

Decline of Native Unionid Bivalves in Lake St. Clair After Infestation by the Zebra Mussel, *Dreissena polymorpha*¹

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To determine impacts of the zebra mussel, *Dreissena polymorpha*, on bivalves in Lake St. Clair, densities of Unionidae in 1990 and 1992 (after *D. polymorpha* invasion) were compared with densities in 1986 (before *D. polymorpha*). Declines in density occurred mainly at sites in the southeastern portion of the lake where unionids were highly infested with *D. polymorpha*. Unionid densities at highly infested sites declined from 2.4/m² in 1986, to 1.8/m² in 1990, and to 0/m² in 1992. Unionid species with light-weight shells that brood larvae over an extended period declined more between 1986 and 1990 than heavy-shelled, short-term brooders. Unionid densities at lightly infested sites located mainly in the northwestern portion of the lake did not decline: mean densities were 1.4/m² in 1986, 1.6/m² in 1990, and 1.4/m² in 1992. While the mean number of *D. polymorpha* per unionid was <1 at these lightly infested sites in 1990, it increased to 35 by 1992. Given this relatively slow increase in *D. polymorpha* per unionid in this portion of the lake, continued monitoring of populations should provide a better understanding of the relationship between the extent of infestations and unionid mortality.

Afin de déterminer quel effet a eu la moule zébrée *Dreissena polymorpha* sur les bivalves du lac Sainte-Claire, on a comparé la densité des unionidés en 1990 et 1992 (après l'invasion de *D. polymorpha*) à ce qu'elle était en 1986 (avant l'invasion). Il y a eu baisse de densité principalement dans les stations situées dans la partie sud-est du lac où les unionidés ont été fortement infestés par *D. polymorpha*. Dans ces stations, la densité des unionidés est passée de 2,4/m² en 1986 à 1,8/m² en 1990 et à 0/m² en 1992. Les espèces des unionidés à la paroi mince qui couvent leurs larves pendant longtemps ont connu un plus grand déclin entre 1986 et 1990 que celles à la coquille épaisse et qui ne couvent pas longtemps. Il n'y a pas eu abaissement de la densité des unionidés dans les stations légèrement infestées, et qui étaient situées principalement dans la partie nord-ouest du lac : la densité moyenne était de 1,4/m² en 1986, de 1,6/m² en 1990 et de 1,4/m² en 1992. Alors qu'il était <1 dans ces stations légèrement infestées en 1990, le nombre moyen de *D. polymorpha* par unionidé était passé à 35 en 1992. Compte tenu de cette augmentation relativement lente du nombre de *D. polymorpha* par unionidé dans cette partie du lac, on pense que le suivi des populations devrait nous permettre de mieux comprendre le rapport entre le degré d'infestation et la mortalité chez les unionidés.

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When the zebra mussel, *Dreissena polymorpha*, was first reported from North America, one of the early concerns was the impact that this species would have on bivalves of the family Unionidae (Hebert et al. 1991; Schloesser and Kovalak 1991; Mackie 1991, 1993). Unionids are filter-feeders that position themselves in substrates with their anterior end buried and their posterior end extending into the overlying water. Being a biofouler, *D. polymorpha* attaches to the exposed portion of the unionid, often reaching numbers as high as 10 000 per individual unionid (Hebert et al. 1991). Heavy infestations may interfere with normal metabolic functions of the unionid such as feeding, respiration, and reproduction and may also impede normal locomotion (Mackie 1991). To date, several surveys of unionids in the Great Lakes region have presented indirect evidence that unionid populations may be declining because of

D. polymorpha infestations (Hunter and Bailey 1992; Haag et al. 1993). However, while these studies imply negative impacts on natural populations, quantitative surveys of unionids conducted before and after the establishment of *D. polymorpha* are presently lacking.

In this study, densities of unionids in Lake St. Clair were determined in 1990 and 1992 and compared with densities found in 1986 (Nalepa and Gauvin 1988). The 1986 survey was conducted 2 yr prior to the first discovery of *D. polymorpha* in the lake and thus provides a baseline for post-invasion comparisons.

Description of Study Site

Lake St. Clair lies at the center of the 125-km-long waterway between Lake Huron and Lake Erie. It has an area of 1100 km², a volume of 3.4 km³, and a mean depth of 3 m. The lake is characterized by two distinct water masses, a northwestern mass and a southeastern mass, that contribute

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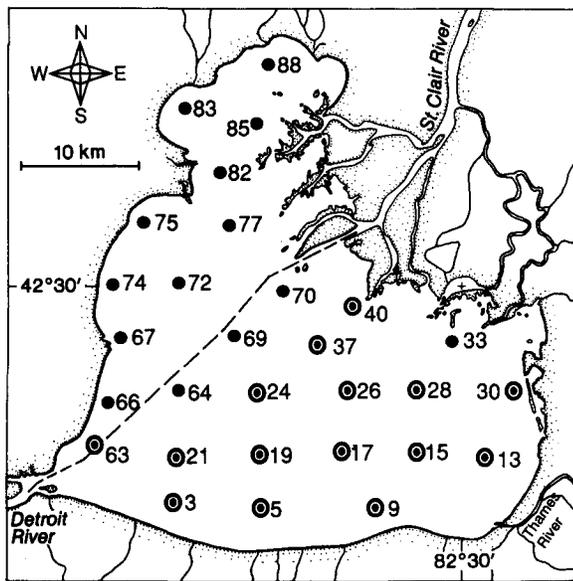


FIG. 1. Location of sampling sites in Lake St. Clair in 1986, 1990, and 1992. Circled sites indicate where unionids were highly infested with *Dreissena polymorpha* in 1990 and prior to 1990 (see text for details). Broken line indicates shipping channel.

to spatial differences in lake productivity (Leach 1972, 1980). Although the areal extent of these two water masses will vary depending on wind speed and direction, the deep channel marking the shipping lane provides a general boundary between the two water masses under the prevailing southwesterly winds (Schwab et al. 1989). A relatively high volume of water (yearly mean = 5100 m³/s) enters the lake from Lake Huron via the St. Clair River, moves through the lake mainly along the western shoreline, and exits via the Detroit River. Inflow from the St. Clair River accounts for 98% of the water entering the lake through distributary channels located northwest of the shipping channel (Fig. 1). This water mass is colder and contains fewer nutrients than the water mass in the southeastern portion of the lake, which is more stable, warmer, and enriched by nutrient loadings from numerous small tributaries and the Thames River. Levels of nutrients and abundances of both phytoplankton and zooplankton increase on a gradient from northwest to southeast (Leach 1972, 1980; Bricker et al. 1976). Although the two water masses are distinct, the lake is vertically well mixed, thermal stratification does not occur, and oxygen concentrations remain close to saturation throughout the year (Herdendorf et al. 1986).

Materials and Methods

Sampling sites and methods in 1990 and 1992 were the same as in 1986. Collections were made in September of each year at 29 sites located throughout the lake (Fig. 1). Site locations (longitude and latitude) were the same as given in Pugsley et al. (1985). In 1986, sites were located using Loran C, and water depth and substrate type were recorded (Table 1 in Nalepa and Gauvin 1988). Loran C was also used for positioning during the 1990 and 1992 surveys.

At each site, SCUBA divers positioned a 0.5-m² frame on the bottom and collected all hard material within the

frame to a depth of 5 cm. The material collected included all living and dead shells of unionids, *D. polymorpha*, and hard substrate. Ten replicate quadrat samples were collected at each site; divers moved about 2–3 m between replicates to insure that each sample was taken in an undisturbed area. Immediately after collection, live unionids were opened and soft tissues placed in preweighed aluminum planchets. Any *D. polymorpha* attached to the unionids were removed and placed in 5% buffered formalin.

In the laboratory, soft tissue and shell dry weights of unionids were obtained separately after drying at 60°C for at least 48 h. Total shell lengths were determined to the nearest millimetre with vernier calipers. The relationship between dry tissue weight and shell length was described by the general allometric equation $W = aL^b$ where W is the tissue weight in grams, L is the shell length in millimetres, and a and b are constants. All *D. polymorpha* were rinsed through a screen with 500- μ m openings, counted, and lengths measured using a digitizer pad (Quigley and Lang 1989). Weights (tissue and shell) of *D. polymorpha* were obtained from length-weight regressions determined from individuals collected on a monthly basis from April to November at two of the sites (stations 3 and 19) (Nalepa et al. 1993). Weights in 1990 and 1992 were determined from separate regressions. Unionid taxonomy followed that of Williams et al. (1993).

Results

On a lakewide basis, the density of unionids was significantly lower (Wilcoxon paired-sample test, $P < 0.001$, $n = 29$) in 1992 than in 1986. Mean density declined from 1.9/m² in 1986, to 1.7/m² in 1990, and to 0.7/m² in 1992. Unionids were not found at four sites in 1986 and 1990, but the number of sites where unionids were not found increased to 15 in 1992. In examining changes in density at individual sites, it was obvious that declines did not occur uniformly over the entire lake, but occurred mainly at sites in the southeastern portion (Fig. 2). This portion of the lake was first extensively colonized by *D. polymorpha* in 1988 (Hebert et al. 1989) and overall densities were higher here than in the northwestern portion of the lake in 1990 and 1992 (T.F. Nalepa, unpublished data; Griffiths 1993).

To determine the relationship between the decline in unionids at individual sites and the number of attached *D. polymorpha*, sampling sites were divided into two categories based on the mean number of *D. polymorpha* per unionid in 1990: highly infested (≥ 55 per unionid) and lightly infested (≤ 3 per unionid) (Fig. 3). The actual number of *D. polymorpha* per individual unionid ranged from 0–1360 at sites in the highly infested category (97% of unionids infested) and ranged from 0–9 at sites in the lightly infested category (14% of unionids infested). The mean ratio between the total weight (shell and soft tissue) of attached *D. polymorpha* and weight of the corresponding unionid was 1.2 (range 0–8.5) at the highly infested sites. Of the 11 sites in the highly infested category, unionid densities at four of the sites were significantly lower (Wilcoxon one-tailed two-sample test, $P < 0.01$) in 1990 compared with densities in 1986 and densities at six sites were significantly lower in 1992 compared with densities in 1990 (Fig. 2). As noted, unionids were not collected at four sites in 1990 and, therefore, could not be categorized as highly infested or lightly infested. However, all of these sites were located in the

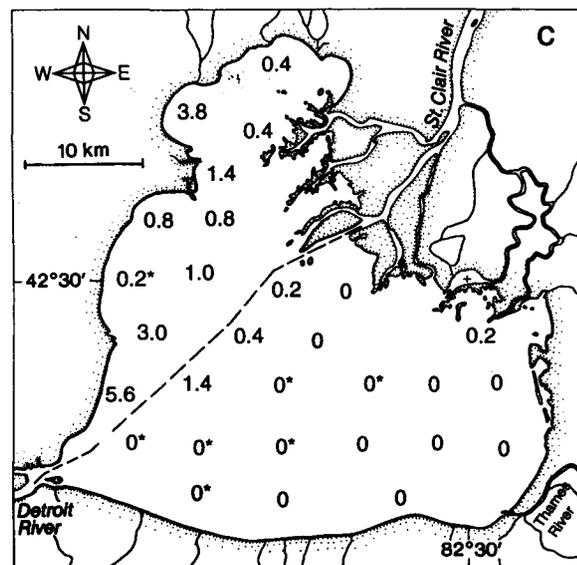
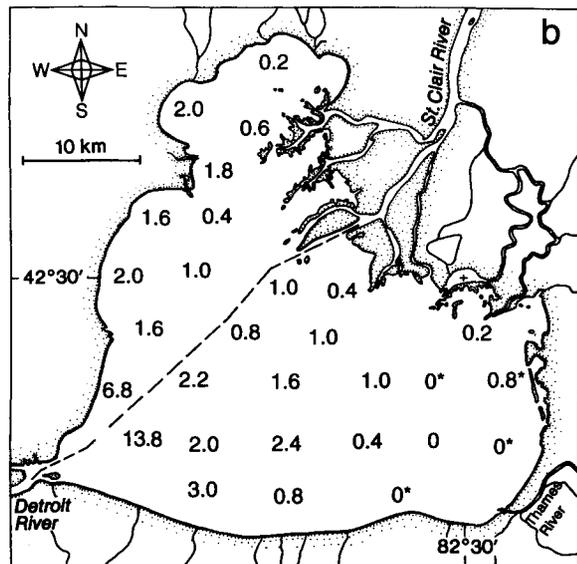
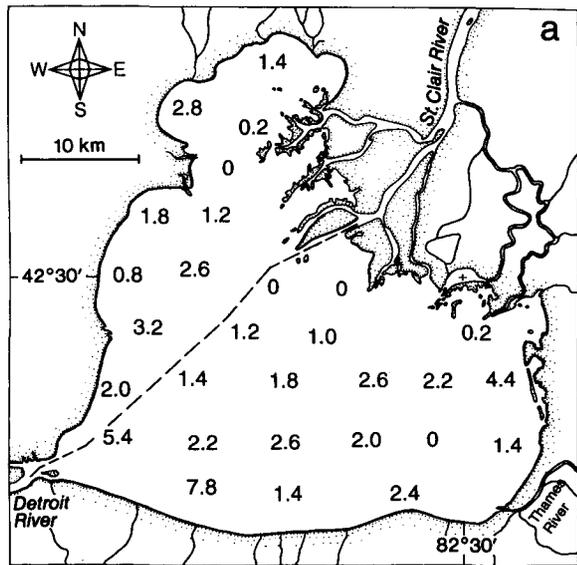


FIG. 2. Mean density (per m^2) of unionids at each of the 29 sampling sites in Lake St. Clair in 1986 (a), 1990 (b), and 1992 (c).

southeastern portion of the lake where unionids were highly infested prior to 1990 (see Fig. 3, Hebert et al. 1991). With these four sites included in the highly infested category, mean densities of unionids at highly infested sites (15 total) declined from $2.4/m^2$ in 1986, to $1.8/m^2$ in 1990, and to $0/m^2$ in 1992. In contrast, unionid densities did not decline (Wilcoxon one-tailed two-sample test, $P > 0.01$) significantly at any of the 14 sites in the lightly infested category between 1986 and 1990, and declined significantly at only one site between 1990 and 1992 (Fig. 2). Mean densities at these sites were $1.4/m^2$ in 1986, $1.6/m^2$ in 1990, and $1.4/m^2$ in 1992. Although densities of unionids did not decline at sites in the lightly infested category over the study period, the mean number of attached *D. polymorpha* per unionid increased from <1 per unionid in 1990 to 32 per unionid in 1992, and from 14% of all unionids infested to 97% infested. The total number of species declined from 18 in 1986, to 17 in 1990, and to 12 in 1992 (Table 1). In field experiments, species in the subfamilies Anodontinae and Lampsilinae were found to be more sensitive (as measured by increased mortality and loss of energy reserves) to fouling by *D. polymorpha* than species in the subfamily Ambleminae (Haag et al. 1993). To determine if differential mortality occurred in these subfamilies in Lake St. Clair over the study period, the relative frequency of anodontines and lampsilines was compared with the frequency of ambleminae at both the highly infested and lightly infested sites (Table 1). At the highly-infested sites, the relative frequency of these two subfamily groups was dependent on sampling year (G -test, $P < 0.01$), with a lower proportion of anodontines and lampsilines being found in 1990 than in 1986. Species that declined the most were *Pyganodon grandis* (75%) and *Lampsilis siliquoidea* (50.6%); however, for other species such as *Leptodea fragilis* and *Lampsilis cardium* the decline was negligible (Table 1). At the lightly-infested sites, the relative frequency of subfamily groups was independent of sampling year (G -test, $P > 0.05$). With sites grouped as in 1990, relative frequencies of subfamilies in 1986 were independent of site groupings, indicating no a priori differences in spatial distributions of subfamilies.

In addition to differential mortality between subfamilies, Haag et al. (1993) found that female *L. radiata* were more sensitive to fouling by *D. polymorpha* than males. In this study, the relative frequency of female and male *L. siliquoidea* was independent of sampling year (G -test, $P > 0.01$) at both the highly infested and lightly infested sites (Table 2), indicating that differential mortality by sex did not occur. Since sublethal stress may occur prior to mortality, the relationship between soft tissue weight and shell length was determined separately for each sex at the highly infested and lightly infested sites. In unionids, this relationship has been used to assess changes in physiological state in response to varying environmental conditions (Payne and Miller 1987). Yearly trends in the dry tissue weight for a standard 60-mm individual (mean shell length of all *L. siliquoidea*) were not apparent for either sex (Table 2).

An asterisk (*) in 1990 indicates a significant decline in density compared with 1986 and an asterisk in 1992 indicates a significant decline in density compared with 1990 (Wilcoxon one-tailed two-sample test, $P < 0.01$).

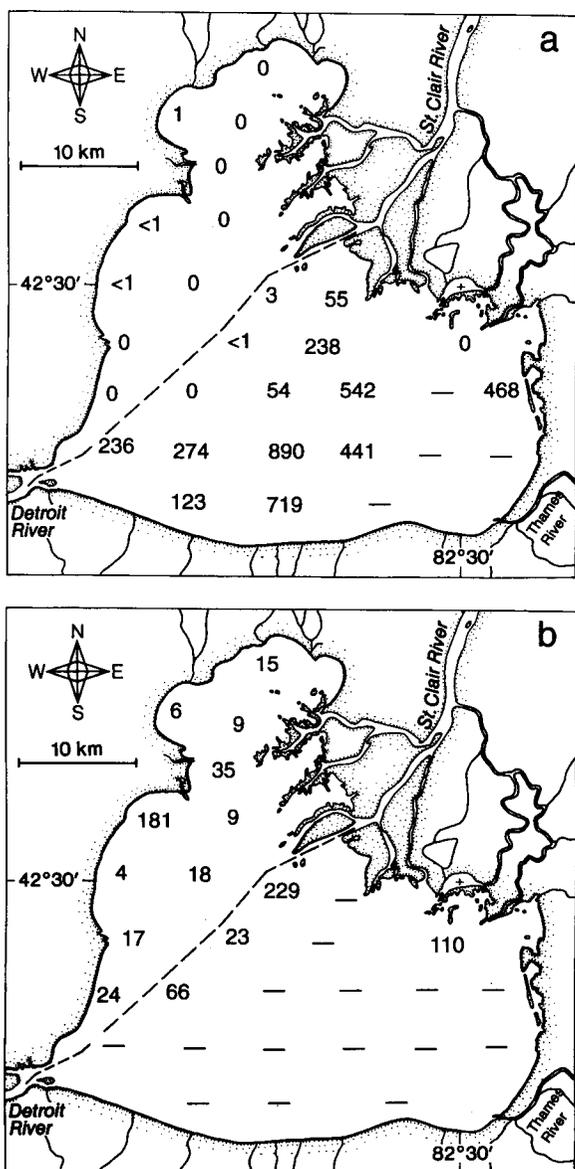


FIG. 3. Mean number of *Dreissena polymorpha* attached to unionids at each of the 29 sampling sites in Lake St. Clair in 1990 (a) and 1992 (b). *Dreissena polymorpha* was not found at any of the sites in 1986. A dash (—) indicates no unionids collected.

Discussion

In comparing temporal changes in unionid populations of Lake St. Clair in 1986 (before *D. polymorpha* invasion) and in 1990 and 1992 (after *D. polymorpha* invasion), the negative impact of *D. polymorpha* on densities of unionids was evident. At sites in the southeastern portion of the lake where unionids were first infested with *D. polymorpha* in 1988 (Hebert et al. 1991), unionid densities began to decline within 2 yr (1990), and no unionids were collected within 4 yr (1992) of infestation. At sites in the northwestern portion of the lake where unionids were not widely infested with *D. polymorpha* until after 1990, declines in densities were not evident in 1992. The delay in unionid infestations in the northwestern portion of the lake can be attributed to the high volume of water flowing into this region from the St. Clair River. This flow probably inhibited *D. polymorpha* larvae from other portions of the lake from easily colonizing

this area. Also, few populations were established in the upstream reaches to serve as a source of larvae (i.e., lower Lake Huron, St. Clair River).

Since the establishment of *D. polymorpha* in North America and the subsequent finding that this species attaches to unionids in large numbers, various authors have predicted that unionids would be negatively affected over the long term (Hebert et al. 1991; Mackie 1991; Schloesser and Kovalak 1991). Others have provided only indirect evidence that natural populations of unionids were declining in areas infested with *D. polymorpha*. For instance, in sampling three sites in Lake St. Clair in 1990, Hunter and Bailey (1992) found that unionid densities were lower at a site in the southeastern portion of the lake than at a site in the southwestern portion. This spatial difference was attributed to the higher number of *D. polymorpha* per unionid at the former site. However, unionid densities tended to be lower in the southeastern portion of the lake before *D. polymorpha* became established (see densities in 1986, Fig. 2). In a survey of various sites in western Lake Erie, Haag et al. (1993) found that the ratio of live individuals to dead individuals of Anodontinae and Lampsilinae was significantly lower than the same ratio for Ambleminae. While this finding supported experimental results that showed higher mortality in the former two subfamilies when infested with *D. polymorpha*, actual declines in densities were not determined. Gillis and Mackie (1994), on the other hand, documented a decline in unionids at several sites in southwestern Lake St. Clair between 1990 and 1992.

Although unionid densities declined to 0/m² between 1986 and 1992 at sites where *D. polymorpha* infestations were the greatest, it is not clear whether the entire unionid population at these sites has been eliminated. Quadrat sampling by divers is the most accurate and preferred method to quantify unionids and detect changes over time (Isom and Gooch 1986; Downing and Downing 1992), but it is not the best method to assess presence-absence because it is labor intensive and usually only a limited area of the bottom can be sampled at a given site (Kovalak et al. 1986). Other methods that assess populations over much larger areas of the bottom, such as diver observations along transects, or towing an epibenthic sled (Schloesser and Nalepa 1994), need to be used to address the specific issue of total population loss.

As noted, during the early years of the *D. polymorpha* infestation (1990 and before) in Lake St. Clair, unionids in the subfamilies Anodontinae and Lampsilinae declined to a greater extent than unionids in the subfamily Ambleminae at sites where individuals were highly infested. This result generally agrees with the short-term (3 mo) field experiments of Haag et al. (1993) in western Lake Erie. It was hypothesized that anodontines and lampsilines are more sensitive to infestations by *D. polymorpha* because they brood larvae for 9–12 mo, while amblemines brood larvae for only a few weeks to 2 mo. Long-term brooders expend more energy in the reproductive process and would be more susceptible to the unfavorable conditions created by *D. polymorpha*. Also, anodontines and lampsilines tend to have lighter shells, and the added weight of *D. polymorpha* would more likely change their center of gravity and require a greater expenditure of energy to maintain their position in the substrate. In Lake St. Clair, while overall density declines were greater in anodontines and lampsilines than in amblemines at highly infested sites, the extent of the decline varied

TABLE 1. Total number of unionids at sites where the mean number of *Dreissena polymorpha* per unionid was high (≥ 55) and low (≤ 3) in 1990. *Dreissena polymorpha* was not found in 1986. Living unionids were not found at the highly infested sites in 1992. The relative frequency of short- and long-term brooders was dependent upon sampling year (1986, 1990) at the highly infested sites (G -test, $P < 0.01$), but independent of year (1986, 1990, 1992) at the lightly infested sites.

Subfamily and Species	Highly infested (15 sites)			Lightly infested (14 sites)		
	1986	1990	1992	1986	1990	1992
Long-term brooders						
Subfamily Anodontinae						
<i>Lasmigona complanata complanata</i>	1	1	0	0	0	0
<i>Pyganodon grandis</i>	8	2	0	6	9	11
<i>Simpsonaias ambigua</i>	0	0	0	0	1	0
<i>Strophitus undulatus</i>	1	0	0	0	0	0
Subfamily Lampsilinae						
<i>Actinonaias ligamentia</i>	0	0	0	0	1	0
<i>Lampsilis cardium</i>	14	13	0	2	3	2
<i>Lampsilis fasciola</i>	1	0	0	0	0	0
<i>Lampsilis siliquoidea</i>	83	41	0	44	38	45
<i>Leptodea fragilis</i>	24	22	0	13	14	5
<i>Ligumia nasuta</i>	3	3	0	5	2	5
<i>Ligumia recta</i>	0	0	0	3	1	1
<i>Obovaria subrotunda</i>	1	2	0	0	0	0
<i>Potamilus alatus</i>	17	12	0	12	11	19
<i>Truncilla donaciformis</i>	1	0	0	0	6	1
<i>Truncilla truncata</i>	2	0	0	1	11	4
Total	156	96	0	86	97	94*
Short-term brooders						
Subfamily Ambleminae						
<i>Amplema plicata plicata</i>	2	0	0	4	0	1
<i>Elliptio dilatata</i>	16	24	0	4	5	3
<i>Fusconaia flava</i>	8	14	0	2	8	1
<i>Quadrula quadrula</i>	0	0	0	2	2	0
<i>Pleurobema coccineum</i>	0	2	0	1	0	0
Total	26	40	0	13	15	5

*Includes one unidentified young-of-the-year.

greatly across species. In contrast to the results of Haag et al. (1993) which showed greater mortality in female than in male *L. radiata*, differences in mortality between male and female *L. siliquoidea* in Lake St. Clair were not apparent.

Over the short term, mortality of infested unionids may certainly differ by subfamily, species, or even by sex, but over the long term, as found in this study, all unionids in heavily infested areas are negatively affected (i.e., densities of all individuals declined to 0/m²). Exact reasons for unionid mortality are not clear, but are likely related to a general decline in the unionid's physiological condition. Infested unionids display a marked, rapid decline in relative condition in just 3 mo as demonstrated by a decrease in glycogen, the main energy reserve, and an increase in stress, as measured by cellulase activity (Haag et al. 1993). Energy stores in heavily infested unionids may be depleted as a result of the following factors, either solely or in combination: (1) food is not filtered from the water effectively because of siphon blockage; (2) filtered water is already cleared of food by *D. polymorpha* or (3) maintenance of position in the substrate with the added weight of attached *D. polymorpha* leads to added metabolic costs. In the experimental treatments of Haag et al. (1993), control groups consisted of specimens of *L. radiata* with *D. polymorpha* removed. Mortality in

these control groups was still 32% after 3 mo. Some mortality may have been due to handling, but this high mortality may indicate that, at least for this species, recovery from prolonged periods of depleted energy reserves does not readily occur. A loss of energy stores is likely the underlying cause of death over the long term; such a loss makes it difficult for unionids to survive periods of stress, as during the winter months. In Lake St. Clair, the greatest number of freshly dead (soft tissue still present) individuals were observed in early spring (T.F. Nalepa, personal observation). Infested unionids may also be more susceptible to the stresses of winter since they cannot effectively burrow into sediments to overwinter (Stansbery 1961; Amyot and Downing 1991).

Although *D. polymorpha* has colonized Europe for over a century and there are a number of reports of this species infesting unionids (Wagner 1936; Sebestyen 1938; Wolff 1969; Lewandowski 1976), changes in densities of unionids related to *D. polymorpha* infestations have generally not been documented. Also not documented is the long-term fate of populations in waters infested with *D. polymorpha*. In one account, Sebestyen (1938) did report large masses of dead unionids washing up on the beaches of Lake Balaton, Hungary, soon after *D. polymorpha* became established. The greatest mortalities in the lake were observed in 1935-36,

TABLE 2. Total number of individuals and tissue dry weight (g) of male and female *Lampsilis siliquoidea* at sites where the mean number of *Dreissena polymorpha* per unionid was high (≥ 55) and low (≤ 3) in 1990. The relative frequency of males and females was independent of year for both the highly infested and lightly infested sites (G -test, $P > 0.05$). Tissue dry weight is for a standard 60-mm individual as calculated from tissue dry weight – shell length regressions. No individuals were found at the highly infested sites in 1992.

	Highly infested			Lightly infested		
	1986	1990	1992	1986	1990	1992
Number collected						
Male	57	30	0	32	27	33
Female	26	11	0	12	11	12
% Female	31.3	26.8	0	27.3	28.9	26.7
Tissue dry weight						
Male	1.35	1.52	0	1.32	1.92	1.50
Female	1.70	1.71	0	1.51	1.98	1.63

about 4 yr after *D. polymorpha* was first discovered. Interestingly, the time lag between the establishment of *D. polymorpha* and greatest unionid mortality in Lake St. Clair closely paralleled that found in Lake Balaton.

Lewandowski (1976) compared the mean dry tissue weight per shell length of unionids with (mean of 20 per unionid) and without attached *D. polymorpha* from Lake Mikolajskie, Poland. There were no differences in the dry weight per shell length relation between the two groups, and this finding has been cited as evidence that unionids are not affected by *D. polymorpha* when infestations are light (Schloesser and Kovalak 1991). For unionids and molluscs in general, this relationship (or tissue weight : shell weight) has been used as an index of relative physiological condition (Russell-Hunter and Eversole 1976; Payne and Miller 1987; Williams and McMahon 1989). During periods of stress, the individual loses tissue biomass relative to the shell either through decreased tissue growth or tissue reabsorption (Russell-Hunter 1985). Although low numbers of attached *D. polymorpha* may indeed have little impact on the physiological condition of unionids, tissue dry weight per shell length did not prove to be a sensitive indicator of stress in this study; that is, there was no apparent decrease in tissue weight of *L. siliquoidea* at heavily infested sites between 1986 and 1990 even though densities declined. In Lake Mikolajskie, the mean number of *D. polymorpha* per unionid increased from 20 in 1972 to 52 in 1974 (Lewandowski 1976). This increase corresponded to a general increase in *D. polymorpha* populations during this period (Stanczykowska and Lewandowski 1993). Subsequently, by 1987, the number and biomass of unionids in Lake Mikolajskie had declined compared with 1972 (Lewandowski 1991). The decline between 1972 and 1987 was attributed to eutrophication, but *D. polymorpha* may have also played a role.

With the recent movement of *D. polymorpha* outside the Great Lakes basin into the major river systems of North America (Tucker et al. 1993), areas with unionid populations that are much more diverse and abundant than those of the Great Lakes are now threatened. Assuming *D. polymorpha* abundances will vary in these systems, an important question to be considered is how many attached *D. polymorpha* can an individual unionid tolerate before it becomes stressed and eventually dies? In southeastern Lake St. Clair,

the maximum number of *D. polymorpha* per unionid increased from 100 in 1988 to a maximum of 10 000 in 1989 (Hebert et al. 1991). In 1990 at the highly infested sites in the southeastern portion of the lake, the maximum number per unionid was 1400, with a mean of 300, just prior to unionid densities decreasing to 0/m² in 1992. These numbers are higher than the 200 per unionid found to cause mortality and a loss of energy reserves in unionid from western Lake Erie (Haag et al. 1993). Certainly an important factor when relating the number of attached *D. polymorpha* and potential impacts on unionids is the relative "health" of populations before *D. polymorpha* becomes established. Despite a mortality event in 1985 (Neves 1987), the unionid population in Lake St. Clair prior to the introduction of *D. polymorpha* has remained generally stable over time. The number of species and their relative abundances in 1986 were little changed since a survey conducted nearly a century earlier (Nalepa and Gauvin 1988). Thus, the time period between infestations by *D. polymorpha* and observed declines in unionids in southeastern Lake St. Clair may be considered typical for a "healthy", relatively unstressed population. In western Lake Erie, where *D. polymorpha* became established at the same time as in Lake St. Clair (Griffiths et al. 1991), unionids apparently declined more rapidly than in Lake St. Clair (Schloesser and Nalepa 1994). This more rapid decline may represent the response of an already stressed population because unionids in western Lake Erie have been in a state of decline over the past few decades (Nalepa et al. 1991). However, it may also be related to the higher number of *D. polymorpha* attached to unionids in western Lake Erie than in Lake St. Clair (Schloesser and Nalepa 1994).

While the increase in number of *D. polymorpha* per unionid in southeastern Lake St. Clair was rapid, and declines in unionid densities were apparent within 2 yr of infestation, increases in the number of *D. polymorpha* per unionid in the northwestern portion of the lake will likely take place over an extended period and may never equal numbers found in the southeastern portion because of cooler temperatures and lower food supplies. Thus, continued monitoring of unionids in this portion of the lake should provide a better understanding of the relationship between the extent of *D. polymorpha* infestations and subsequent mortality in unionids.

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