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# Impact of Zebra and Quagga Mussels (Dreissena spp.) o Freshwater Unionids (Bivalvia: Unionidae) in the Detroi River of the Great Lakes

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ABSTRACT.—To assess the impact of zebra and quagga mussel (*Dreissena* spp.) infestatio on unionids, unionids (Bivalvia: Unionidae) were sampled in the Detroit River in 1982–1983 before mussels invaded the river, and in 1992 and 1994, after mussels invaded the river. Liv unionids at four stations along the southeastern shore accounted for 97% (20 species) of al shells collected in 1982–1983, whereas live unionids accounted for only 10% (13 species) i 1992. A similar decline in live unionids occurred at nine stations along the northwester shore, except the decline occurred over the three sampling periods: in 1982–83, 84% (2 species) were live; in 1992, 65% (26 species) were live; and, in 1994, only 3% (13 species were live. The difference in time to near-total mortality of unionids along the southeaster and northwestern shores is attributed to differences in the time of invasion and abundanc of zebra mussel veligers in distinct water masses emanating from Lake St. Clair located im mediately upstream of the Detroit River. Although individuals of all species of all unioni subfamilies declined between 1982 and 1992/1994, members of the subfamilies Anodontina and Lampsilinae declined more than Ambleminae. Between 1986 and 1992/1994, five An odontinae, three Lampsilinae and 0 Ambleminae species have been extirpated from the rive due to dreissenid mussel infestation. Numbers of individuals of commonly found specie declined more than numbers of individuals of uncommonly found species. However, th number of uncommon species declined 47% (17 to 9) along both the southeastern an northwestern shores, whereas common species remained the same (3 species) along th southeastern shore and declined only 40% (5 to 3 species) along the northwestern shore This study, and others, suggest that high mortality of unionids can occur between 4 and yr after initial invasion by dreissenids or up to 8 yr depending on water current pattern Infestation-induced mortality of unionids in the Detroit River is similar to that observed a a few locations in other rivers, but is higher over a larger area than that measured in othe rivers to date, probably because the Detroit River was the first to be colonized by dreisseni mussels in North America.

## INTRODUCTION

Invasion of the Laurentian Great Lakes by zebra mussels (*Dreissena polymorpha*) was acterized by rapid dispersal and explosive population growth (Griffiths *et al.*, 1991; N and Schloesser, 1993). Zebra mussels rapidly colonized (*i.e.*, infested, Schloesser an valak, 1991) shells of native unionids (Bivalvia: Unionidae) (Hebert *et al.*, 1989). Wi short time, the intensity of infestations in the Great Lakes was greater than previou ported in Europe (Lewandowski, 1976; Hebert *et al.*, 1991; Schloesser and Kovalak, 1 High infestation intensities raised concern about the long-term impact of zebra muss unionids throughout North America (Schloesser and Kovalak, 1991; Mackie, 1993; Ma *et al.*, 1993; Schloesser and Nalepa, 1995). Then in 1991, another species of drei mussel (quagga mussel; *Dreissena bugensis*), which has life history characteristics sim

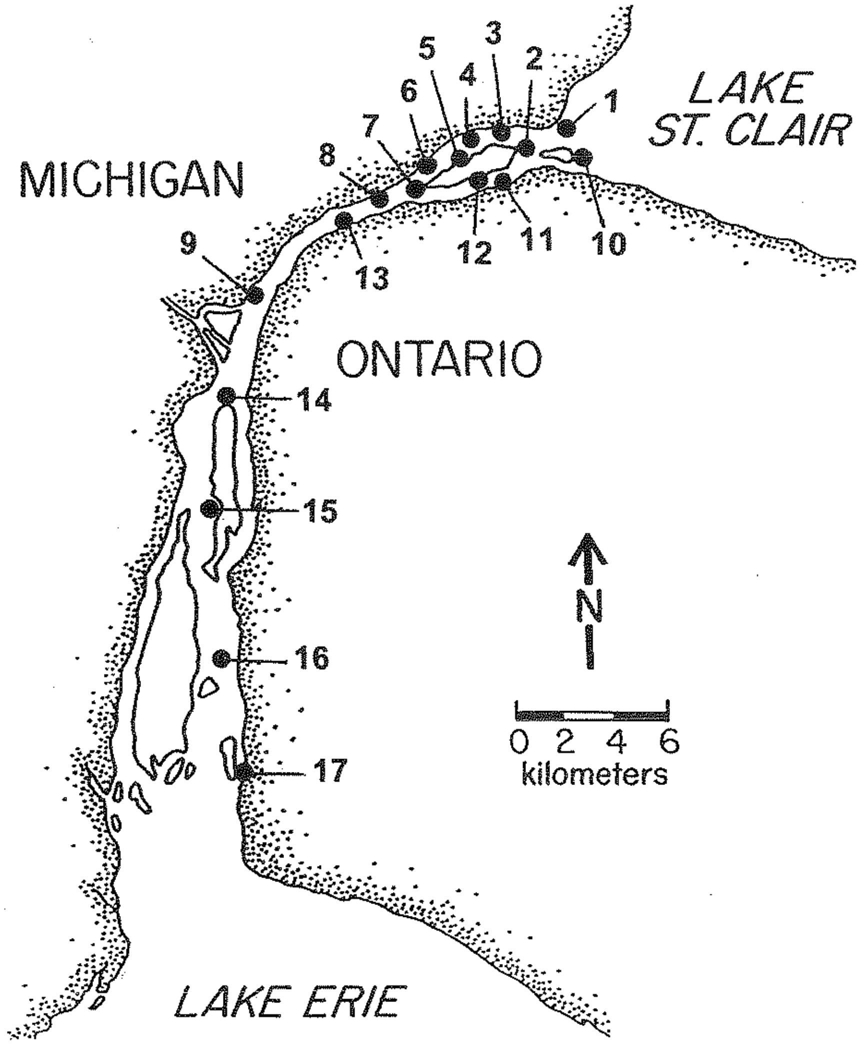


FIG. 1.—Locations of 17 sampling stations where unionids were collected in the Detroit River between Lake St. Clair and Lake Erie 1982–1983 (stations 1–9, 12, and 15–17), 1992 (stations 1–9 and 10–17) and 1994 (stations 1–9)

the zebra mussel, was discovered. It was probably introduced 1 to 2 yr after zebra mussels (May and Marsden, 1992; Mills *et al.*, 1996).

Impacts of zebra mussels on unionids in open waters of lakes immediately above and below the Detroit River (*i.e.*, Lake St. Clair and western Lake Erie; Fig. 1) have been severe and have resulted in unionid mortality approaching 100% (Gillis and Mackie, 1994; Nalepa, 1994; Schloesser and Nalepa, 1994; Nalepa *et al.*, 1996). Lake St. Clair, western Lake Erie and the Detroit River were invaded by zebra mussels in 1986 (Griffiths *et al.*, 1991). Low infestation intensities (*i.e.*, <100 mussels/unionid) occurred in the lakes for about 3 yr

(1986–1989; Hebert *et al.*, 1989; Griffiths *et al.*, 1991) before zebra mussels increased ra in abundance in summer/autumn 1989 and infestation intensities rose (*i.e.*, >10,000 sels/unionid) (reviewed in Schloesser and Kovalak, 1991; Mackie, 1993; Nalepa and Sch ser, 1993). Within 3 yr (1990–1993) of the rapid increase in abundance of zebra muss Lakes St. Clair and Erie most unionids were dead (Gillis and Mackie, 1994; Nalepa, Schloesser and Nalepa, 1994, 1995; Nalepa *et al.*, 1996).

At present, dreissenid mussels are spreading rapidly through large river systems thro out North America (Schloesser, 1995; Strayer *et al.*, 1996). These large rivers are beli to be preferred habitat for mussel colonization and growth (Strayer, 1991). If impac dreissenid mussel infestation in rivers are as severe as those observed in lakes, the uni fauna in large rivers of North America may be in danger (Schloesser and Kovalak, Williams *et al.*, 1993). The Detroit River was selected for the present study because i the first large river colonized by dreissenid mussels, the unionid fauna was surveyed be the colonization by mussels and because it connects Lake St. Clair and western Lake where impacts of zebra mussels on unionids have been documented (Gillis and Ma 1994; Nalepa, 1994; Schloesser and Nalepa, 1994; Nalepa *et al.*, 1996). Results of the pre study may be useful to predict what will happen to the unionid fauna in other large r where less study of unionid infestations has been conducted (*e.g.*, Illinois and Missis rivers, Tucker *et al.*, 1993; Tucker, 1994; and St. Lawrence River of the Great Lakes, Ricc *et al.*, 1996).

## METHODS

Native freshwater unionids (Bivalvia: Unionidae) and attached dreissenid mussels sampled using SCUBA in the Detroit River in August–September 1982–1983, July–Au 1992 and October 1994 (Fig. 1). The 1982–1983 data were collected before the invasio zebra mussels (Griffiths *et al.*, 1991; Nalepa and Schloesser, 1993) and provide a bas reference, against which impacts are evaluated. Sampling methods were the same (di boat, equipment, identification level, etc.) for all three sampling periods. Thirteen sta were sampled in 1982–1983 (1–9, 12 and 15–17). In 1992, the 13 stations sampled in 1 1983 and an additional four stations (10, 11, 13 and 14) were sampled. In 1994, only stations (1–9) were sampled because few live unionids were found SE of the shipping c nel in 1992. The shipping channel carries most of the water flowing down the Detroit and separates stations 1–9 located on the northwestern side and stations 10–17 locate the southeastern side of the shipping channel.

Unionids were sampled using SCUBA by hand picking all live and dead unionids vi on the substrate within a 25-m radius of an anchored boat for 60 min. When few unic were found, additional 50- to 75-m searches were made for an additional 15–30 min adja to the station to ensure that the sampled area was representative of the area and sampling was not performed in the same location where unionids were removed du earlier sampling periods. No visible evidence was found that sampling contributed to extirpation of unionids. Water temperatures during all three sampling periods range tween 15 and 21 C. Possible sampling bias caused by unionid burrowing is unlikely bec unionids are believed to burrow and hibernate at water temperatures below 10 C, possibly lower (van der Schalie, 1938; D. Strayer, Institute of Ecosystem Studies, Millbr New York, pers. comm.). At each station, collections were brought to the surface, live un ids were individually bagged, dead unionids were collectively bagged and taken to the oratory. In the laboratory, individual half shells of dead unionids that could be pa together were included in the present study and unpaired half shells were discarded. I unionids were included in the present study because their presence in a population e riencing rapid mortality can be a useful indicator of population trends in the presence o: dreissenid mussels (Nalepa, 1994; Schloesser and Nalepa, 1994; Nalepa *et al.*, 1996; Ricciard: *et al.*, 1996; Schloesser *et al.*, 1998). In 1992, infestation intensities of up to 100 unionid: per station were determined by obtaining individual dry weights (48 h at 100 C) of hos unionids and infesting zebra mussels.

Unionids were identified following Clarke (1981) and by comparisons with taxonomic reference collections (Detroit Edison Company, Detroit Michigan). Unionid nomenclature follows Williams *et al.* (1993) with the exception that *Lampsilis radiata radiata* (Gmelin 1791) was combined with *Lampsilis siliquoidea* (Barnes, 1823) because the ranges of these two species overlap and Clarke (1981) suggested that they interbreed in the Great Lakes Although no quagga mussels (*Dreissena bugensis*) were observed in the present study, it is possible there was a small percentage (ca. <1% ?) of this species present (Rosenberg and Ludyanskiy, 1994; Mills *et al.*, 1996). Mean numbers of unionids per taxon, station and subfamily were tested by Student's t-test of $\log_{(10)}(X+1)$ transformed data (Snedecor and Cochran, 1967).

## RESULTS

Of a total of 7236 individuals and 28 species of unionids found, 2990 were live individuals of 27 species and 4246 were dead individuals of 28 species (Table 1). Of the 28 species *Villosa fabalis* was the only species not represented by a live individual. Live individuals of five species (*Quadrula quadrula, Anodontoides ferussacianus, Strophitus undulatus, Epioblasma triquetra* and *Obovaria subrotunda*) were found along the northwestern shore, but not along the southeastern shore of the river. No live individuals of any species was unique to the southeastern shore.

In all, unionid populations declined between 1982–1983 and 1992/1994, but they declined along the southeastern shore between 1982–1983 and 1992, whereas they declined along the northwestern shore between 1992 and 1994 (Tables 1 and 2). Along the southeastern shore, total numbers of live unionids declined from 422 (97% of total) to 40 (10%) and dead individuals increased from 14 (3% of total) to 374 (90%) between 1982–1983 and 1992. Similarly, the number of species represented by one or more live individuals declined from 20 to 13 and the number of species of dead individuals increased from 6 to 19 between 1982–1983 and 1992. In addition, mean numbers of live individuals per species declined significantly from 19 to 2 per species and mean numbers of dead individuals increased significantly from <1 to 17 per species between 1982–1983 and 1992. Mean numbers of live unionids per station along the southeastern shore declined from 106 (±30.7) in 1982–1983 to 10 (±10.0) in 1992. In 1992, percentages of live and dead unionids (2% and 98%, respectively) at four stations (stations 10, 11, 13 and 14) along the southeastern shore of the river sampled only in 1992 were similar to those (10% and 90%, respectively) found at stations 12 and 15–17 sampled only in 1992. Along the northwestern shore, total numbers of live unionids increased from 857 (84% of the total) in 1982–1983 to 1592 (65%) in 1992 then decreased to 58 (3%) in 1994; dead individuals increased from 165 (16% of the total) to 954 (35%) to 1959 (97%); and, the number of species represented by one or more live individuals increased from 22 to 26, then decreased from 26 to 13 and the numbers of dead species increased from 17 to 25 to 26 in successive sampling periods between 1982–1983 and 1994. In addition, mean numbers of live individuals per species increased from 31 to 56 per species, then decreased from 56 to 2 per species, whereas the number of dead individuals per species increased from 6 to 34 to 70 between successive sampling periods. Mean numbers (±SE) of live unionids per station along the northwestern shore increased between 1982–1983 (95 ± 20.3) and 1992 (177 ± 30.9), then decreased between

1992 (177 ± 30.9) and 1994 (6 ± 2.2). Substantial increases in the number of live unic occurred at all stations along the northwestern shore between 1982–1983 (range 8 to and 1992 (50 to 290), except station 7, which exhibited a threefold decrease. The r number of live species per station increased significantly from 22 to 26 between 1982– and 1992, then decreased from 26 to 13 between 1992 and 1994.

Numbers of individuals and species of live unionids collected at individual stations cate that impacts of infestation were more severe at stations farthest downstream w each river area (Table 2). Along the southeastern shore in 1992, no individuals were fo at the three most downstream stations (15–17), whereas between 2 and 40 individuals found at the five most upstream stations (10–14). Along the southeastern shore, the r dry weight of infesting zebra mussels (±SE, n = 52, 55 ± 10.5) exceeded the mean we of unionids (46 ± 4.3) in 1992. Along the northwestern shore in 1992 and 1994, sm numbers of individuals were found at the three most downstream stations (7–9) than a six most upstream stations (1–6). Along the northwestern shore in 1992, the mean weight of infesting zebra mussels (n = 166, 42 ± 1.9) was less than the mean weigl unionids (67 ± 1.6).

In general, unionids within Anodontinae and Lampsilinae were impacted more by m infestation than those of Ambleminae between 1982–1983 and 1992/1994 (Tables 1 3). All 6 of 6 species of Ambleminae occurred in the river at last sampling in 1992 or 1 whereas 0 of 5 species of Anodontinae and 13 of 16 live species of Lampsilinae were fo at last sampling. The number of species of Ambleminae and Lampsilinae along the so eastern shore declined between 1982–1983 (17 species) and 1992 (13 species), but n of the three species of Anodontinae were found in 1992. Along the northwestern sh species of Anodontinae disappeared and species of Lampsilinae declined from 15 whereas the number of Ambleminae remained the same at six species between 1982–19 1992 and 1994. Mean numbers of individuals per species of the Lampsilinae decline fold along the southeastern shore between 1982–1983 and 1992, and 40-fold along northwestern shore between 1982–1983/1992 and 1994, whereas mean numbers of Am minae declined only 5-fold along the southeastern shore between 1982–1983 and 1992 along the northwestern shore between 1982–1983/1992 and 1994.

Although numbers of common species (>10% of live unionids in 1982–1983) decl more than uncommon species (<10%), taxa of uncommon species were more likely t extirpated than common species from the Detroit River between 1982–1983 and 1992/ (Table 1). Along the southeastern shore, numbers of live individuals of commonly fo species declined 97% (from 302 to 9 individuals) and numbers of uncommonly fo individuals declined 76% (120 to 29 and 2 *Epioblasma torulosa rangiana* not preser 1982–1983). Along the northwestern shore, commonly found individuals declined (from 675 to 22 individuals) and uncommonly found individuals declined 83% (182 t and 6 *Amblema plicata plicata* not present in 1982–1983) between 1982–1983 and 1 However, in 1982–1983 along the southeastern shore, there were 17 uncommon an common (*Lampsilis siliquoidea, Leptodea fragilis* and *Potamilus alatus*) live species; in 1 only 9 of 17 (53%) of the uncommon species were found, whereas all three of the com species found in 1982–1983 were present. Similarly, in 1982–1983 along the northwes shore, there were 17 uncommon and 5 common (*Lampsilis ovata, L. siliquoidea, Lept fragilis, Liguma recta* and *Potamilus alatus*) live species; in 1994, only 8 of 17 (47%) o uncommon species were found, whereas 3 of 5 (60%) common species found in 1982– were present.

TABLE 1.—Numbers of dead, live and total unionids collected at stations located along shores in the Detroit River 1982–1983, 1992 and 1994. Mean number per species with same superscripts indicate significant differences ($P \leq 0.05$)

| | Southeastern Shore | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Stations 12 and 15–17 | | | | | | Stations 10, 11, 13 and 14 | | |
| | 1982–1983 | | | 1992 | | | 1992 | | |
| Subfamily/Species | Dead | Live | Total | Dead | Live | Total | Dead | Live | Total |
| Ambleminae | | | | | | | | | |
| *Amblema plicata plicata* | 0 | 2 | 2 | 1 | 3 | 4 | 2 | 1 | 3 |
| *Fusconaia flava* | 0 | 7 | 7 | 1 | 2 | 3 | 7 | 1 | 8 |
| *Quadrula quadrula* | 0 | 0 | 0 | 1 | 0 | 1 | 5 | 0 | 5 |
| *Cyclonaias tuberculata* | 1 | 1 | 2 | 3 | 0 | 3 | 15 | 1 | 16 |
| *Elliptio dilatata* | 0 | 14 | 14 | 20 | 1 | 21 | 58 | 6 | 64 |
| *Pleurobema cordatum* | 0 | 5 | 5 | 2 | 2 | 4 | 1 | 0 | 1 |
| Anodontinae | | | | | | | | | |
| *Pyganodon grandis* | 0 | 11 | 11 | 3 | 0 | 3 | 3 | 0 | 3 |
| *Anodontoides ferussacianus* | | | | | | | | | |
| *Lasmigona c. complanata* | 0 | 2 | 2 | 0 | 0 | 0 | 3 | 0 | 3 |
| *L. costata* | 0 | 1 | 1 | 0 | 0 | 0 | 15 | 0 | 15 |
| *Strophitus undulatus* | | | | | | | | | |
| Lampsilinae | | | | | | | | | |
| *Actinonaias ligamentina* | 0 | 1 | 1 | 4 | 0 | 4 | 15 | 0 | 15 |
| *Epioblasma torulosa rangiana* | 1 | 0 | 1 | 2 | 2 | 4 | 2 | 0 | 2 |
| *E. triquetra* | | | | | | | 1 | 0 | 1 |
| *Lampsilis ovata* | 0 | 30 | 30 | 50 | 15 | 65 | 73 | 4 | 77 |
| *L. siliquoidea* | 7 | 77[a/] | 84 | 62 | 1 | 63 | 60 | 0 | 60 |
| *Leptodea fragilis* | 1 | 109[a/] | 110 | 89 | 6 | 95 | 163 | 0 | 163 |
| *Ligumia nasuta* | 0 | 10 | 10 | 7 | 0 | 7 | 7 | 0 | 7 |
| *L. recta* | 0 | 21 | 21 | 19 | 3 | 22 | 60 | 1 | 61 |
| *Obliquaria reflexa* | | | | | | | 0 | 3 | 3 |
| *Obovaria olivaria* | 0 | 5 | 5 | 3 | 1 | 4 | 1 | 0 | 1 |
| *O. subrotunda* | | | | | | | 1 | 1 | 2 |
| *Potamilus alatus* | 3 | 116[a/] | 119 | 98 | 2 | 100 | 212 | 0 | 212 |
| *Ptychobranchus fasciolaris* | 1 | 1 | 2 | 5 | 0 | 5 | 35 | 0 | 35 |
| *Truncilla donaciformis* | 0 | 1 | 1 | 0 | 0 | 0 | 9 | 0 | 9 |
| *T. truncata* | 0 | 6 | 6 | 3 | 1 | 4 | 26 | 0 | 26 |
| *Villosa fabalis* | | | | | | | | | |
| *V. iris* | 0 | 2 | 2 | 1 | 1 | 2 | 6 | 3 | 9 |
| Total Number | 14 | 422 | 436 | 374 | 40 | 414 | 780 | 21 | 801 |
| Percent Total | 3 | 97 | 100 | 90 | 10 | 100 | 98 | 2 | 100 |
| Number of species | 6 | 20 | 22 | 19 | 13 | 19 | 24 | 9 | 25 |

TABLE 1.—Continued

| Subfamily/Species | Northwestern shore Stations 1–9 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1982–1983 | | | 1992 | | | 1994 | | |
| | Dead | Live | Total | Dead | Live | Total | Dead | Live | Total |
| Ambleminae | | | | | | | | | |
| *Amblema plicata plicata* | 1 | 0 | 1 | 6 | 13 | 19 | 3 | 6 | 9 |
| *Fusconaia flava* | 0 | 1 | 1 | 7 | 15 | 22 | 12 | 3 | 15 |
| *Quadrula quadrula* | 0 | 1 | 1 | 0 | 2 | 2 | 2 | 1 | 3 |
| *Cyclonaias tuberculata* | 3 | 4 | 7 | 4 | 10 | 14 | 12 | 6 | 18 |
| *Elliptio dilatata* | 19 | 49 | 68 | 84 | 114 | 198 | 123 | 10 | 133 |
| *Pleurobema cordatum* | 1 | 9 | 10 | 1 | 9 | 10 | 10 | 2 | 12 |
| Anodontinae | | | | | | | | | |
| *Pyganodon grandis* | 1 | 11 | 12 | 26 | 7 | 33 | 9 | 0 | 9 |
| *Anodontoides ferussacianus* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Lasmigona c. complanata* | 0 | 4 | 4 | 5 | 11 | 16 | 18 | 0 | 18 |
| *L. costata* | 1 | 4 | 5 | 10 | 9 | 19 | 21 | 0 | 21 |
| *Strophitus undulatus* | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 1 |
| Lampsilinae | | | | | | | | | |
| *Actinonaias ligamentina* | 0 | 3 | 3 | 15 | 49 | 64 | 28 | 3 | 31 |
| *Epioblasma torulosa rangiana* | 5 | 12 | 19 | 38 | 93 | 131 | 21 | 0 | 21 |
| *E. triqueta* | 0 | 0 | 0 | 1 | 2 | 3 | 3 | 0 | 3 |
| *Lampsilis ovata* | 13 | 98[a/] | 111 | 134 | 247 | 381 | 256 | 8 | 264 |
| *L. siliquoidea* | 21 | 190[a/] | 211 | 155 | 84 | 239 | 288 | 7 | 295 |
| *Leptodea fragilis* | 48 | 163[a/] | 211 | 139 | 289 | 428 | 418 | 0 | 418 |
| *Ligumia nasuta* | 11 | 37 | 48 | 14 | 4 | 18 | 34 | 0 | 34 |
| *L. recta* | 5 | 103[a/] | 108 | 76 | 129 | 205 | 158 | 0 | 158 |
| *Obliquaria reflexa* | 0 | 0 | 0 | 0 | 6 | 6 | 2 | 1 | 3 |
| *Obovaria olivaria* | 0 | 4 | 4 | 1 | 0 | 1 | 1 | 0 | 1 |
| *O. subrotunda* | 1 | 2 | 3 | 4 | 2 | 6 | 1 | 0 | 1 |
| *Potamilus alatus* | 9 | 121[a/] | 130 | 145 | 316 | 461 | 448 | 7 | 455 |
| *Ptychobranchus fasciolaris* | 8 | 15 | 23 | 30 | 63 | 93 | 54 | 2 | 56 |
| *Truncilla donaciformis* | 7 | 7 | 14 | 3 | 5 | 8 | 2 | 0 | 2 |
| *T. truncata* | 11 | 18 | 30 | 51 | 92 | 143 | 25 | 0 | 25 |
| *Villosa fabalis* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *V. iris* | 0 | 1 | 1 | 3 | 19 | 22 | 9 | 2 | 11 |
| Total Number | 165 | 857 | 1022 | 954 | 1592 | 2546 | 1959 | 58 | 2017 |
| Percent Total | 16 | 84 | 100 | 35 | 65 | 100 | 97 | 3 | 100 |
| Number of species | 17 | 22 | 23 | 25 | 26 | 28 | 26 | 13 | 26 |
| Mean number (±se) /species | 6 ± 1.03 | 21 ± 10.04 | | [illegible] | [illegible] | | [illegible] | [illegible] | |

TABLE 2.—Numbers of individual and species of live unionids collected at stations in the Detı River 1982–1983, 1992 and 1994. Total number of species and mean number of individuals per stat with the same superscript indicate significant differences ($P \le 0.05$)

| | 1982–1983 | | 1992$^{a/}$ | | 1994 | |
|---|---|---|---|---|---|---|
| Shore/Station | Individuals | Species | Individuals | Species | Individuals | Specie |
| Southeastern shore | | | | | | |
| 10 | | | 2 | 2 | | |
| 11 | | | 5 | 3 | | |
| 12 | 176 | 18 | 40 | 13 | | |
| 13 | | | 4 | 2 | | |
| 14 | | | 10 | 4 | | |
| 15 | 55 | 6 | 0 | 0 | | |
| 16 | 53 | 8 | 0 | 0 | | |
| 17 | 138 | 6 | 0 | 0 | | |
| Total | | 20$^{1}$ | | 13$^{1}$ | | |
| $\bar{x} \pm$ SE | 106 ± 30.7$^{2}$ | | 10 ± 10.0$^{2}$ | | | |
| Northwestern shore | | | | | | |
| 1 | 123 | 13 | 290 | 19 | 1 | 1 |
| 2 | 136 | 11 | 212 | 20 | 8 | 6 |
| 3 | 70 | 14 | 290 | 18 | 12 | 6 |
| 4 | 58 | 13 | 210 | 17 | 5 | 4 |
| 5 | 185 | 9 | 235 | 16 | 17 | 7 |
| 6 | 78 | 13 | 155 | 14 | 14 | 8 |
| 7 | 167 | 9 | 50 | 11 | 0 | 0 |
| 8 | 8 | 4 | 73 | 7 | 1 | 1 |
| 9 | 32 | 7 | 77 | 11 | 0 | 0 |
| Total | | 22$^{3}$ | | 26$^{3}$ | | 13$^{3}$ |
| $\bar{x} \pm$ SE | 95 ± 20.3$^{4}$ | | 177 ± 30.9$^{4}$ | | 6 ± 2.2$^{4}$ | |

$^{a/}$ Only stations 12 and 15–17 used in tests of significance

TABLE 3.—Mean numbers of individual unionids (±SE) per species and, in parentheses, numbers live species in subfamily groups collected along shores in the Detroit River 1982–1983, 1992 and 19! Mean numbers of individuals per species with same superscript indicate significant difference (P 0.05)

| | Southeastern shore (Stations 12 and 15–17) | | Northwestern shore (Stations 1–9) | | |
|---|---|---|---|---|---|
| Subfamily | 1982–1983 | 1992 | 1982–1983 | 1992 | 1994 |
| Ambleminae | 5 ± 2.1 (5) | 1 ± 0.5 (4) | 11 ± 7.8 (5) | 27 ± 17.5$^{1}$ (6) | 5 ± 1.4$^{1}$ (6) |
| Anodontinae | 5 ± 3.2 (3) | 0 (0) | 4 ± 2.0 (3) | 6 ± 2.1$^{2}$ (5) | 0$^{2}$ (0) |
| Lampsilinae | 29 ± 11.8$^{3}$ (12) | 2 ± 1.1$^{3}$ (9) | 46 ± 15.4 (14) | 82 ± 25.5$^{4}$ (15) | 2 ± 0.7$^{4}$ (7) |

## DISCUSSION

We attribute changes in native freshwater unionid populations in the Detroit Rive tween the early 1980s and the mid-1990s to mortality induced by dreissenid mussel i tation. Historically, 28 to 39 species of unionids were found in the Detroit River betv the turn of the century and the early 1980s (Walker, 1913; Goodrich, 1932; van der Sch 1938; Freitag, 1984; van der Schalie, 1986; T. Freitag, U.S. Army Corps of Engineers, De Michigan, pers. comm.). Earlier studies were conducted before dreissenid mussels bec abundant in the Lake St. Clair-Detroit River system in 1989 (Hebert *et al.*, 1989; Grif *et al.*, 1991; Nalepa and Schloesser, 1993). After about 8 yr of infestations by zebra mus unionids declined dramatically. Episodic mortality of unionids has been observed in w of North America before the invasion of dreissenid mussels, but the severity and exte mortality was less than observed in the area between Lakes Huron and Erie in the 1990s (Neves, 1987; Schloesser and Nalepa, 1995).

Infestation of unionids by zebra mussels has been shown to cause high mortality of ur ids, especially in the initial invasion period, in one European lake (Lake Balaton, Hun Sebestyen, 1938), in the St. Lawrence and Hudson rivers (Ricciardi *et al.*, 1996; Strayer Smith, 1996), in open waters of the Great Lakes (Gillis and Mackie, 1994; Schloesser Nalepa, 1994; Schloesser, 1995; Nalepa *et al.*, 1996) and in portions of small rivers and l outside the Great Lakes (*e.g.*, Tucker, 1994; Tucker and Atwood, 1995; Hunter *et al.*, 1 D. Garton, Indiana University, Kokomo, pers. comm.). The near-total mortality of unio observed in the present study is similar to that observed in Lake St. Clair, where mort patterns closely parallel those observed along shores of the Detroit River (Nalepa *et* 1996). In the Hudson River, total mean density of unionids declined 56% between 1 1992 and 1995, and in the St. Lawrence River, densities of unionids declined between and 100% at five sites between 1992 and 1995 (Ricciardi *et al.*, 1996; Strayer and Sn 1996). In the Mississippi River, unionid mortality was observed and attributed to ha alterations by zebra mussels (Tucker, 1994). In the Detroit River, higher proportion uncommon than common unionid species were extirpated along both shores of the between 1982–1983 and 1992/1994. Similarly, infestation in Presque Isle Bay of eas Lake Erie, resulted in 8 of 11 (73%) uncommon taxa and only 1 of 4 (25%) common being extirpated between 1991 and 1993 (E. Masteller, Pennsylvania State University, pers. comm.). In Lake St. Clair, Nalepa *et al.* (1996) found 13 of 15 (87%) uncommon and 1 of 3 (33%) common taxa became extirpated due to zebra mussel infestation betv 1986 and 1994. Of the estimated 297 species of unionids in North America, 213 (7 were considered endangered, threatened, or of special concern before the additional pacts of zebra mussels were taken into account (Williams *et al.*, 1993). Most of the species classified as endangered, threatened, and of special concern were designated cause of their relatively low abundances.

We believe the temporal difference in near-total mortality of unionid populations a the southeastern shore (occurred by 1992) and northwestern shore (occurred between and 1994) is attributable to the temporal difference in the abundance of dreissenid mu in Lake St. Clair and the resulting probable dispersal of mussel veligers into the De River. Lake St. Clair contains two semipermanent (disrupted by wind), water masse southern and a northern) that have distinct physical and chemical properties (Leach, 1 1991). The southern and northern water masses in the lake primarily flow down the sc eastern and northwestern shores around a large island at the headwaters of the De River, respectively (Ayers, 1964; U.S. Army Corps of Engineers, 1975). In 1990, the south water mass probably contained large numbers of veligers as a result of high densities

4000/m$^2$) of dreissenid mussels on underlying substrates, but the northern water mass probably contained few veligers because few mussels (ca. 5/m$^2$) were found on substrates (Nalepa *et al.*, 1996). The distribution of veligers and the resulting settlement of mussels has been shown to depend on substrate densities of mussels and water currents (Stanczykowska and Lewandowski, 1993; Sprung, 1993). Therefore, heavy infestations of unionids probably occurred earlier along the southeastern shore (stations 10–17), and along the northwestern shore below the island at the head of the river (stations 7–9) where waters from both shores mix, than at stations 1–6 along the northwestern shore. In the southern portion of Lake St. Clair, little unionid mortality was measured in 1990, but near-total mortality occurred by 1992 (Nalepa, 1994). Along the southeastern shore of the Detroit River, near-total mortality was also evident in 1992. In the northern portion of Lake St. Clair, near-total mortality of unionids occurred between 1992 and 1994 (Nalepa *et al.*, 1996). Similarly, near total mortality occurred along the northwestern shore of the Detroit River between 1992 and 1994.

Causes for differential impacts on subfamilies of unionids demonstrated in the present study are unknown. Schloesser *et al.* (1996) reviewed several characteristics that are believed to be important in determining the vulnerability of unionids to infestation. In general, most studies support the hypothesis that species of Anodontinae and Lampsilinae are impacted sooner and more severely than species of Ambleminae. The present study supports this generalization. However, in Lake St. Clair, Nalepa (1994) and Nalepa *et al.* (1996) found no significant differences in mortality between subfamilies, but did find a trend in which numbers of Anodontinae and Lampsilinae declined less (60% decline) than the number of Ambleminae (80% decline) between 1986 and 1992. The work of Nalepa *et al.* (1996) is similar to that of the present study where significant declines occurred in mean numbers of individuals in all three unionid subfamilies. Similar to the present study, Strayer and Smith (1996) found the density of anodontines dropped 90%, lampsilines dropped 61% and amblemines dropped only 36% within 3 yr of infestation.

To date, high infestation-induced mortality of unionids appears to occur within 8 yr of colonization by zebra mussels. The period between initial colonization by mussels and near-total mortality of unionids in studies conducted to date are; 3–4 yr in the St. Lawrence River, 4 yr in open waters of western Lake Erie, 4 yr in Presque Isle Bay of eastern Lake Erie, >4 yr in the Hudson River, 6 yr in southern Lake St. Clair and along the southeastern shore of the Detroit River, 7 yr in nearshore waters of western Lake Erie and 8 yr in northern Lake St. Clair and along the northwestern shore of the Detroit River (Schloesser and Nalepa, 1994; Nalepa *et al.*, 1996; Ricciardi *et al.*, 1996; Schloesser *et al.*, 1996; Strayer and Smith, 1996; Schloesser *et al.*, 1998). However, in some studies differential mortality between subfamilies makes the determination of the time to near-total mortality of all unionids difficult. For example, near-total mortality of Anodontinae and Lampsilinae unionids has been documented in the Hudson River, but a relatively large proportion of the Ambleminae unionids still exist (Strayer and Smith, 1996). In addition, near-total mortality has not been documented at several sites in the St. Lawrence River (Ricciardi *et al.*, 1996). However, only 4 yr of mussel colonization and infestation of unionids had occurred in the Hudson and St. Lawrence rivers. After 6 yr of colonization of the Detroit River by dreissenid mussels (primarily zebra mussels), live unionids along the southeastern shore accounted for only 5% of the collections, but along the northwestern shore live unionids accounted for 65%; after 8 yr of colonization along the northwestern shore, live unionids accounted for only 3% of the collections. Comparisons between years of colonization by dreissenid mussels in the Hudson and St. Lawrence rivers with that in the Detroit River and Lake St. Clair indicate that more mortality of unionids in the Hudson and St. Lawrence rivers may be expected.

To date, there have been several attempts to predict if and what impacts zebra mussel

FIG. 2.—Unionid mollusk, *Potamilus alatus,* infested with zebra mussels collected near the head the Detroit River

infestation may have on unionids in North America. Early in the invasion of zebra muss and infestation of unionids, Hebert *et al.* (1991) and Schloesser and Kovalak (1991) us visual inspection of infested unionids to predict that infestation could cause substan mortality of unionids (Fig. 2). Subsequent work in Lakes St. Clair and Erie has confirm that unionid mortality may approach 100% when unionids are heavily encrusted with ze mussels (Schloesser and Nalepa, 1994; Nalepa *et al.,* 1996). Quantitative and empiri review of available data led Ricciardi *et al.* (1995) and Schloesser *et al.* (1996) to state t direct measurement of field densities and infestation intensities of zebra mussels could used to predict unionid mortality. In general, these predictions indicate that severe mortal (>90%) of unionids would occur when substrate densities of zebra mussels are >500 6000/m$^2$ and infestation intensities are >100–200 adult dreissenid mussels per unionid. addition, Schloesser *et al.* (1996) suggested that these critical levels needed to occur in t presence of heavy zebra mussel recruitment and the earliest warning of possible unio mortality due to infestation by zebra mussels is "the presence of heavy encrustation exposed unionid shells." Similarly, studies indicate that when infestation weights are ab equal to or exceed host unionids, mortality of unionids approaches 80 to 100% withi year (Schloesser and Kovalak, 1991; Schloesser and Nalepa, 1994; Ricciardi *et al.,* 199 This occurred in the present study in 1992 along the southeastern shore where infestati weights exceeded host weights and mortality was high, but not along the northwestern sh where infestation weights were ca. 60% of host weights, and mortality had not occurr High mortality did occur along the northwestern shore at the next sampling 2 yr later

1994. However, work of Ricciardi *et al.* (1996) at a few locations in the St. Lawrence Riv and Strayer and Smith (1996) in the Hudson River indicate that unionid mortality occu at low substrate densities <2500/m$^2$ and infestation intensities <10/unionid. Strayer an Smith (1996) discuss possible explanations for the apparent discrepancy between predicti measures and observations in the Hudson River and suggest that food in the water colun may be the limiting factor for unionids and that this limitation is created by consumptio of available food by zebra mussels. Some data indicate that infestation intensities tend be lower at sites with moving (lotic) water than at sites with slower moving (lentic) wate (Ricciardi *et al.*, 1995). In addition, densities of mussels are generally lower in riverine tha in lentic waters (Mellina and Rasmussen, 1994). However, some of the highest infestatio intensities (*i.e.*, >10,000/unionid) and substrate densities (800,000/m$^2$) occurred in a r erine habitat of a power plant canal (Schloesser and Kovalak, 1991; Kovalak *et al.*, 199 At present, the predictive measures described by Ricciardi *et al.* (1995) and Schloesser *al.* (1996) are useful indicators of possible mortality, but more measures are needed if v are to be able to predict all conditions under which zebra mussels may cause mortality unionids.

Although fewer individuals were collected at station 12 in 1992 (40) than in 1982–19 (176), the number collected at this station represents 66% of the total live (61) individu collected in 1992. This may be because unionids were abundant at station 12 in 1982–19 and 6 yr of infestation by dreissenid mussels at this site may not have been long enough reduce the numbers of unionids. Work by Nalepa *et al.* (1996) in Lake St. Clair, locate immediately upstream of the Detroit River supports the hypothesis that more infestatio induced mortality will occur in the Detroit River because in 1994 a few (2% of the 19 population representing species of all three subfamilies) unionids were present in Lake S Clair, but in 1996 no unionids occurred (T. Nalepa, Great Lakes Environmental Researc Laboratory, Ann Arbor, Michigan, pers. comm.). Or, perhaps station 12 is a 'refuge' si where unionids appear to survive in the presence of dreissenid mussel colonization. Sever refugia habitats have been found. For example, in nearshore waters (small bays, wave swe shores, and wetlands) of western Lake Erie unionids appear to survive in the presence dreissenid mussels (both zebra and quagga mussels) (Schloesser *et al.*, 1998; D. Wilco Great Lakes Science Center, Ann Arbor, Michigan, pers. comm.). Some studies have pr posed that sites like these be managed to ensure survival of unionid populations, althoug long-term studies have not been completed (Clarke, 1992; Masteller *et al.*, 1993; Tuck and Atwood, 1995; reviewed in Schloesser *et al.*, 1996). Therefore, we do not know if i festations will permanently reduce unionid populations or extirpate unionid species over broad geographic region in North America. In Europe, some species of unionids ha survived in the presence of dreissenid mussels for decades (Lewandowski, 1976). Howeve little quantitative information about unionid populations before the invasion of dreissen mussels in Europe is available (Sebestyen, 1938; Lewandowski, 1976; reviewed in Schloess and Kovalak, 1991).

The present study documents extensive and severe mortality of unionids caused by drei senid mussel infestations in the Detroit River of the Great Lakes. Infestation caused a 95 reduction in the number and extirpated eight species of unionids between 1986 (whe zebra mussels were first introduced into the system) and 1992/1994. This study, and other suggest that: (1) high mortality of unionids can occur between 4 and 6 yr after initi invasion by dreissenids or up to 8 yr depending on water current patterns; (2) species i the subfamilies Anodontinae and Lampsilinae were more vulnerable to infestation tha species of Ambleminae; (3) numbers of individuals of commonly found species decline more than numbers of individuals of uncommonnly found species; and (4) numbers uncommonly found taxa declined more than numbers of commonly found taxa. Ir Detroit River, unionids along opposite shores and in up-river and down-river areas exhil a 2-yr difference in high mortality that is attributed to differences in the abundan veligers in headwaters of the river. Therefore, examination of the abundance of dreis mussel veligers entering a river may be an important consideration in assessing if uni are threatened by infestations in a riverine system. Unfortunately, in the Detroit River, s mortality did eventually occur throughout the river and, at present, it is not known maining unionid populations in the Detroit River will survive.

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