Zebra Mussel Infestation of Unionid Bivalves (Unionidae) in North America

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SYNOPSIS. In 1989, zebra mussels received national attention in North America when they reached densities exceeding 750,000/m^2 in a water withdrawal facility along the shore of western Lake Erie of the Laurentian Great Lakes. Although water withdrawal problems caused by zebra mussels have been of immediate concern, ecological impacts attributed to mussels are likely to be the more important long-term issue for surface waters in North America. To date, the epizoic colonization (*i.e.*, infestation) of unionid bivalve mollusks by zebra mussels has caused the most direct and severe ecological impact. Infestation of and resulting impacts caused by zebra mussels on unionids in the Great Lakes began in 1988. By 1990, mortality of unionids was occurring at some locations; by 1991, extant populations of unionids in western Lake Erie were nearly extirpated; by 1992, unionid populations in the southern half of Lake St. Clair were extirpated; by 1993, unionids in widely separated geographic areas of the Great Lakes and the Mississippi River showed high mortality due to mussel infestation. All infested unionid species in the Great Lakes (23) have become infested and exhibited mortality within two to four years after heavy infestation began. Data indicate that mean zebra mussel densities >5,000–6,000/m^2 and infestation intensities >100–200/unionid in the presence of heavy zebra mussel recruitment results in near total mortality of unionids. At present, all unionid species in rivers, streams, and lakes that sympatrically occur with zebra mussels have been infested and, in many locations, negatively impacted by zebra mussels. We do not know the potential consequences of infestation on the 297 unionid species found in North America, but believe zebra mussels pose an immediate threat to the abundance and diversity of unionids.

INTRODUCTION

Colonization of substrates, water withdrawal facilities, and hard-bodied invertebrates is a distinctive characteristic of the zebra mussel (*Dreissena polymorpha*) in Europe and now in North America (Clarke, 1952; Nalepa and Schloesser, 1993). Development of controls to keep water withdrawal facilities free of zebra mussels was the immediate concern during the invasion and early proliferation of mussel populations (Clarke, 1952; Griffiths *et al.*, 1989).

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FIG. 1. Zebra mussel infested unionid (*Megalonaias nervosa*) removed from the Illinois River 1993 (photo courtesy of D. Blodgett, Illinois Natural History Survey, Havana, Illinois).

However, epizoic colonization (*i.e.*, infestation) of snails, crayfish, and especially unionids is believed to be the most direct and ecologically destructive characteristic of zebra mussels (Hebert *et al.*, 1989, 1991; Schloesser and Kovalak, 1991; Hunter and Bailey, 1992; Mackie, 1993). In addition, the discovery and spread of a second dreissenid species (*Dreissena* (*rostriformis*) *bugensis*) has raised even more concern for the survival of unionids (Mills *et al.*, 1993; Spidle *et al.*, 1994).

Infestation of unionids is beginning to occur throughout the range of the zebra mussel in North America (Tucker *et al.*, 1993; personal communications). Zebra mussels have invaded and are becoming abundant in major river systems of the United States such as the Illinois, Mississippi, Tennessee, Ohio, Arkansas, and Hudson (Schloesser, 1995). In the Illinois River, where zebra mussels first invaded and became abundant outside the Great Lakes water basin, infestation at some locations is as heavy as that found in the Great Lakes (Fig. 1). Similar heavy infestations have been observed in the Mississippi River and some inland lakes (personal communication, D. Garton, Indiana University, Kokomo, Indiana). To date, low to medium infestations have been observed in all large rivers where mussels and unionids are sympatrically occurring.

The present study reviews the colonization of zebra mussels on unionids in North America. A major portion of this review is devoted to the impacts of mussels on unionids as documented in the Great Lakes because infestation first occurred and has been most documented in this area.

ZEBRA MUSSEL ATTACHMENT

Zebra mussels have four life-history characteristics that allow them to attach to and successfully colonize unionids: 1) The reproductive and planktonic distribution period of zebra mussels occurs at a time when unionids extend their shells out of the sediment to feed and reproduce, thus promoting direct colonization of unionid shells (Schloesser and Kovalak, 1991; Nalepa and Schloesser, 1993). 2) Zebra mussels have high reproductive and, when habitat conditions are favorable, survival potential (Walz, 1978; Sprung, 1993). 3) Early settled pediveligers and juveniles actively search for and select hard substrates, such as unionid shells, for attachment (Lewandowski, 1976; Martel, 1993; Yankovich and Haffner, 1993). 4) Juvenile and adult zebra mussels produce byssal threads that allow them to attach to firm substrates and maintain physical contact with unionids (Eckroat *et al.*, 1993).

INFESTATION

Unionid species

To date, infestation of unionids has been documented for 31 species in North America (Table 1). In the Great Lakes, 23 species have been infested. In major rivers, 24 species have been infested (Tucker *et al.*, 1993; Strayer *et al.*, 1994; Tucker, 1994). It is likely that there will be many more species infested as zebra mussels continue to invade and colonize rivers, streams, and inland lakes (Stolzenburg, 1992; Schloesser, 1995). Potentially, zebra mussels could infest all 297 unionid species in North America (Williams *et al.*, 1993).

Mortality

Infestation and resulting mortality of unionids has been most intensively studied in Lake St. Clair and western Lake Erie of the Great Lakes (Hebert *et al.*, 1989, 1991; Schloesser and Kovalak, 1991; Hunter and Bailey, 1992; Mackie, 1993; Gillis and Mackie, 1994; Nalepa, 1994; Schloesser and Nalepa, 1994). This is attributed to the first discovery of zebra mussels in Lake St. Clair in 1988, but first introducted into both Lake St. Clair and western Lake Erie in 1986 (as determined by life-history characteristics), and an exponential increase in abundance in the summer of 1989 (Hebert *et al.*, 1989; Griffiths *et al.*, 1989; Nalepa and Schloesser, 1993). To date, all 18 species that have been intensively studied in Lake St. Clair and western Lake Erie have exhibited high mortality attributed to infestation by zebra mussels (Table 1; Gillis and Mackie, 1994; Nalepa, 1994; Schloesser and Nalepa, 1994). In addition, near total mortality of five additional species in Presque Isle Bay in east-central Lake Erie has also occurred (DWS, unpublished data). To date, all species that have experienced heavy infestation for several years have exhibited near total mortality.

Infestation was first observed in Lake St. Clair in 1988 during a preliminary survey to determine the abundance and distribution of zebra mussels shortly after their discovery (Hebert *et al.*, 1989). In 1988, the maximum infestation intensity was 38 zebra mussels/unionid and the maximum substrate density was 200 mussels/m^2. By 1989, the maximum infestation intensity was 10,500/unionid and the maximum substrate density was 4,500/m^2 (Hebert *et al.*, 1991). Unionids were described as being covered with a 4- to 6-cm-deep layer over the entire unionid shell that extended out of the sediments. In western Lake Erie, the maximum infestation intensity was 48/unionid and the maximum substrate density was about 100/m^2 in winter 1989 and by August 1989, the maximums had increased to 10,700/unionid and 750,000/m^2 (Schloesser and Kovalak, 1991; Nalepa and Schloesser, 1993). In both Lake St. Clair and western Lake Erie, increased infestation intensities in the summer of 1989 were primarily attributed to young-of-the-year recruitment. This period included only about four weeks of post-planktonic veliger settling of zebra mussels (Garton and Haag, 1993).

High to near total mortality of unionids occurred in Lake St. Clair within three to five years after heavy infestation intensities began in summer 1989 (Gillis and Mackie, 1994; Nalepa, 1994). Gillis and Mackie (1994) intensively studied infestation of unionids at two sites in southern Lake St. Clair from 1990 to 1992. Densities of unionids decreased from 1 to 0/m^2 at one site between 1990 and 1992 and from 2 to $<1/m^2$ at another site between 1991 and 1992. At a 4-m depth contour, unionids decreased from 8/m^2 in 1986, to 2/m^2 in 1990, to 0/m^2 in 1992. In 1986, 10 species were found, in 1990, 12 were found, in 1991, 4

TABLE 1. *Species list of unionid mollusks infested by zebra mussels in the Great Lakes and major connecting rivers in North America 1989–1994.**

	Great Lakes			Major rivers	
**Amblema plicata plicata*	LSC	WLE	PI	IMR	
Anodonta implicata					HR
**Anodontoides ferussacianus*			PI		
Arcidens confragosus				IMR	
Ellipsaria lineolata				IMR	
**Elliptio complanta*	LSC				HR
**Elliptio dilatata*	LSC		PI	IMR	
**Fusconia flava*	LSC		PI		
**Lampsilis cardium*	LSC	WLE	PI	IMR	
**Lampsilis siliquoidea (& radiata)*	LSC	WLE	PI	IMR	HR
Lampsilis teres				IMR	
**Lasmigona complanata complanata*	LSC			IMR	
**Lasmigona costata*			PI		
**Leptodea fragilis*	LSC	WLE	PI	IMR	
Leptodea ochracea					HR
**Ligumia nasuta*	LSC		PI		HR
**Ligumia recta*	LSC		PI		
Megalonaias nervosa				IMR	
**Obliquaria reflexa*	LSC			IMR	
**Pleurobema coccineum*	LSC				
**Potamilus alatus*	LSC	WLE	PI	IMR	
**Potamilus ohiensis*		WLE		IMR	
**Ptychobranchus fasciolaris*	LSC		PI		
**Pyganodon grandis*	LSC	WLE	PI	IMR	
Quadrula nodulata				IMR	
**Quadrula pustulosa pustulosa*		WLE	PI	IMR	
**Quadrula quadrula*			PI	IMR	
**Strophitus undulatus*			PI		
**Truncilla donaciformis*			PI	IMR	
**Truncilla truncata*	LSC		PI	IMR	
Utterbackia imbecillus				IMR	

* An asterisk indicates species where mortality has been attributed to infestations. LSC = Lake St. Clair; Gillis and Mackie (1994); Hunter and Bailey (1992). WLE = western Lake Erie; Haag *et al.* (1993); Schloesser and Nalepa (1994). PI = eastern Lake Erie, Presque Isle; unpublished, DWS. IMR = Illinois and Mississippi rivers; Tucker *et al.* (1993); Tucker (1994). HR = Hudson River; Strayer *et al.* (1994); Strayer, personal communication.

species were found, and by 1992 no live species were found (Nalepa and Gauvin, 1988; Gillis and Mackie, 1994). Nalepa (1994) conducted a lake wide survey of unionids in Lake St. Clair in 1986, 1990, and 1992. Mean lake-wide densities of unionids remained relatively stable at $2/m^2$ between 1986 and 1990 and then declined to $1/m^2$ in 1992. The total number of unionids collected declined from 281 to 248, and to 99 in each of the three years, respectively. Because of physical characteristics and water current patterns, infestation and subsequent unionid mortality varied substantially within Lake St. Clair. In high-infested regions, unionids were still present in 1990, but the average number of zebra mussels per unionid was about 400. By 1992, no unionids were collected in this region. In low-infested regions, the average number of zebra mussels per unionid was <3 in 1990, and unionids were still present in 1992. However by 1994, unionids in Lake St. Clair were nearly extirpated (TFN, unpublished data).

Unionid mortality also occurred in western Lake Erie, but it occurred within one to two years after heavy infestations instead of three to five years as documented in Lake St. Clair. Schloesser and Nalepa (1994) documented the swift decline of unionids at one site in offshore waters of western Lake Erie (Fig. 2). In fall 1989 when all live unionids were infested, the unionid collection consisted of 53% live and 47% dead individuals. In May–June 1990, the collection was 17% live and 83% dead, and by September 1990, no live unionids could be

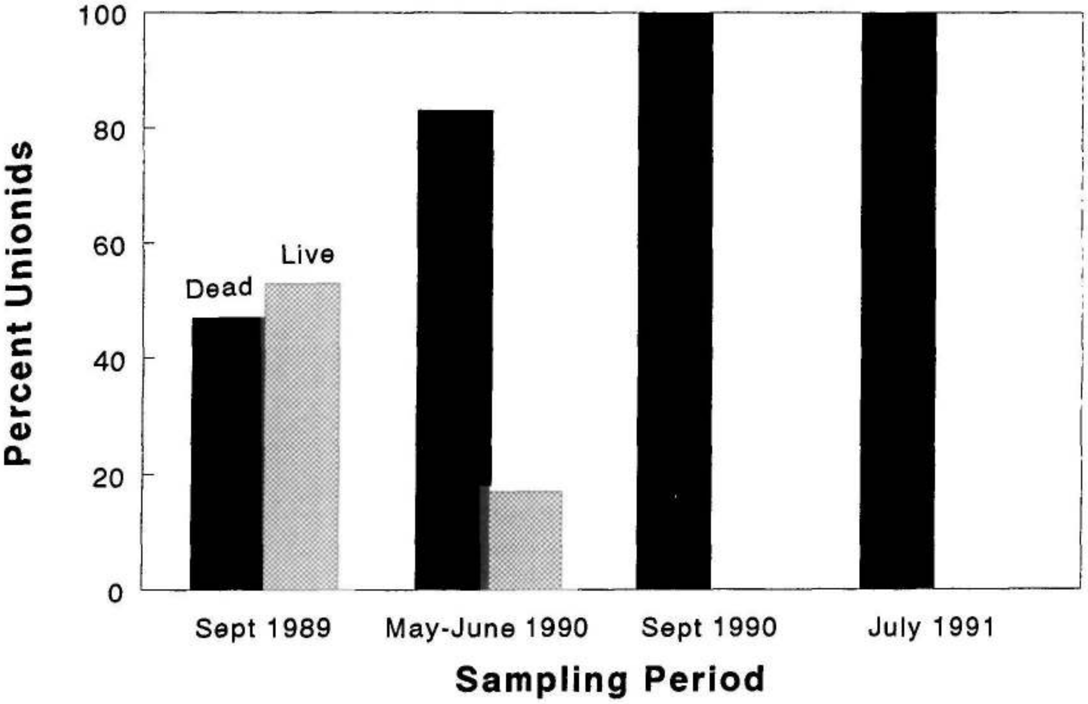

FIG. 2. Percent live and dead unionids collected at one site in offshore waters of western Lake Erie 1989–1991 (Schloesser and Nalepa, 1994).

found. Maximum infestation intensities were 11,550/live unionid and 14,393/dead unionid. In addition, Schloesser and Nalepa (1994) sampled 17 historical stations located throughout western Lake Erie. In 1991, they found only 4 live and 187 dead unionids. The near total absence of unionids in most of western Lake Erie, like that in Lake St. Clair in the early 1990s, is unprecedented because unionids had existed in these waters for centuries.

Zebra mussels have been found outside the Great Lakes water basin in several rivers including, the Illinois, Mississippi, Tennessee, Ohio, Arkansas, and Hudson (Schloesser, 1995). Many of these sightings were of isolated, single individuals that probably did not represent established populations that threatened unionids at the time of their discovery. However, established populations of zebra mussels were present in the lower Illinois River and adjoining area of the Mississippi River in 1991. These populations probably became established in 1990 from veligers contained in water flowing in canals that connect the Illinois River to Lake Michigan (Schloesser, 1995). If infestations and resulting impacts similar to those observed in the Great Lakes are to occur outside the Great Lakes, one would expect them to be found in the area of confluence near the Illinois and Mississippi rivers before they occur in other inland waters.

Indeed, zebra mussels have infested 20 species of unionids near the confluence of the Illinois and Mississippi rivers, and observations and descriptions of infestations are similar to those observed in the Great Lakes (Table 1; Schloesser and Kovalak, 1991; Nalepa and Schloesser, 1993; Tucker *et al.*, 1993; Tucker, 1994). Length-frequency distributions of zebra mussels collected in the area of confluence of the two rivers indicate that mussels probably became established in the study area in 1990 (Tucker *et al.*, 1993). Between 1991 and 1993, mussel densities increased dramatically; in the Illinois River, maximum densities of mussels on substrates were about 10/m^2 in 1991 and about 100,000/m^2 in 1993 (unpublished data, S. Whitney, Illinois Natural History Survey, Havana, Illinois). In 1992, zebra mussels in Alton pool of the Mississippi River infested 9 of 25 unionid species, occurred on 27% of the unionids, and averaged about 2 mussels/unionid (Tucker *et al.*, 1993). In 1993, infestation in Alton pool occurred on all 18 species collected and on 100% of the unionids and averaged 37/unionid (Tucker, 1994). Several other pools located around the confluence of the Illinois and Mississippi rivers showed similar, but lower average infestation intensities than that observed in Alton pool of the Mississippi River (Tucker *et al.*, 1993). At one site (pool 26 of the Mississippi River), Tucker (1994) described substrate densities as "... zebra mussels not only colonized unionids but also essentially covered the entire surface of the gravel bar.... They formed a pavement made up of zebra mussel shells interconnected by byssal threads." Data presented by Tucker (1994) indicate that during the early infestation period in the Mississippi River, there was a high degree of variability of infestation intensities based on unionid species. This high variability of infestation has been characteristic of early infestation periods in the Great Lakes (Hebert *et al.*, 1989; Schloesser and Kovalak, 1991; Nalepa, 1994).

Available information indicates that at low infestation intensities unionids can survive in the presence of zebra mussels (Lewandowski and Stanczykowska, 1975; Lewandowski, 1976). However, critical infestation intensities and corresponding substrate densities of zebra mussels at which impacts on unionids occur are unknown. Lewandowski (1976) indicates a direct relationship between non-lethal infestation intensities (<200/unionid) and substrate densities below about 2,000/m^2. Our review of available data in North America indicates that substrate densities >5,000–6,000/m^2 and infestation intensities >100–200 juvenile and adult mussels/unionid in the presence of heavy zebra mussel recruitment, which may substantially increase numbers of mussels in summer and fall, causes mortality of unionids (Hebert *et al.*, 1989, 1991; Schloesser and Kovalak, 1991; Nalepa, 1994; Schloesser and Nalepa, 1994; Ricciardi *et al.*, in press).

To date there have been several techniques to evaluate real and potential impacts of infestation including: 1) numbers of infesting zebra mussels, 2) visual estimate of infestation intensity, 3) weight of infesting zebra mussels, 4) energy reserves of unionids, 5) deformities of unionid shells, 6) growth of unionids, and 7) mortality of unionids. Unfortunately, the most common evaluation technique used to date (*i.e.*, mortality) occurs too late for mitigation of impacts on unionids. More evaluation techniques are needed during the early infestation period. Such techniques would indicate the potential for negative impacts and the need to take active measures to preserve the affected unionid population. At present, the earliest warning of negative impacts of infestation on unionids appears to be the presence of heavy encrustations on exposed unionid shells (*e.g.*, Fig. 1). Evidence indicates that unionid populations exposed to such heavy infestations will experience near total mortality.

CAUSES OF MORTALITY

At present, the causal mechanism(s) of unionid mortality as a result of infestation by zebra mussels is(are) unknown. Several possible mechanisms have been proposed (Schloesser and Kovalak, 1991). Existing evidence for proposed mechanisms of mortality is derived primarily from field and laboratory observations and some laboratory analysis of indicators of unionid health, such as energy reserves (*e.g.*, glycogen content). More research is needed to characterize the causal mechanism(s) of unionid mortality; such efforts will be useful to determine if impacts can be mitigated through active conservation efforts to save unionids.

Valve movement and deformities

Visual observations of infested unionids indicate that zebra mussels restrict and/or prevent normal valve movement of unionids (Fig. 1). In addition, observations of unionid shells cleaned of infesting mussels indicate that unionid shell deformities are often observed (Fig. 3). Hunter and Bailey

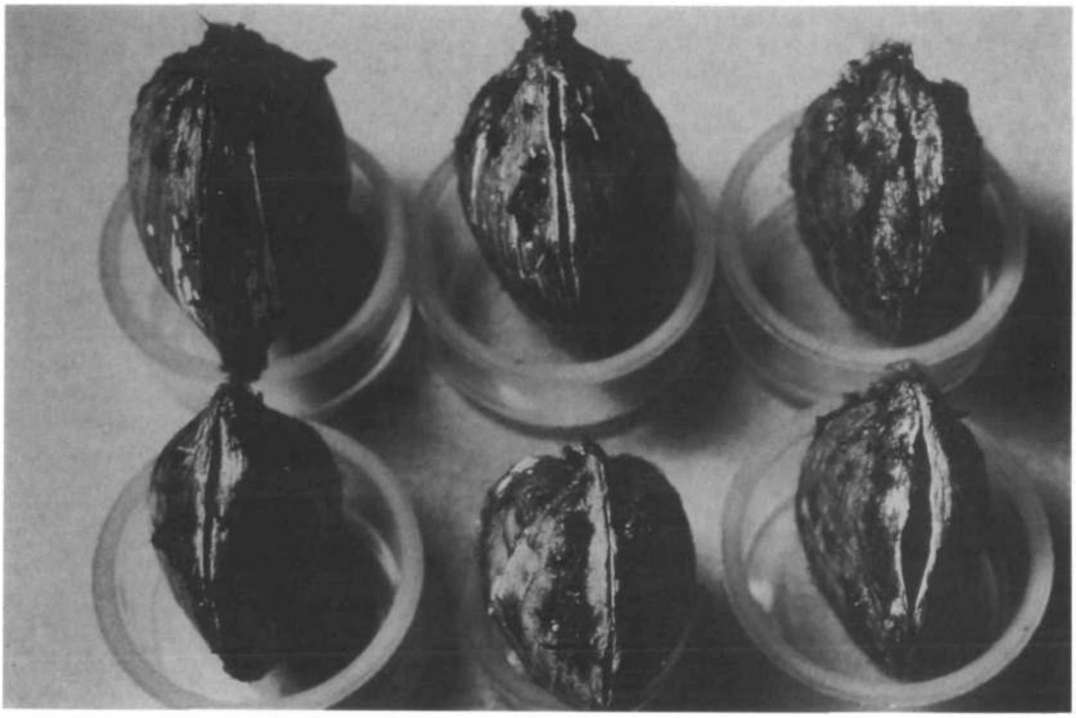

FIG. 3. Posterior views of *Lampsilis siliquoidea* exibiting varying degrees of shell deformities attributed to infestation by zebra mussels in Lake St. Clair of the Great Lakes. (photo courtesy of R. D. Hunter, Oakland University, Rochester, Michigan).

(1992) reported the most extensive observations of the mechanical disruption of valve closing and opening, smothering of siphons, and shell deformities. Descriptions indicate that mussels colonize unionids at such high intensities that unionid valves cannot open and close. Unionid valves were pulled by byssal threads with such tension that new growth and old shell material was deformed for 78% of the unionid population.

Available foods

The reduction of available foods for infested unionids as a result of zebra mussel feeding has been partially studied in the Great Lakes (Hebert *et al.*, 1989; Haag *et al.*, 1993). Both elimination of foods in the water column by zebra mussels and direct interference of food gathering siphons of unionids by zebra mussels are possible mechanisms that may contribute to lower food supplies reaching infested unionids. When found at substantial densities, zebra mussels have been found to reduce available phytoplankton in entire lake systems (MacIsaac *et al.*, 1992; Madenjian, 1996). Gillis (1993) reported interference competition between zebra mussels and unionids and showed that the position of attached zebra mussels, rather than the number attached, was the largest contributing factor to altering the filtration activities of host unionids. Infestations of up to 2,000 zebra mussels/unionid resulted in total occlusion of the siphon openings of host unionids. Hebert *et al.* (1991) and Haag *et al.* (1993) showed physiological food reserves of infested unionids to be lower than non-infested unionids. Infested unionids had lipid reserves 50% lower than non-infested unionids. Similarly, Haag *et al.* (1993) reported lower glycogen and cellulase activity of infested unionids than non-infested unionids (Table 2).

Impair movement

Impairment of movement of unionids caused by infestation by zebra mussels has

TABLE 2. *Percent survival, glycogen content* (i.e., *index of fitness*), *and enzyme activity* (i.e., *index of stress*) *of two species of infested and non-infested unionids held in cages* (ca. *90 days*) *in near shore waters of western Lake Erie July–October 1990.* (*Haag* et al., *1993*).

Species	Treatment	Percent survival	Glycogen content (mg/g)	Enzyme activity (units/μg)
Lampsilis siliquoidea				
male	Infested	64	0.08	111.5
	Non-infested	68	0.13	200.5
female	Infested	17	0.04	151.6
	Non-infested	68	0.08	399.6
Amblema plicata plicata				
	Infested	100	0.67	87.8
	Non-infested	100	1.90	257.4

been observed and is believed to be a common cause of unionid mortality. Gillis and Mackie (1994) attributed the presence of many dead, thin shelled, alate unionids (*e.g., Potamolus alatus* and *Leptodea fragilis*) found on their sides with large colonies of zebra mussels attached, as evidence that they were dislodged from the substrate by infestations. In contrast, rounded species (*e.g., Pyganodon grandis*) were found lying on their sides less frequently than thin-shelled, alate species. Hunter and Bailey (1992) observed infestations where mussels formed layers on unionids in excess of 2 cm and extended from the sides of the infestation layers laterally on to adjacent sediments probably immobilizing unionids. Tucker (1994) observed infested unionids lying on their sides along the shores in windrows in Pool 26 of the Mississippi River. He believed "a pavement" like bottom covered by zebra mussels prevented unionids from burrowing into sediments once they were dislodged. Unionids were thus stranded and exposed to fluctuating water levels that Tucker (1994) believed caused unionid mortality. Schloesser and Nalepa (1994) attribute mortality of infested unionids to smothering by sediments caused by the inability of unionids to maintain themselves at the mud-water interface due to the additional weight of infesting mussels. Weight of infesting zebra mussels may exceed host unionid weight by a factor of four, but has been noted to be as high as 8.5 (Hebert *et al.,* 1991; Schloesser and Kovalak, 1991; Nalepa, 1994).

Accumulation of toxic metabolic feces

Zebra mussels bio-deposit much of what they filter as feces and pseudofeces. Accumulation of deposited materials by infesting mussels around unionid beds may cause degraded water quality unsuitable for unionid survival. Direct observations support rapidly changing benthic habitat conditions near heavily infested unionids (Schloesser and Kovalak, 1991; Gillis and Mackie, 1994). In Lake St. Clair, there was a noticeable increase in the overlying depositional layer between 1990 and 1991 when high mortality of infested unionids occurred (Gillis and Mackie, 1994). In near-shore waters of western Lake Erie, benthic habitat showed evidence of anoxia (*e.g.,* bubbles, black surface sediment, and decaying benthic fauna) near heavily infested unionids and high densities of accumulating zebra mussels (SCUBA observations, Schloesser and Kovalak, 1991).

FACTORS AFFECTING INFESTATION

Available data indicate that life history characteristics of species, sex, and/or shell morphology of unionids may play an important part in determining when impacts of zebra mussels occur on unionids (even though the result of heavy infestations is the same over a two to four year period, *i.e.,* near total mortality, discussed above). Data by Haag *et al.* (1993) suggest that there may be differences in impacts of infestation based on life history characteristics of unionid species. The subfamilies Lampsilinae and Anodontinae (*e.g., Lampsilis sili-*

quoidea) are long-term brooders (*i.e.*, usually 9–12 months), while Ambleminae (*e.g.*, *Amblema plicata plicata*) are short term brooders (*i.e.*, usually <2 months) of young (Clarke, 1981). Over the short term, infested individuals of the Lampsilinae had lower energy reserves (*i.e.*, glycogen content) than individuals of the Ambleminae (Table 2). Field surveys confirmed higher mortality for lampsilines than amblemines. Mortality was also greater for female than male *L. siliquoidea*, indicating that mortality was linked to stress of brooding young. Haag *et al.* (1993) also mentioned shell morphology as a possible contributing factor to differences in mortality of subfamilies of unionids. Lampsilines and anodontines have thin shells, and amblemines have thick shells. Some data from Gillis and Mackie (1994) and Nalepa (1994) support the hypothesis that thin alate species are impacted sooner than species with inflated and round shells. However, for another species, *A. p. plicata*, no mortality was observed, but fitness and stress were substantially affected. Surveys of infested unionid populations support the generalization that species of the Lampsilinae subfamily (*i.e.*, *L. siliquoidea*, *Leptodea fragilis*, and *Potamilus alatus*) were more likely to have lower energy reserves and experience mortality sooner than species of the subfamily Ambleminae (*A. p. plicata* and *Quadrula pustulosa*) (Haag *et al.*, 1993). Of the heavily infested unionids found in a survey of Lake St. Clair by Nalepa (1994), species in the subfamilies Anodontinae and Lampsilinae declined sooner than species in the subfamily Ambleminae. However, results of Hunter and Bailey (1992) at several sites in Lake St. Clair suggest that lampsilines were less susceptible to impacts of infestation than several other species including species of Ambleminae.

Personal observations and communications indicate that some unknown factor(s) reduces the intensity of unionid infestation by zebra mussels, thus decreasing unionid mortality in some areas where unionids and zebra mussels co-exist. For example, at one site in near-shore western Lake Erie all individuals of *Amblema plicata plicata* became heavily infested and were extirpated within two years, whereas at another nearby site the same species were heavily infested and have not shown high mortality in four years (DWS, unpublished data). A similar observation has been made in a large bay of Lake Erie (Presque Isle Bay), a large interconnecting river of the Great Lakes (St. Clair River), and a small river in Michigan (Clinton River) (personal communications, E. Masteller, Penn State University, Erie, Pennsylvania, R. Smithee, Detroit Edison, Detroit, Michigan, and J. Lazar, Tennessee Technological University, Cookeville, Tennessee). At present, it is believed that there is(are) a unique characteristic(s) of these habitats that allow unionids to escape heavy infestation and resulting mortality.

SUMMARY

To date, infestation and the causual mechanisms leading to impacts on unionids is not a well documented observation in North America. The Great Lakes experience shows us that zebra mussel densities $>5{,}000/m^2$ cause infestation intensities >150 one-year-old and older zebra mussels/unionid. This infestation level in the presence of heavy zebra mussel recruitment seems lethal to all unionid species within several years after infestation begins. This may be why a review of the European literature by Lewandowski (1976) only found mean infestation intensities below 180/unionid.

If zebra mussel infestation occurs at relatively low intensities (*i.e.*, <200/unionid) in some areas of North America, then there is reasonable expectation, based on the coexistence of zebra mussels and unionids in Europe, that impacts of infestation on unionids in North America may vary dramatically from that documented in the Great Lakes.

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REFERENCES

Clarke, A. H. 1981. *The freshwater molluscs of Canada.* National Museum of Natural Resources, National Museums of Canada. Ottawa, Canada.

Clarke, K. B. 1952. The infestation of waterworks by *Dreissena polymorpha*, a freshwater mussel. Institute of Water Engineers 6:370–379.

Eckroat, L. R., E. C. Masteller, J. C. Shaffer, and L. M. Steele. 1993. The byssus of the zebra mussel (*Dreissena polymorpha*): Morphology, byssal thread formation, and detachment. *In* T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 239–262. Lewis/CRC Press, Inc., Boca Raton, Florida.

Garton, D. and W. Haag. 1993. Seasonal reproductive cycles and settlement patterns of *Dreissena polymorpha* in western Lake Erie. *In* T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 111–128. Lewis/CRC Press, Inc., Boca Raton, Florida.

Gillis, P. L. 1993. The impact of *Dreissena polymorpha* on populations of unionidae and their effect on the host unionids' filtration activity and growth rate in Lake St. Clair. M.Sc. Thesis, University of Guelph, Guelph, Ontario.

Gillis, P. L. and G. L. Mackie. 1994. Impact of zebra mussels, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. Canad. J. Zool. 72:1260–1271.

Griffiths, R. W., W. P. Kovalak, and D. W. Schloesser. 1989. The zebra mussel, *Dreissena polymorpha* (Pallas 1771), in North America: Impacts on raw water users. In *Proceedings of the Service Water Reliability Improvement Seminar*, pp. 11–26. Electric Power Research Institute, Palo Alto, California.

Haag, W. R., D. J. Berg, D. W. Garton, and J. L. Farris. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. Canad. J. Fisher. Aquat. Sci. 50:13–19.

Hebert, P. D. N., B. W. Muncaster, and G. L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): A new mollusc in the Great Lakes. Canad. J. Fisher. Aquat. Sci. 46: 1587–1591.

Hebert, P. D. N., C. C. Wilson, M. H. Murdoch, and R. Lazar. 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. Canad. J. Zool. 59:405–409.

Hunter, R. D. and J. F. Bailey. 1992. *Dreissena polymorpha* (zebra mussel): Colonization of soft substrata and some effects on unionid bivalves. The Nautilus 106:60–67.

Lewandowski, K. 1976. Unionidae as a substratum for *Dreissena polymorpha* Pall. Polskie Archiwum Hydrobiologii 23:409–420.

Lewandowski, K. and A. Stanczykowska. 1975. The occurrence and role of bivalves of the family unionidae in Mikolajakie Lake. Ekologia Polska 23(2):317–334.

MacIsaac, H. J., W. G. Sprules, O. E. Johannsson, and J. H. Leach. 1992. Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. Oecologia 92:30–39.

Mackie, G. L. 1993. Biology of zebra mussels (*Dreissena polymorpha*) and observations of mussels colonization on unionid bivalves in Lake St. Clair of the Great Lakes. *In* T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 153–173. Lewis/CRC Press, Inc., Boca Raton, Florida.

Madenjian, C. P. 1996. Removal of algae by the zebra mussel (*Dreissena polymorpha*) population in western Lake Erie: a bioenergetics approach. Canad. J. Fisher. Aquat. Sci. 52:000–000. (In press)

Martel, A. 1993. Dispersal and recruitment of zebra mussels (*Dreissena polymorpha*) in a nearshore area in west-central Lake Erie: Significance of postmetamorphic drifting. Canad. J. Fisher. Aquat. Sci. 50(1):3–12.

Mills, E. L., R. M. Dermott, E. F. Roseman, D. Dustin, E. Mellina, D. B. Conn, and A. P. Spidle. 1993. Colonization, ecology, and population structure of the quagga mussel (Bivalvia, Dreissenidae) in the lower Great Lakes. Canad. J. Fisher. Aquat. Sci. 50(11):2305–2314.

Nalepa, T. F. 1994. Decline of native bivalves (Unionidae: Bivalvia) in Lake St. Clair after infestation by the zebra mussels *Dreissena polymorpha*. Canad. J. Fisher. Aquat. Sci. 51:2227–2233.

Nalepa, T. A. and J. M. Gauvin. 1988. Distribution, abundance, and biomass of freshwater mussels (Bivalvia: Unionidae) in Lake St. Clair. J. Great Lakes Res. 14:411–419.

Nalepa, T. A. and D. W. Schloesser. (eds.) 1993. *Zebra mussels: Biology, impacts, and control*. Lewis/CRC Press, Inc., Boca Raton, Florida.

Ricciardi, A., F. G. Whoriskey, and J. B. Rasmussen. Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. Canad. J. Fisher. Aquat. Sci. 52:000–000. (In press)

Schloesser, D. W. 1995. Introduced species, zebra mussels in North America. In *Encyclopedia of environmental biology*, pp. 337–356. Academic Press, Inc., San Diego, California.

Schloesser, D. W. and W. Kovalak. 1991. Infestation of unionids by *Dreissena polymorpha* in a power plant canal in Lake Erie. J. Shellfish Res. 10(2): 355–359.

Schloesser, D. W. and T. F. Nalepa. 1994. Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after the invasion by the zebra mussel, *Dreissena polymorpha*. Canad. J. Fisher. Aquat. Sci. 51:2234–2242.

Spidle, A. P., J. E. Marsden, and B. May. 1994. Identification of the Great Lakes quagga mussel as *Dreissena* (*rostriformis*) *bugensis* from the Dnieper River, Ukraine based on allozyme variation. Canad. J. Fisher. Aquat. Sci. 51(7):1485–1489.

Sprung, M. 1993. The other life: An account of present knowledge of the larval phase of *Dreissena polymorpha*. *In* T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control*, pp. 39–53. Lewis/CRC Press, Inc., Boca, Raton, Florida.

Stolzenburg, W. 1992. The mussels' message. Nature Conservancy 42(6):16–23.

Strayer, D. L., D. C. Hunter, L. C. Smith, and C. K. Borg. 1994. Distribution, abundance, and roles of freshwater clams (Bivalvia, Unionidae) in the freshwater tidal Hudson River. Freshwater Biol. 31:239–248.

Tucker, J. K. 1994. Colonization of unionid bivalves by the zebra mussel, *Dreissena polymorpha,* in pool 26 of the Mississippi River. J. Freshwater Ecol. 9:129–134.

Tucker, J. K., C. H. Theiling, K. D. Blodgett, and P. A. Theil. 1993. Initial occurrence of zebra mussels (*Dreissena polymorpha*) on freshwater mussels (Family Unionidae) in the upper Mississippi River system. J. Freshwater Ecol. 8:245–251.

Walz, N. 1978. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. II. Reproduction. Archiv fuer Hydrobiologie Supplement 55(1):106–119.

Williams, J. D. *et al.* 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18:6–22.

Yankovich, T. L. and G. D. Haffner. 1993. Habitat selectivity by the zebra mussel (*Dreissena polymorpha*) on artificial substrates in the Detroit River. *In* T. F. Nalepa and D. W. Schloesser (eds.), *Zebra mussels: Biology, impacts, and control,* pp. 175–181. Lewis/CRC Press, Inc., Boca Raton, Florida.