

Dramatic Decline of Unionid Bivalves in Offshore Waters of Western Lake Erie After Infestation by the Zebra Mussel, *Dreissena polymorpha*

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Unionid bivalves and attached epizoic zebra mussels (*Dreissena polymorpha*) were collected at one index station in 1989, 1990, and 1991 and at 17 stations in 1991 in offshore waters of western Lake Erie of the Laurentian Great Lakes. Sampling at the index station revealed that the proportion of live unionids declined from 53% in September 1989 to 17% in May–June 1990 and to 0% in September 1990: this 100% mortality coincided with heavy infestation by zebra mussels. Quantitative sampling with a Ponar grab at the 17 stations in 1991 revealed a widespread and dramatic reduction in unionid populations. In 1982, five unionid species occurred at 35% of the stations at a density of 4/m², whereas in 1991, no live unionid species were found. Qualitative sampling with an epibenthic sled at the 17 stations in 1991 yielded only 4 live specimens of 2 species (*Amblema plicata plicata* and *Fusconaia flava*) and 187 dead specimens of 10 species. These and other results indicate that unionid populations are being negatively affected by zebra mussels in the Great Lakes. Similar impacts on unionids are expected to occur where zebra mussels become abundant throughout North America.

Des bivalves unionidés et des moules zébrées épizoïques (*Dreissena polymorpha*) ont été prélevés à une station de référence en 1989, 1990 et 1991, ainsi qu'à 17 stations en 1991 au large dans les eaux de la partie ouest du lac Érié, l'un des Grands Lacs laurentiens. L'échantillonnage de la station de référence a révélé que la proportion des unionidés vivants est passée de 53% en septembre 1989 à 17% en mai–juin 1990 et à 0% en septembre 1990. Cette mortalité complète coïncidait avec une intense infestation par des moules zébrées. L'échantillonnage quantitatif au moyen d'une benne preneuse du type Ponar à 17 stations, en 1991, a mis en évidence une réduction à la fois étalée et spectaculaire des populations d'unionidés. En 1982, cinq de ces espèces étaient observées à 35% des stations en densité de 4/m², alors qu'en 1991, aucun sujet vivant de ces espèces n'était trouvé. L'échantillonnage qualitatif au moyen d'un traîneau épibenthique dans les 17 stations, en 1991, n'a rapporté que 4 spécimens vivants de 2 espèces (*Amblema plicata plicata* et *Fusconaia flava*), et 187 spécimens morts qui appartenaient à 10 espèces. Ces résultats, comme d'autres, indiquent que les populations d'unionidés souffrent de la présence de la moule zébrée dans les Grands Lacs. On pense que des effets similaires sur les unionidés devraient se produire lorsque la moule zébrée deviendra abondante partout en Amérique du Nord.

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Invasion of the zebra mussel, *Dreissena polymorpha* (Bivalvia: Dreissenidae), into the Laurentian Great Lakes is of great concern because, at high densities, mussels may negatively affect raw water users and indigenous fauna and flora (Griffiths et al. 1989; Hebert et al. 1989; Gannon et al. 1990; Schloesser et al. 1990; Sblendorio et al. 1991). In 1989, zebra mussel populations in the Great Lakes increased rapidly and reached maximum densities (> 700 000 / m²) far greater than those recorded in European waters (reviewed in Nalepa and Schloesser 1993). At present, it is not known if zebra mussels will reach high densities in all waters that they invade, but they are expected to spread throughout much of North America during the next 20 yr (Griffiths et al. 1989, 1991; Strayer 1991; Neary and Leach 1992).

The epizoic colonization of hard-bodied invertebrates including snails, crayfish, and unionid bivalves by zebra mussels has been an observed characteristic of the zebra mussel invasion in the Laurentian Great Lakes (Nalepa and Schloesser 1993). In Europe, zebra mussels are especially epizoic on unionid bivalves (Lewandowski 1976), where they attach to shells by byssal structures (Fig. 1). Infestation of unionids by zebra mussels in the Great Lakes has been observed in nearshore waters of Lake St. Clair (Hebert et al. 1989, 1991; Mackie 1991, 1993; Hunter and Bailey 1992; Nalepa 1994; Gillis and Mackie 1994), western Lake Erie (Schloesser and Kovalak 1991; Garton and Haag 1991; Haag et al. 1993), eastern Lake Erie (D.W. Schloesser, personal observation), Lake Huron (T.F. Nalepa, personal observation), and Lake Michigan (E. Marsden, Illinois Natural History

Survey, Zion, IL 60099, personal observation). There is concern, but little confirmatory evidence, about detrimental effects of infestation on naturally occurring unionid populations (reviewed in Schloesser and Kovalak 1991).

The present study was conducted to assess the effects of zebra mussels on unionids in offshore waters of western Lake Erie. This information should be valuable in determining the potential effects of zebra mussel infestations on unionids elsewhere in North America.

Methods

Unionid bivalves and infesting zebra mussels were collected in offshore waters of western Lake Erie at one index station (9L) in September 1989, May–June and September 1990, and July 1991, and at 17 stations in June–July 1991; all 17 stations were previously sampled for unionid bivalves in 1961, 1972, and 1982 (Fig. 2; Carr and Hiltunen 1965).

Qualitative sampling was performed with an epibenthic sled (46 × 25 cm) at the index station (9L) during all four sampling periods (Fig. 2). The sled was similar to that used by Miller et al. (1989). The sled was repetitively pulled (ca. 5 min per tow) with a small boat for about the same accumulative amount of time (i.e., 4 h) each sampling period. A minimum 3:1 ratio of tow rope length to water depth was maintained, and the rope was manually monitored to ensure contact of the sled with substrates during sampling. Sediments were composed of soft, pudding-like mud under a thin layer (ca. 1 cm) of silt. Unionids and attached zebra mussels were removed from the sled, individually preserved in a 5% buffered (CaCO₃) formalin solution, and taken to the laboratory.

Qualitative and quantitative sampling were performed at the 17 stations located throughout western Lake Erie in June–July 1991 (Fig. 2). At each station, one epibenthic sled tow (qualitative, 5 min per station) was performed as described above. In addition, three replicate Ponar grab (quantitative, 0.05 m²) samples were collected at each station to compare with the published literature (Nalepa et al. 1991). Sediments consisted primarily of soft mud, which filled 100% of the Ponar at all stations except 4R, 5R, 5M, and 4L, where sediments consisted of a combination of silt, mud, and sand, which filled between 1/2 and 1/8 of a Ponar sample. Samples were washed in a U.S. Standard No. 30 sieve (0.65 mm mesh), individually preserved in a 5% buffered (CaCO₃) formalin solution, and taken to the laboratory.

In the laboratory, samples were washed over a U.S. Standard No. 60 sieve (0.25-mm mesh). Unionid shells were removed from debris. Individual half shells of dead unionids that could be paired were included in the present study and unpaired half shells were discarded. Unionids and attached zebra mussels were identified, counted, measured, and weighed. Unionids were identified following Clarke (1981) and by comparisons with bivalve taxonomic reference collections. Taxonomic nomenclature follows Turgeon et al. (1988) and Williams et al. (1993) with the exception of combining *Lampsilis siliquioidea* (Barnes, 1823) and *L. radiata radiata* (Gmelin, 1791) as *L. siliquioidea* because these two species interbreed (Clarke 1981). Dry weights (105°C for 48 h) of individual unionids and infesting mussels <6-mm long and whole millimetre size categories >6 mm (i.e., 6 mm, 7 mm, ...) long were determined. Length–frequency distributions were constructed from shell length measurements

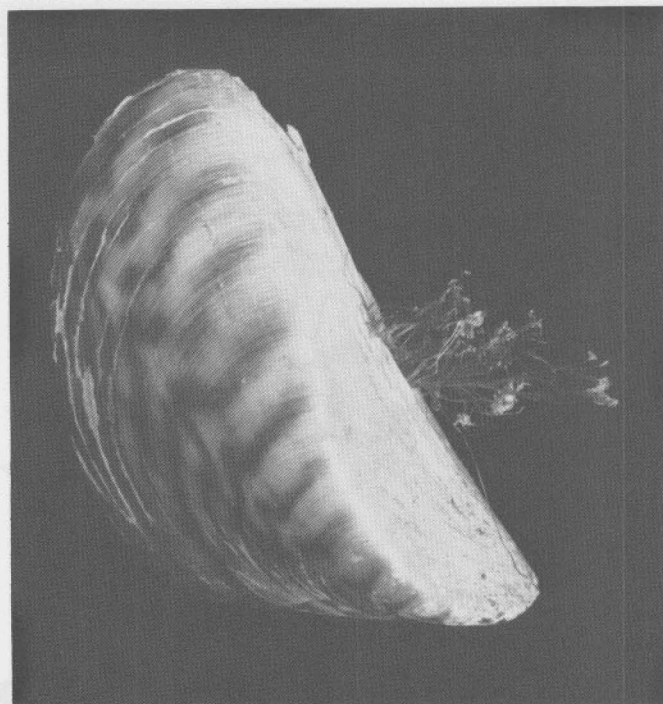


FIG. 1. The zebra mussel, *Dreissena polymorpha*, showing the ventrally located byssal structures that enable this species to be epizoic on unionid bivalves.

in 1-mm size classes. A randomly selected subsample of 200–300 mussels <6-mm long per unionid and all mussels >7-mm long were measured for each sampling period. Length–frequency distributions of unmeasured mussels <6 mm were based on the proportions of measured subsampled mussels in each whole millimetre size group. Cohort groups were based on lengths corresponding to the smallest number of mussels between length–frequency distribution peaks. Age determinations of young-of-the-year and young-of-the-year-plus mussels were based on a January 1 spawn date (Griffiths et al. 1991; Schloesser and Kovalak 1991). This procedure is adequate to separate annual size groups of mussels during the sampling period in the study area (Schloesser and Kovalak 1991). Infestation is used to describe the colonization of unionids by zebra mussels following the concept that mussels are ectoparasites as described by Margolis et al. (1982), used by Schloesser and Kovalak (1991), and demonstrated in the present study.

Results

Index Station

Total proportions of live and dead unionids changed dramatically at the index station between September 1989 and July 1991 (Fig. 3). In September 1989, the unionid collection consisted of 53% live individuals (of 54 total individuals); in May–June 1990, the population was 17% live (54 individuals). In September 1990 (56 individuals) and July 1991 (46 individuals) no live unionids were collected.

Eight unionid species were collected. These taxa, and the percent composition of the total number of individuals (210) include: *Lampsilis siliquioidea* (65%), *Ligumia nasuta* (20%), *Leptodea fragilis* (6%), *Pyganodon grandis* (4%), *Potamilus*

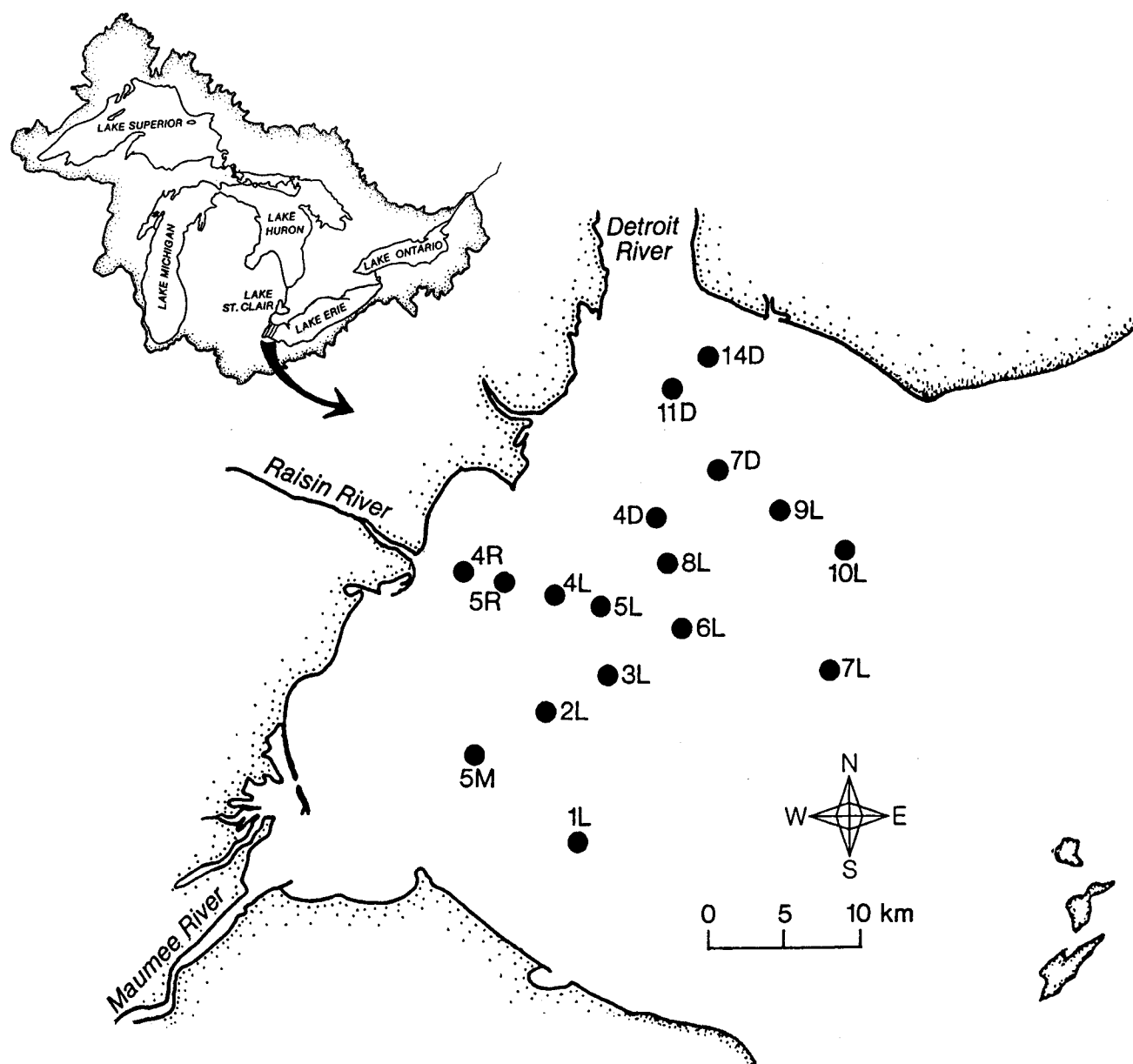


FIG. 2. Locations of one index station (9L) and 17 stations where unionid bivalves and infesting zebra mussels (*Dreissena polymorpha*) were collected in western Lake Erie 1989–91.

alatus (2%), *Lampsilis cardium* (1%), *Amblema plicata plicata* (1%), and *Elliptio dilatata* (<1%). The only consistently collected species was *L. siliquioidea*, which accounted for the majority of changes of live (89% of the total number) and dead (60% of the total number) individuals.

All live unionids were infested by zebra mussels (Table 1). Proportions of dead unionids showing infestation declined from 77% in September 1989 to 26% in July 1991. This decline was not accompanied by an increase in the proportion of dead unionids exhibiting byssal threads. Proportions of dead unionids showing no evidence of infestation increased from 23% in September 1989 to 74% in July 1991.

There was substantial variation in intensity of infestation between sampling periods (Table 2). Total mean intensities per sampling period ranged between 79 and 7022 individuals per unionid and 3 and 37 g per unionid, whereas intensities on individual unionids ranged between 4 and 14 393 per

unionid and 1 and 104 g per unionid. Mean intensities on successive sampling dates indicate that infestation declined in winters and increased in summer. Mean intensities of live and dead unionids were similar in September 1989 and higher for live than for dead unionids during May–June 1990. Maximum individual intensities of live and dead unionids were 11 550 and 14 393 unionid, respectively. In September 1989, mean weights of infesting mussels exceeded unionid mean weights by a factor of about three; in May–June 1990, infestation weights dropped to about one-third of host unionids; in September 1990, weights of mussels and unionids were about equal; and, in July 1991, weights of mussels were substantially lower than weights of unionids.

The zebra mussel population was composed of two size groups or age-classes, which declined substantially during the winter months when unionids bury in substrates (Fig. 4). The total density of infesting mussels was 7022 per unionid

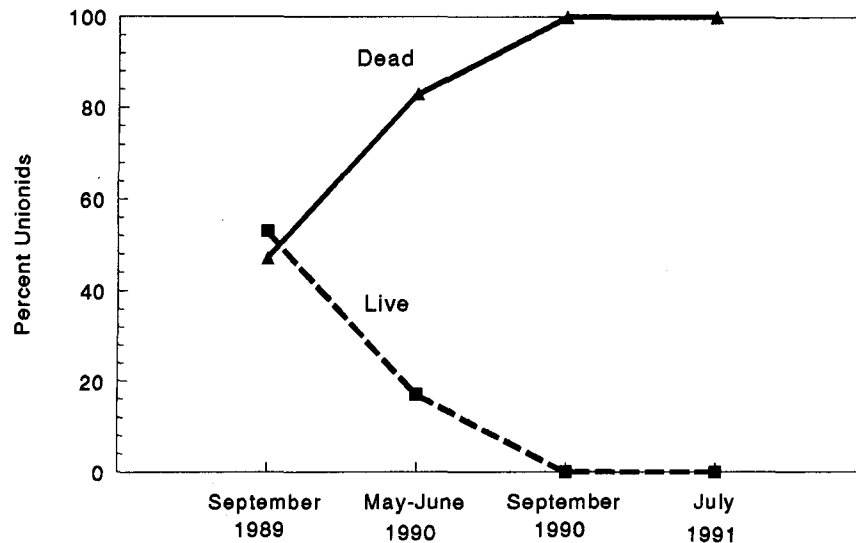


FIG. 3. Percent live and dead unionids collected at index station 9L in western Lake Erie 1989–91.

TABLE 1. Proportions (%) of live and dead unionids showing infestation (attached mussels and byssal threads only) and no infestation by zebra mussels (*Dreissena polymorpha*) at an index station (9L; Fig. 2). in western Lake Erie 1989–91.

	Sept. 18, 1989	May 20, June 26, 1990	Sept. 20, 1990	July 11 1991
Showing infestation				
Attached mussels				
Live	100	100	—	—
Dead	77	42	61	26
Byssal threads only				
Live	0	0	—	—
Dead	0	22	7	0
Total				
Live	100	100	—	—
Dead	77	64	68	26
No infestation				
Live	0	0	—	—
Dead	23	36	32	74

in September 1989, 260 per unionid in May–June 1990, 1124 per unionid in September 1990, and 79 per unionid in July 1991. Increased numbers of zebra mussels between successive sampling periods only occurred between May–June 1990 and September 1990 when small freshly spawned mussels increased densities from 248 per unionid to 1049 per unionid. In general, the mean density of smaller mussels was greater than the density of older, larger mussels, except in July 1991 when large mussels were about three times more abundant than small mussels. In September 1990 and July 1991, many of the zebra mussels, especially the larger mussels, were loosely attached and some appeared freshly dead, as evidenced by open shells and decaying tissues.

Length–frequency distributions of zebra mussels on live and dead unionids were different in September 1989 and May–June 1990 (Fig. 5). In September, live unionids were colonized by more mussels of most length classes than were dead unionids. In May–June 1990, more mussels of most length classes colonized dead rather than live unionids.

Seventeen Stations

In 1991, no live unionids were collected with the Ponar sampler at 17 historically sampled stations where live unionids had been found in the previous three decades (Table 3). Unionid diversity and abundance declined from 1961 to 1982 when five unionid species occurred at 6 of 17 stations (35%) and the mean density at all stations was 4/m². A total of 23 dead unionids representing 5 unionid species (*Lampsilis siliquoidea* (15), *Ligumia nasuta* (3), *Potamilus alatus* (3), *Amblema plicata plicata* (1), and *Fusconaia flava* (1)) were found.

Only four live specimens were collected with the epibenthic sled at the 17 stations in June–July 1991; three were *Amblema plicata plicata* (from stations 11D, 14D, and 2L) and one was *Fusconaia flava* (from station 14D); however, a total of 187 dead specimens representing 10 species, mostly *Lampsilis siliquoidea*, *Ligumia nasuta*, *Potamilus alatus*, and *A. p. plicata*, were collected (Table 4). The largest number

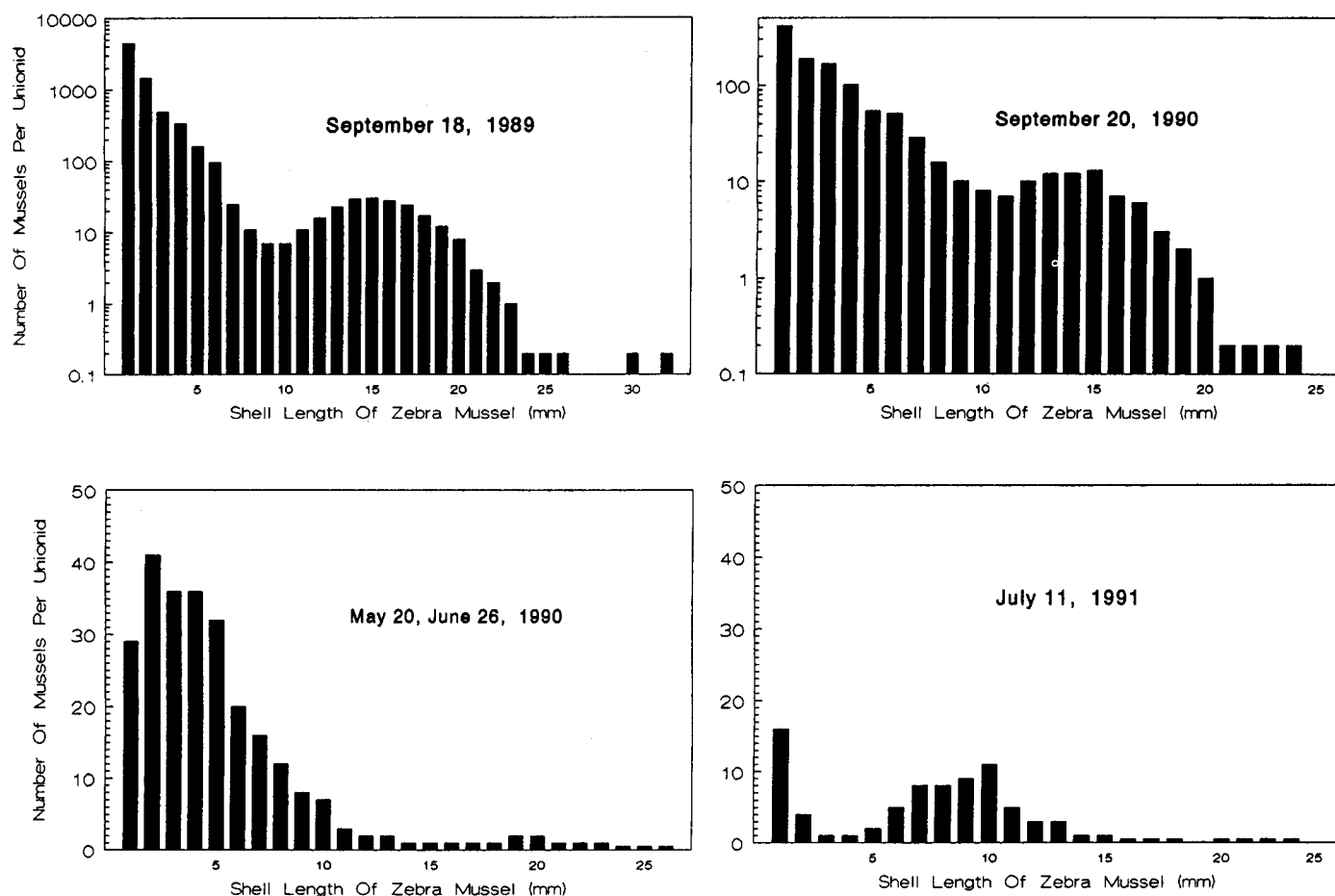


FIG. 4. Length-frequency distributions of zebra mussels (*Dreissena polymorpha*) removed from unionids collected at index station 9L in western Lake Erie 1989-91.

TABLE 2. Mean (\pm SE) numbers and dry weights of zebra mussels (*Dreissena polymorpha*) per infested unionid, and in parentheses, numbers and mean dry weight of unionids at an index station (9L; Fig. 2) in western Lake Erie 1989-91.

	Live		Dead		Total	
	No.	Weight (g)	No.	Weight (g)	No.	Weight (g)
Sept. 18, 1989	6805 \pm 622.7 (29)	36 \pm 3.5 (14 \pm 1.7)	9120 \pm 1218.7 (3)	48 \pm 9.52 (15 \pm 2.2)	7022 \pm 584.0 (32)	37 \pm 3.3 (15 \pm 1.5)
May 20, June 26, 1990	346 \pm 95.0 (9)	9 \pm 2.1 (19 \pm 4.1)	216 \pm 98.5 (19)	5 \pm 1.7 (24 \pm 3.7)	260 \pm 73.4 (28)	7 \pm 1.3 (22 \pm 2.8)
Sept. 20, 1990			1225 \pm 218.7 (33)	13 \pm 3.4 (16 \pm 1.8)	1225 \pm 218.7 (33)	13 \pm 3.4 (16 \pm 1.8)
July 11, 1991			79 \pm 24.4 (12)	3 \pm 1.4 (17 \pm 1.7)	79 \pm 24.4 (12)	3 \pm 1.4 (17 \pm 1.7)

of dead unionids was collected at station 5L (61 specimens), located about in the middle of the sampled area.

Discussion

Present Study

Our study reveals that live Unionidae were nearly extirpated in a large portion of western Lake Erie between 1989 and 1991. Live unionids were present at an index station in 1989 but disappeared by 1990, and no live unionids were

found in 1991 at 17 quantitatively sampled stations, where unionids had been present for decades. In addition, qualitative sampling revealed that only 4 of 191 total specimens were live, and all of these were infested by zebra mussels. Dramatic exponential increases of zebra mussel densities occurred in western Lake Erie in 1989 (reviewed in Nalepa and Schloesser 1993). These increased densities of mussels coincided with rapid and massive infestation of unionids and their subsequent decline in western Lake Erie. We believe that the invasion of zebra mussels into western

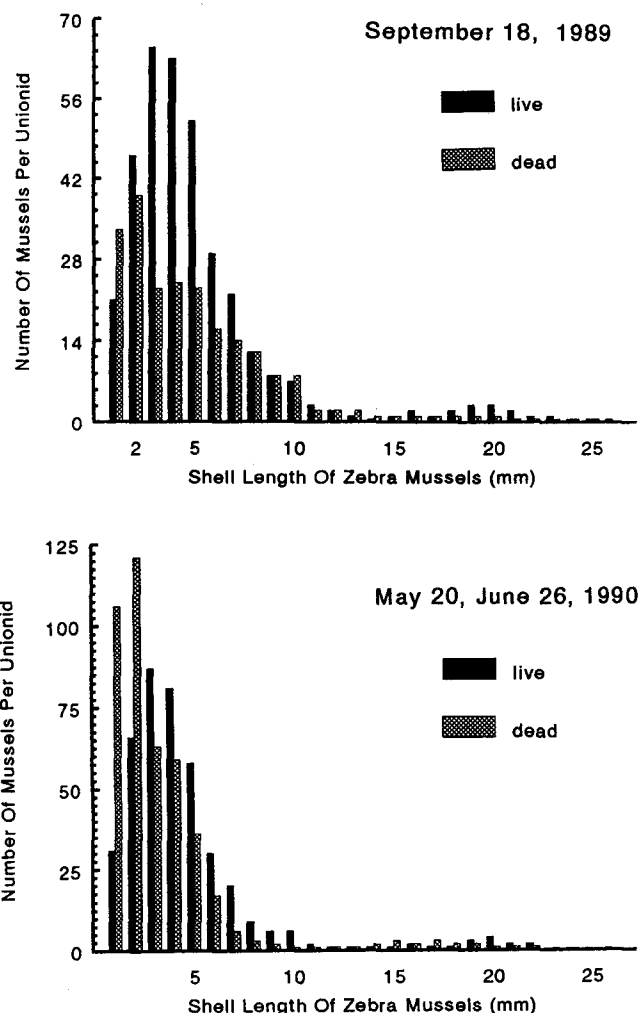


FIG. 5. Length-frequency distributions of zebra mussels (*Dreissena polymorpha*) removed from live and dead unionids collected at index station 9L in western Lake Erie September 1989 and May-June 1990.

Lake Erie in 1986 (Griffiths et al. 1991), plus the dramatic increase in mussel densities and massive infestation of unionids in the summer of 1989, indicate that zebra mussels caused near extinction of unionids in a large portion of western Lake Erie by 1990.

Infestation intensities, length-frequency distributions of infesting zebra mussels, and proportions of unionids showing evidence of infestation indicate that unionid mortality due to zebra mussels primarily occurred shortly after the present study was initiated. In fall 1989, infestation intensities and length-frequency distributions of zebra mussels on live and dead unionids were similar, indicating that infested live and dead unionids collected in fall 1989 were exposed to the same exponential population growth of mussels that occurred in the summer of 1989 (Nalepa and Schloesser 1993). In fall 1989, most dead, and all live unionids, showed no evidence of being buried in soft sediments at the index station, indicating that they had maintained themselves at the sediment-water interface during the summer of 1989. However, a few dead unionids appeared to have been buried in sediments for a short period (as evidenced by odor, decaying tissues, and the presence of black subsurface sediments in mussel and unionid shells); such mortality is attributed

TABLE 3. Percent composition of live unionid species collected with a quantitative sampler at 17 historically sampled stations (Fig. 2) in western Lake Erie 1961, 1972, and 1982 (Nalepa et al. 1991), and 1991 (present study).

	1961	1972	1982	1991
<i>Lampsilis siliquoidea</i>	33	63	40	0
<i>Ligumia nasuta</i>	33	8	30	0
<i>Pyganodon grandis</i>	17	8	10	0
<i>Potamilus ohioensis</i>	6	8	0	0
<i>Elliptio dilatata</i>	3	0	0	0
<i>Obliquaria reflexa</i>	3	0	0	0
<i>Leptodea fragilis</i>	3	0	0	0
<i>Potamilus alatus</i>	3	4	10	0
<i>Lampsilis cardium</i>	0	8	0	0
<i>Amblema plicata plicata</i>	0	0	10	0
No. of Species	8	6	5	0
Stations with unionids (%)	94	65	35	0
Mean No./m ²	10	6	4	0

to the inability of unionids to maintain themselves at the water-sediment interface because of the three-fold increase in weight of infesting mussels and subsequent smothering in the sediment. Dead unionids that showed no infestation (23%) were mostly old, decalcified specimens that appeared to have been buried and not exposed to zebra mussel colonization in 1989. By spring 1990, length-frequency distributions of mussels on dead unionids were substantially different than those for mussels on live unionids, and 22% of dead unionids showed evidence (i.e., byssal threads attached) of having been infested. Most of the small number of zebra mussels that were attached to unionids in spring 1990 were dead, black, smelled of decaying flesh, and appeared to have been buried in substrates when sampled. These freshly dead zebra mussels probably died from suffocation during winter months when unionids typically burrow into the substrate (Morton 1993). In addition, freshly dead unionids were found in spring 1990 and fall 1990. No freshly dead unionids were found in summer 1991.

Increasing proportions of dead unionids and unionids showing evidence of infestation would be expected throughout the period of study if the zebra mussel infestation was the primary cause of mortality. However, observations of byssal threads attached to unionid shells buried in sediments of western Lake Erie and artificially suspended in the water column indicate that visible evidence of zebra mussel infestation only remains on unionids for 3-4 mo after unionids die and are buried in soft sediments (D.W. Schloesser, personal observation). Thus, the use of byssal threads as an indicator of unionid infestation and resulting mortality is possible for only a short period of time after unionids become buried in soft sediments.

Historical Unionid Studies

The near total absence of live Unionidae in 1990 and 1991, and the speed at which the decline occurred between 1989 and 1991 is historically unprecedented in the offshore waters of western Lake Erie. Nalepa et al. (1991) documented the long-term decline of Unionidae in the western basin using available data collected with Ponar-type samplers from several previous studies. Nalepa's study showed that densities of unionids declined from 10/m² in 1961 to 6/m² in 1972 to 4/m² in 1982; the proportion of stations

TABLE 4. Number of dead unionid species collected in an epibenthic sled (5 minute tows) at 17 stations (Fig. 2) in western Lake Erie June 17 and July 11, 1991.

Species	1L	2L	3L	4L	5L	6L	7L	8L	9L	10L	4D	7D	11D	14D	4R	5R	5M	Total
<i>Lampsilis siliquoidea</i>	1	18	4	3	40	4	2	2		1				14	1	23		113
<i>Amblema plicata plicata</i>		3	2									1			1	2		9
<i>Potamilus alatus</i>		3			6		1	2										12
<i>Elliptio complanata</i>		2			2											2		6
<i>Pyganodon grandis</i>			2		4													6
<i>Ligumia nasuta</i>					8	2	1	2						17		5		35
<i>Ligumia recta</i>					1								1					2
<i>Obliqueria reflexa</i>																1		1
<i>Quadrula pustulosa</i>																1		1
<i>Fusconaia flava</i>																2		2
Total	1	26	8	3	61	6	4	6		1		1		32	2	36		187

with live unionids declined from 94% in 1961 to 65% in 1972, to 35% in 1982, while the number of species declined from 8 in 1961, to 6 in 1972, to 5 in 1982. Although the reason for the long-term decline is uncertain, Nalepa et al. (1991) believed it to be related to reduced water and substrate quality. Between 1982 and the present study, unionid densities at the index station declined from 4 to 0/m², the percentage of stations with unionids declined from 35 to 0%, and the number of unionid species declined from 5 to 0. The near total absence of live unionids at the 17 stations sampled by the Ponar sampler is confirmed by results from epibenthic sled samples. Species composition of dead unionids in sled samples was similar to the composition of live unionids found in earlier studies (Nalepa et al. 1991).

Although declines of unionid abundance have been documented throughout western Lake Erie for every 10-yr period since 1961, the rapid decline of Unionidae at the index station between fall 1989 and spring 1990 and the total absence of live unionids in fall 1990 and summer 1991 indicate that substantial changes occurred which affected unionid survival over a very brief time. Rapid declines of unionids in other water bodies have been attributed to diseases, parasites, short-term fluctuations in water quality, and unknown causes (reviewed by Neves 1987). Examination of unionids in fall 1989 revealed no morphological evidence of unionid disease or parasites. Historically, western Lake Erie has been subject to catastrophic, short-term declines in water quality, such as low oxygen levels (Britt 1955; Carr and Hiltunen 1965; Wood 1973). However, observations while sampling in the present study indicate good habitat conditions, as evidenced by the presence of other live benthic organisms (i.e., amphipods, isopods, oligochaetes, chironomids, etc.) throughout the sampled area. In addition, benthic quality surveys of western Lake Erie indicate that habitat conditions improved dramatically between 1979 and 1991 (Farara and Burt 1993) and were good in 1993 (as evidenced by the presence of *Hexagenia* spp. nymphs; D.W. Schloesser, unpublished data). These surveys indicate that improved habitat conditions may have allowed the historically declining unionid populations to increase in abundance in western Lake Erie. However, if unionid recovery in western Lake Erie is to occur, it will probably take much longer after the severe mortality caused by the zebra mussel.

Other Zebra Mussel – Unionid Interaction Studies

The dramatic decline of unionids as documented in the present study is similar to that in Lake St. Clair located

immediately upstream of western Lake Erie (Fig. 2; Nalepa 1994; Gillis and Mackie 1994). Potential negative effects of zebra mussels on unionids in the Great Lakes were first noted in Lake St. Clair in 1988 by Hebert et al. (1989), who found a maximum of 35 mussels on one unionid and suggested that zebra mussels may be an interference competitor of native unionids. After zebra mussels spawned in Lake St. Clair in 1989, Hebert et al. (1991) noted a maximum infestation intensity exceeding 10 000 mussels per unionid but provided no individual data. Hebert et al. (1991) determined that infested unionids had 50% lower levels of lipids in body tissues than noninfested unionids and suggested that the long-term survival of unionids in Lake St. Clair may be threatened. Additional studies by Mackie (1991, 1993) in Lake St. Clair indicated a maximum infestation intensity of 625 and a mean intensity of 210 mussels per unionid. Nalepa (1994) surveyed Lake St. Clair and found that in areas of high zebra mussel infestation (>55 per unionid) unionids disappeared in a large portion of the lake between 1990 and 1992. Nalepa found some unionid populations in northwestern Lake St. Clair where infestation intensities were below 3 per unionid.

Near extirpation of unionids in Lake Erie occurred about 1 yr (1990) earlier at the index station in the present study than in southern Lake St. Clair (1991), even though zebra mussels invaded both areas in 1986 (Gillis and Mackie 1994; Griffiths et al. 1991). In general, mean intensities in western Lake Erie are about 7- to 10-fold higher than in Lake St. Clair (Hunter and Bailey 1992; Leach 1993). In 1989, Schloesser and Kovalak (1991) determined that unionids in nearshore waters of western Lake Erie were infested by mussels at a maximum intensity of 10 732 and a mean intensity of 6777 per unionid and suggested that the survival of unionids with these intensities was unlikely. In the present study, maximum infestation intensities of live (11 550) and dead (14 393) unionids exceed those reported earlier.

Higher infestations in western Lake Erie than Lake St. Clair are attributed to differences in substrate densities of zebra mussels. Maximum densities in western Lake Erie have been reported to exceed 342 000/m², whereas in Lake St. Clair maximum densities have not exceeded 19 000/m² (Leach 1993; Hunter and Bailey 1992). As shown by Lewandowski (1976), there is a direct relationship between unionid infestation rates and relatively low environmental densities of zebra mussels. At low environmental densities in Europe, there are few documented effects of infestation on unionids (Lewandowski 1976; Schloesser and Kovalak 1991). However, high infestation

intensity did occur in Lake Balaton, Hungary, in the 1930s and caused high unionid mortality (Sebestyen 1938; reviewed by Schloesser and Kovalak 1991).

Mechanisms of Unionid Mortality

At present, the causal mechanism(s) of increased mortality of unionids as a result of zebra mussel infestation is unknown. This is partly because declines have only recently been attributed to mussel infestations, and because it is difficult to separate interactions between habitat characteristics and infestation impacts. There are several hypothetical causal mechanisms, which may not be the same for all habitat conditions (Schloesser and Kovalak 1991; Mackie 1991).

-
- impair normal locomotion and burrowing activities
 - prevent valve closure, thus exposing the unionid to predation, parasitism
 - prevent valve opening, thus stopping respiration
 - smother siphons, thus stopping metabolic activities
 - reduce available food for the unionid
 - cause shell deformities, thus preventing normal growth
 - generate metabolic wastes, thus causing toxic effects
 - add weight to the unionid shell, thus causing unionid to sink into soft sediments and be smothered
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However, even at relatively low infestation rates and low environmental densities of zebra mussels, unionids have shown physiological effects (e.g., reduced lipid content, Hebert et al. 1991; reduced glycogen content, Haag et al. 1993) and complete mortality (Gillis and Mackie 1994). A reduction in metabolic reserves of infested unionids has been observed in controlled studies in western Lake Erie and in natural populations in Lake St. Clair (Hebert et al. 1991; Haag et al. 1993).

We attribute unionid mortality to reduced metabolic reserves, as evidenced by high mortality and poor condition of unionids collected in spring. Many dead unionids collected in spring 1990 contained decaying flesh and appeared to have been buried in the soft sediments. Reduced metabolic reserves of unionids caused by infesting mussels in the summer 1989 combined with increased weight of infesting mussels prevented unionids from surviving winter and (or) prevented burrowing unionids from reaching the substrate surface in 1990 when water temperatures increased.

We have documented dramatic reductions in unionid populations in western Lake Erie. The rapid, large invasion of the study area by zebra mussels corresponded with a near 100% mortality of unionids. To date, all studies support predictions (French 1990; Hebert et al. 1991; Schloesser and Kovalak 1991) that high densities of zebra mussels will result in high infestation intensities and that these would cause mortality of unionids in the Great Lakes, and possibly throughout much of North America.

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