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# A Refuge for Native Freshwater Mussels (Bivalvia: Unionidae) from Impacts of the Exotic Zebra Mussel (*Dreissena polymorpha*) in Lake St. Clair

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# A Refuge for Native Freshwater Mussels (Bivalvia: Unionidae) from Impacts of the Exotic Zebra Mussel (*Dreissena polymorpha*) in Lake St. Clair

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***ABSTRACT.*** *The introduction and spread of the exotic zebra mussel* (Dreissena polymorpha) *throughout the Great Lakes has decimated native unionid populations. However, significant communities have continued to survive in several nearshore areas of Lake Erie. This study documents the discovery of a "refuge" site for unionids in Lake St. Clair. Ninety-five sites in various areas around the lake were surveyed between 1998 and 2001, and 2,356 live unionids of 22 species were found alive at 33 of these sites. Almost all sites (31) were in shallow (mainly < 1 m) waters of the St. Clair delta, in habitats similar to refugia in Lake Erie, i.e., nearshore areas with firm sandy substrates and marshy bays with soft, muddy sediments. Species richness ranged from 1 to 12 species per site, and relative abundance ranged from 2 to 302 unionids per person-hour of sampling effort. Densities at nine sites ranged from 0.03 to 0.07 per* $m^2$*. Five species considered to be at risk were found alive. Infestation rates at sites near the St. Clair delta ranged from 0 to 286 zebra mussels per unionid, which is slightly higher than rates at other known refuge sites. The community is now dominated by thick-shelled species such as* Fusconaia flava *and* Lampsilis cardium, *which are known to be least susceptible to zebra mussels. Further studies are needed to determine if unionid populations in the delta are stable, and to understand the mechanisms responsible for unionid survival at this and other refugia. Such information could be used to predict the locations of other natural sanctuaries and to guide their management for the preservation of the Great Lakes unionid fauna.*

***INDEX WORDS:*** *Unionidae, freshwater mussels, zebra mussels, Lake St. Clair, refuge.*

## INTRODUCTION

North America historically supported the greatest diversity of freshwater mussels (Mollusca: Unionacea) in the world. Nearly 300 species and subspecies, representing one-third of the world's freshwater mussel fauna, are native to this continent (Williams *et al.* 1993, Bogan 1993). Forty of Canada's 53 freshwater mussel species occur in the lower Great Lakes drainage basin, and 32 of these have been recorded from Lake St. Clair (Metcalfe-Smith *et al.* 1998). The introduction and spread of the exotic zebra mussel (*Dreissena polymorpha*) throughout the Great Lakes in the late 1980s deci-

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mated native unionid populations (Schloesser *et al.* 1996). Zebra mussels attach to a unionid's shell, where they interfere with activities such as feeding, respiration, excretion, and locomotion, and effectively starve it to death (Haag *et al.* 1993; Baker and Hornbach 1997). Ricciardi *et al.* (1998) estimated that the invasion of the Mississippi River basin by zebra mussels would increase freshwater mussel extinction rates in that system by 10-fold, from about 1.2% of species per decade to 12% per decade.

Native mussel communities were virtually extirpated from the offshore waters of western Lake Erie by 1990 (Schloesser and Nalepa 1994) and the offshore waters of Lake St. Clair by 1994 (Nalepa *et al.* 1996). Similar declines were documented in some nearshore areas, including southwestern Lake St. Clair (Gillis and Mackie 1994) and the inner harbor of Presque Isle Bay, Lake Erie (Schloesser and Masteller 1999). However, significant unionid communities have continued to survive in several nearshore locations in Lake Erie. Schloesser *et al.* (1997) found 11 species of unionids living in firm, compacted sand substrate at a depth of 1 to 2 m near the mouth of the Raisin River in western Lake Erie in 1993. Nichols and Wilcox (1997) collected about 6,000 individuals of 21 species from soft, silt-clay substrates in 1 m of water in Metzger Marsh, on the south shore of western Lake Erie, in 1996. Further, a small community of nine species was discovered in Thompson Bay, the outer harbor of Presque Isle Bay, in shallow (< 1 m) water on silt-sand sediments with relatively little vegetation in 1990 to 1992 (E.C. Masteller, the Pennsylvania State University at Erie, Erie PA, personal communication, December 2001). The objective of this study was to determine if significant unionid communities also persist in similar nearshore areas of Lake St. Clair.

## METHODS

### Study Area

Lake St. Clair is situated between Lake Huron and Lake Erie. It is fed by the St. Clair River and drains into Lake Erie via the Detroit River. It is heart-shaped, with a maximum natural depth of 6.5 m and a surface area of 1,115 km$^2$ (Leach 1991). Because of the lake's shallowness, it has no commercial harbors. A navigation channel dredged to a depth of 8.3 m bisects the lake approximately along the Canada/U.S.A. border to accommodate heavy commercial vessel traffic between Lake Erie and Lake Huron (Edsall *et al.* 1988). The southern and western/northwestern shores of the lake are heavily urbanized (cities of Windsor, Ontario, and Detroit, Michigan, and their suburbs), with improved shorelines, i.e., sea walls, to prevent storm erosion. The northeastern shore consists of a large delta with natural marshland, much of it within the territory of the Walpole Island First Nation, and the eastern shore of the lake is mainly rural farmland. Leach (1991) described the substrate of Lake St. Clair as consisting of muddy sand in the central part of the lake and gravel or sand closer to shore. Prior to the zebra mussel invasion, unionids provided the only hard substrate in many areas (Nalepa *et al.* 1996). At present, most of the hard substrate in offshore areas is made up of unionid shells and zebra mussels (Hunter and Bailey 1992, Nalepa *et al.* 1996).

### Survey Sites and Sampling Methods

A total of 95 sites were surveyed for unionids between 1998 and 2001 (Fig. 1). In 1998, surveys were conducted at three depths (1 m, 2.5 m, and 4 m) along ten transects in the vicinity of Puce and Belle River on the south shore of the lake. At each of these 30 sites, 20 Ekman grabs were taken from a boat, and five 1 m$^2$ quadrats were sampled using SCUBA. Gillis and Mackie (1994) reported that unionids had been virtually eliminated from this area by 1992 due to increasing densities of zebra mussels. The area was re-surveyed in 1998 to determine if any unionids still survived.

Seventy sites were surveyed in 1999, including 10 sites that had been examined in 1998 (5 of 10 transects were re-surveyed at depths of 2.5 and 4 m). Surveys were also conducted at three depths (< 1 m, 2–3 m, and > 4 m) along four transects off Grosse Point, Michigan. Gillis and Mackie (1994) observed that this location was 3 years behind Puce in terms of the intensity of zebra mussel infestation, and they predicted that unionid densities would decline severely by 1994. Substrates in the Puce, Belle River, and Grosse Pointe areas were sandy to a depth of 1 m or less, and consisted of soft silty mud at greater depths. The remaining 48 sites were located at varying depths and distances from the eastern shore of the lake and in Canadian waters off the St. Clair delta, including 12 sites in marshy bays. Substrates consisted of sand at depths of less than 1 m, sand or sand and gravel at depths between 1 and 3 m, and silty mud at depths greater than 3 m. Shallow sites in marshy bays had soft muddy substrates. None of these sites had been surveyed be-

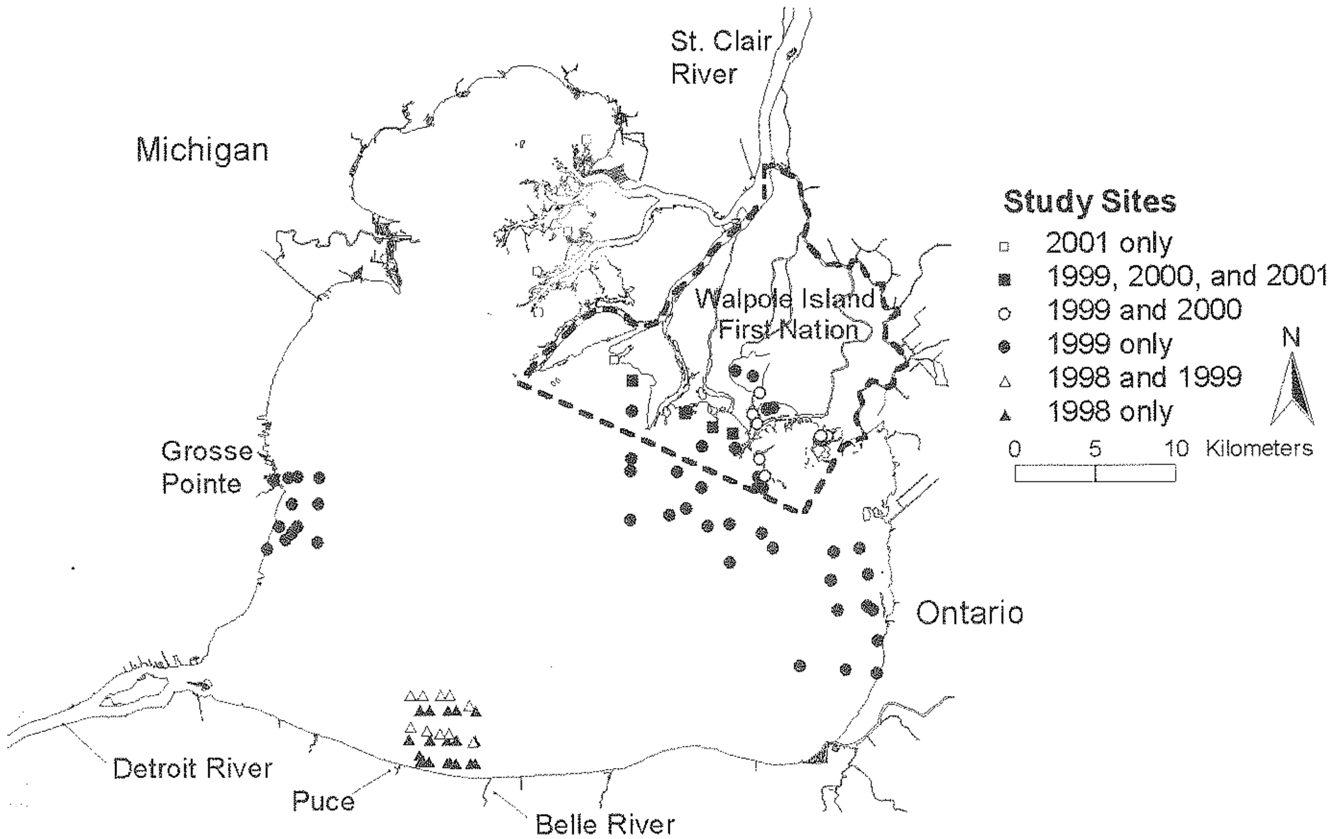


*FIG. 1. Study sites in Lake St. Clair from 1998 to 2001.*

fore. At sites deeper than 2 m, SCUBA searches were conducted by two divers for a total of 0.5 person-hours (p-h). In water shallower than 2 m, searches were conducted by three surveyors using mask and snorkel for a total of 0.75 p-h. At sites where live unionids were found (all were shallow), snorkel searches were extended to a total of 1.5 p-h.

Ten sites where unionids were found to be the most abundant in 1999 were re-surveyed in 2000; all sites were located in shallow water near the delta. Snorkel searches (1.5 p-h duration) were repeated at these sites, and ten 1 $m^2$ quadrats were sampled to estimate unionid densities. Quantitative sampling was conducted in 2001 at four of the sites where mussels were most abundant, using the following technique: two divers searched the area until a live unionid was found. An iron stake was planted next to the animal, and a 4.55 m line was attached at one end to the stake and at the other end to the diver. The diver swam around the stake in circles of ever-decreasing diameter until the entire area (65 $m^2$) had been covered. The technique was very effective in areas with clear water and firm, sandy substrates. In areas with soft substrates, the divers' movements tended to stir up the sediment and reduced visibility to the point where sampling had to be done by feel. Although sampling by feel took more time, it is likely that it was just as thorough. Five additional sites near the delta were also surveyed using the same technique. Ten quantitative samples were taken from each of the nine sites, except that one site was abandoned after five samples had been taken due to deteriorating weather conditions, and 21 samples were taken from one of the most productive sites. It is recognized that sampling technique used in this study may give an overestimate of unionid densities in the area, but because of the non-clumped distribution and sparse density of unionids in the area the overestimate would be very slight. Habitat in the areas sampled in Lake St. Clair was very uniform (generally sand or mud), leading to less selection of specific substrates and a less aggregated distribution of mussels in the area. Downing and Downing (1992) reported that many freshwater mussel populations are not significantly aggregated in their habitat. Sparse populations with

<10 unionids per $m^2$ were much less likely to be spatially aggregated than dense populations (Downing and Downing 1992); the unionid population in Lake St. Clair fits with this analysis. This sampling technique was used because it was much more efficient than using quadrats in areas where unionids densities are very sparse. A large area (65 $m^2$) can be sampled more effectively, in a much shorter time, and many more unionids collected with this method than with random placing of 1 $m^2$ quadrats. Limited quadrat sampling in 2000 found this method unsatisfactory in terms of effort and number of mussels collected, so no data were recorded.

Live unionids were identified to species using the nomenclature of Turgeon *et al.* (1998). All specimens were counted and returned to the substrate. The degree of zebra mussel infestation was determined for all of the sites surveyed in 1999 and 2000 by counting the number of zebra mussels attached to the shells of the first few animals of each unionid species collected. The degree of zebra mussel infestation was also determined at six of the sites surveyed in 2001, by counting the number of live adult zebra mussels attached to the shells of all 233 live unionids collected. The presence of young-of-the-year zebra mussels was also noted, but they were not counted. Field surveys were conducted in July to early August in 1998 and 1999, mid-June in 2000, and late August to early September in 2001.

## RESULTS

No live unionids were found at any of the 42 sites surveyed in western and southwestern Lake St. Clair near Grosse Point, Puce, and Belle River. Shells of many different species were found, including species reported live near Puce in 1990 and Grosse Point in 1991 by Gillis and Mackie (1994); however, all of these shells were weathered (dull nacre, worn periostracum and hinge teeth), indicating that the animals had died years earlier. Many of the shells were infested with live zebra mussels or had byssal threads attached to them.

A total of 2,356 unionids of 22 species were found alive at 33 of the 53 sites surveyed in waters off the St. Clair delta and along the eastern shore of the lake between 1999 and 2001 (Table 1). Thirty-one of these sites were off the delta or in the bays, and the remaining two sites were along the eastern shore between Mitchell's Bay and the mouth of the Thames River. Most of the sites supporting live unionids were shallower than 1 m (26 of 31 sites). Only 11 species (Table 1) were found at depths greater than 1 m, and only one live specimen (*L. cardium*) was found at a depth of greater than 2 m. Members of the Subfamilies Lampsilinae and Ambleminae accounted for 56% and 42%, respectively, of all unionids collected, while members of the Subf. Anodontinae accounted for only 2%.

Species richness at the sites where live unionids were found ranged from one to 12 species (Fig. 2). Richness was based on a timed search of 1.5 p-h/site for the 28 sites surveyed in 1999, and a sampling area of 325 to 650 $m^2$ for the five sites surveyed in 2001. Four sites were surveyed in both 1999 (using a timed search of 1.5 p-h) and 2001 (using a sampling area of 650 to 780 $m^2$). This additional sampling effort did not result in any new species being found at these sites. Similarly, additional 1.5 p-h timed searches conducted in 2000 at 10 of the sites surveyed in 1999 did not add any new species to the species lists for these sites. These results suggest that 1.5 p-h timed searches were probably adequate for determining the number of species occupying a site.

Relative abundance of unionids at the 28 sites where unionids were found in 1999 ranged from 2 to 302 individuals per 1.0 p-h of sampling effort (Fig. 3). Average catch-per-unit-effort was lower in 2000 (21 unionids/p-h) than in 1999 (46 unionids/p-h) at the 10 sites sampled in both years. Since the 2000 surveys were conducted earlier in the year than the 1999 surveys, i.e., mid-June vs. July to early August, it is possible that many animals had not yet returned to the surface after winter. Density estimates were calculated for the nine sites surveyed in 2001, and these ranged from 0.03 per $m^2$ at site off Squirrel Island to 0.07 per $m^2$ at site in Big Muscamoot Bay (Fig. 3). Average density varied significantly among sites ($p = 0.02$), but not within sites ($p = 0.45$).

The most frequently encountered species, i.e., those found at the most sites, were *L. siliquoidea* (88% of sites), *L. cardium* (76%), *L. nasuta* (48%), *P. alatus* (48%), *F. flava* (45%), and *V. iris* (42%) (Table 1). Remaining species were found at seven or fewer sites, with six of these species (*Alasmidonta marginata*, *Anodontoides ferussacianus*, *Epioblasma torulosa rangiana*, *Quadrula pustulosa*, *Quadrula quadrula*, and *Strophitus undulatus*) found at only one site each. Frequency of occurrence and abundance were highly correlated in 1999 ($r = 0.95$), and in the combined data from 1999 to 2001 ($r = 0.89$). Nevertheless, several species tended to be locally abundant (especially *F. flava*, *O. subrotunda*, and *Pleurobema sintoxia*), while

***TABLE 1. Numbers of unionids collected from Lake St. Clair in 1999, 2000, and 2001, and percent of sites where each species was found (% occurrence is calculated as percent of sites where live unionids were found).***

| Species | 1999 | 2000 | 2001 | % Occurrence |
|---|---|---|---|---|
| *Alasmidonta marginata*[a] | – | – | 1 | 3% |
| *Amblema plicata*[a,b] | 25 | 2 | 4 | 27% |
| *Anodontoides ferussacianus*[a] | 1 | – | – | 3% |
| *Elliptio dilatata*[a,b] | 10 | 2 | 2 | 9% |
| *Epioblasma torulosa rangiana*[a] | 1 | – | – | 3% |
| *Fusconaia flava*[a,b] | 752 | 93 | 62 | 45% |
| *Lampsilis cardium*[a,b,c] | 246 | 28 | 55 | 76% |
| *Lampsilis fasciola*[a,b] | 14 | 2 | 3 | 15% |
| *Lampsilis siliquoidea*[a,b] | 537 | 53 | 117 | 88% |
| *Lasmigona costata*[a] | 8 | 3 | 1 | 18% |
| *Leptodea fragilis*[a] | 9 | 1 | – | 18% |
| *Ligumia nasuta*[a,b] | 70 | 5 | 2 | 48% |
| *Ligumia recta*[a] | 3 | – | 1 | 6% |
| *Obovaria subrotunda*[a,b] | 25 | 15 | 13 | 15% |
| *Pleurobema sintoxia*[a] | 1 | 10 | 31 | 9% |
| *Potamilus alatus*[a,b] | 38 | 3 | 12 | 48% |
| *Ptychobranchus fasciolaris*[a,b] | 6 | – | 1 | 18% |
| *Pyganodon grandis*[a] | 32 | – | 2 | 21% |
| *Quadrula pustulosa*[a] | 2 | – | – | 3% |
| *Quadrula quadrula*[a] | 1 | – | – | 3% |
| *Strophitus undulatus*[a] | 3 | – | – | 3% |
| *Villosa iris*[a,b] | 35 | 2 | 11 | 42% |
| Totals | 1,819 | 219 | 318 | 33 sites |

[a]species found at sites in water < 1 m deep.
[b]species found at sites in water 1 to 2 m deep.
[c]species found at sites in water > 2 m deep.

other species (*Leptodea fragilis* and *P. fasciolaris*) were widely distributed but sparse.

Community composition varied among the nine sites sampled quantitatively in 2001 (Table 2). With the exception of one site in Goose Bay, sites south of the main channel (Canadian waters) supported a richer mussel community (6 to 8 species/site) than those north of the channel (U.S. waters) (3 to 5 species/site). The three sites off Squirrel Island were dominated by *P. sintoxia*, *F. flava*, and *O. subrotunda*; the site off Bassett Island was dominated by *F. flava* and *L. cardium*; and the site off Pocket Bay was mainly populated by *L. siliquoidea* and *L. cardium*. Between 78 and 89% of unionids collected from three of the sites in American waters were *L. siliquoidea*. The fourth site supported a community of eight species, with *L. siliquoidea* accounting for 56% of individuals collected.

Numbers of zebra mussels attached to the shells of unionids at sites surveyed around the St. Clair delta in 1999 averaged 107 ± 18.7 SE/unionid (n = 113). The infestation of unionids at sites outside

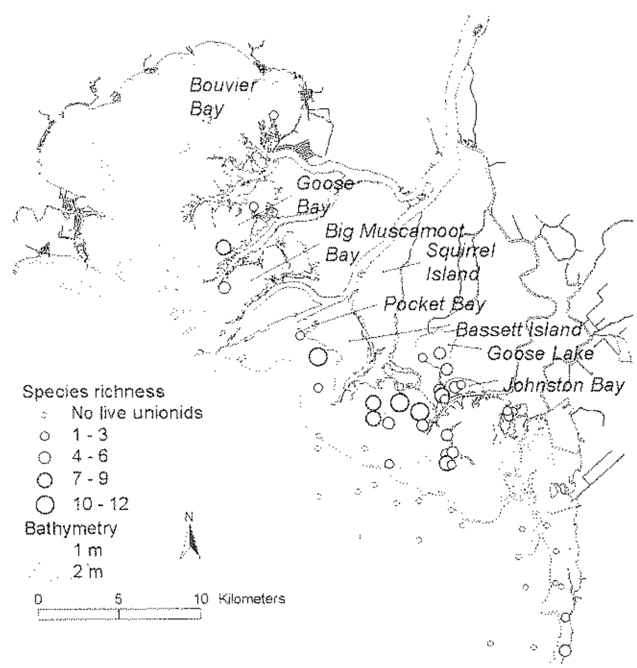


***FIG. 2. Unionid species richness at sites in northeastern Lake St. Clair (1998 to 2001).***

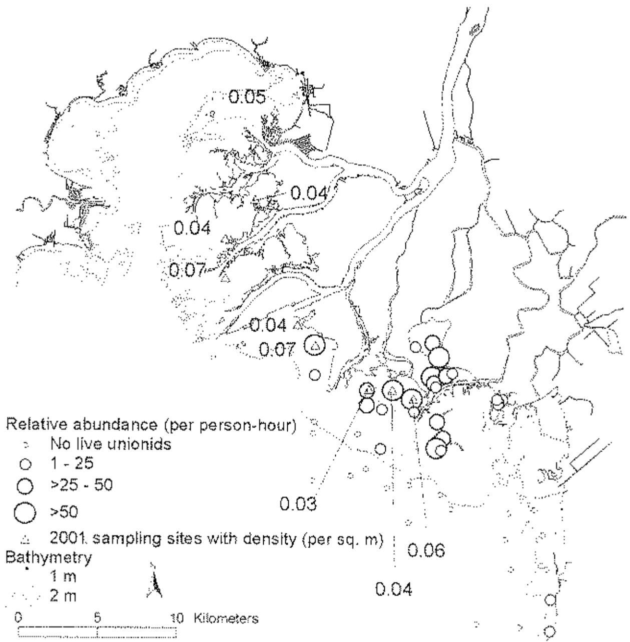


***FIG. 3. Relative abundance of unionids at 1999 study sites, based on a 1.0 person-hour sampling effort. Densities (unionids per m²) are shown for sites sampled quantitatively in 2001.***

the delta proper was much lower than at sites in Goose Lake and Johnston Bay (Fig. 2). The mean number of zebra mussels at sites in the delta excluding the eight sites in Goose Lake and Johnston Bay was 61.4 (n = 79). The mean number of zebra mussels infesting unionids at sites in Goose Lake and Johnston Bay was 177 (n = 34). At the two sites surveyed in 1999 near the mouth of the Thames River an average of 3,366 zebra mussels (n = 7) were estimated to be infesting unionid shells, with many young-of-the-year zebra mussels present. In 2000 an average of 31 ± 6.4 SE (n = 28) zebra mussels were found to be infesting unionid shells at sites surveyed near the St. Clair delta. Numbers of adult zebra mussels attached to the shells of unionids varied significantly ($p < 0.001$) among seven sites surveyed in 2001 (n = 233). The degree of infestation ranged from 3 ± 1.2 SE zebra mussels/unionid in Pocket Bay to 47 ± 5.0 SE/unionid at a site in Goose Bay. The latter site was one of two sites where young-of-the-year zebra mussels were also present; the other site was in Big Muscamoot Bay.

***TABLE 2. Numbers of live unionids collected during quantitative sampling at nine sites in the St. Clair delta in 2001.***

| | Canadian waters | | | | | U.S. waters | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Squirrel Island | | | Bassett Island | Pocket Bay | Big Muscamoot Bay | Goose Bay | | Bouvier Bay |
| *Alasmidonta marginata* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Amblema plicata* | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| *Elliptio dilatata* | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Fusconaia flava* | 0 | 8 | 8 | 40 | 0 | 1 | 3 | 0 | 2 |
| *Lampsilis cardium* | 1 | 1 | 6 | 38 | 5 | 1 | 2 | 0 | 1 |
| *Lampsilis fasciola* | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *Lampsilis siliquoidea* | 0 | 1 | 7 | 7 | 7 | 34 | 13 | 21 | 27 |
| *Lasmigona costata* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Ligumia nasuta* | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Ligumia recta* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Obovaria subrotunda* | 1 | 3 | 9 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pleurobema sintoxia* | 14 | 14 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Potamilus alatus* | 1 | 0 | 0 | 3 | 0 | 5 | 2 | 1 | 0 |
| *Ptychobranchus fasciolaris* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Pyganodon grandis* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 1 | 0 | 1 | 0 | 0 | 3 | 2 | 4 | 0 |
| Total unionids | 20 | 29 | 36 | 95 | 13 | 44 | 25 | 26 | 30 |
| Species richness | 6 | 7 | 8 | 8 | 3 | 5 | 8 | 3 | 3 |
| Area surveyed (m²) | 650 | 650 | 650 | 1,365 | 325 | 650 | 650 | 650 | 650 |

## DISCUSSION

This study documents the existence of a significant refuge site for unionids in Lake St. Clair, 15 years after zebra mussels invaded the system. Twenty-two of the 32 species known to occupy the lake historically were found alive in shallow (mainly < 1m) waters of the St. Clair delta, including nearshore areas with firm sand or sand/gravel substrates and marshy bays with soft, muddy sediments. The St. Clair delta (this study) and Metzger Marsh in western Lake Erie (Nichols and Wilcox 1997) may support the richest remnant communities of unionids to have survived the zebra mussel invasion of the lower Great Lakes. Recent surveys of other marshes near Metzger Marsh and sites near Bass Island and along the southwest shore of Lake Erie were largely fruitless (H.L. Dunn, Ecological Specialists, Inc., O'Fallon, Missouri, personal communication, December 2001), as were searches of the Detroit River (P.J. Marangelo, The Nature Conservancy, East Lansing, Michigan, personal communication, December 2001) and Rondeau Bay on the north shore of Lake Erie (by the authors).

The unionid community of the St. Clair delta includes several species considered to be at risk. The northern riffleshell (*E. t. rangiana*) is listed as endangered in both Canada (Staton *et al.* 2000) and the U.S.A. (U.S. Fish and Wildlife Service 1994). The wavy-rayed lampmussel (*L. fasciola*) is also listed as endangered in Canada (Metcalfe-Smith *et al.* 2000), and is listed as threatened in Michigan (Peter Badra, Michigan Natural Features Inventory, personal communication, September 2001). The round hickorynut (*O. subrotunda*) is state-endangered in Michigan, and the Canadian status of this species and the kidneyshell (*P. fasciolaris*) are under evaluation (by the authors) for listing in 2003. A fifth species, the round pigtoe (*P. sintoxia*), is on the priority list for evaluation in Canada.

It is difficult to determine if there have been long-term changes in the richness or composition of the unionid community of the St. Clair delta because no sampling was previously conducted in such shallow water. In 1986, before the introduction of the zebra mussel, Nalepa and Gauvin (1988) surveyed 29 sites throughout Lake St. Clair at depths ranging from 3.0 to 7.3 m, and reported 18 live species and an average density of 2 unionids/m$^2$. Densities at the three sites nearest to the delta (3.3 to 4.5 m deep) were lower than this average (0, 0.2 and 0.2 per m$^2$), but still generally higher than the densities of 0.03 to 0.07 per m$^2$ observed in 2001. The densities recorded in 2001 may be slight overestimations due to the sampling method used, meaning that the decline in unionid density may have been even greater. The frequency of occurrence of some species differed substantially between 1986 and 1999 (Fig. 4). *Lampsilis siliquoidea* was a dominant member of the community in both years, although less so in 1999. *Leptodea fragilis*, *P. alatus*, *E. dilatata*, and *P. grandis* have declined in relative abundance, while *L. cardium* and especially *F. flava* have increased. Gillis and Mackie (1994) compared species composition from the 4-m contour at a site near Puce in 1990 with Nalepa and Gauvin's (1988) data from a depth of 5.2 m at this site in 1986, and observed a similar shift in community composition, i.e., *P. grandis*, *L. siliquoidea*, *L. fragilis*, and *P. alatus*, as well as *Truncilla truncata*, declined in density by 80 to 100%, while densities of *F. flava* and *L. cardium* did not change. They suggested that thin-shelled, alate species (*L. fragilis*) would be the most likely to tip and have their siphons become fouled in the substrate under an accumulation of zebra mussels, thereby suffering the greatest mortality. By 1992, however, all individuals regardless of species had dissappeared. Schloesser and Masteller (1999) showed the same general trend for unionid populations at Presque Isle Bay, Lake Erie. Zebra mussels invaded the bay in 1990, within 2 years of zebra mussels colonizing the bay, *L. fragilis*, *P. alatus*, *P. grandis*, and *E. dilatata* had declined in abundance by 81 to 90%, while populations of *F. flava*, *Q. quadrula*, and *Amblema plicata* remained unchanged. One year later, *L. siliquoidea* had also declined by 87%, and by 1995 (5 years from zebra mussel introduction) all species were lost. Since the shifts in community structure that preceded the demise of unionids at Puce and Presque Isle Bay have also occurred in the St. Clair delta, it is not certain that the St. Clair "refuge" will persist.

It is believed that species belonging to the subfamilies Anodontinae and Lampsilinae are impacted earlier and more severely by zebra mussels than members of the Ambleminae (Schloesser *et al.* 1998). In the St. Clair delta, the Lampsilinae declined from 80% to 42% of the community and the Anodontinae from 6% to 2% between 1986 and 1998 to 2001, while the Ambleminae increased from 14% to 56%. At a site in western Lake Erie

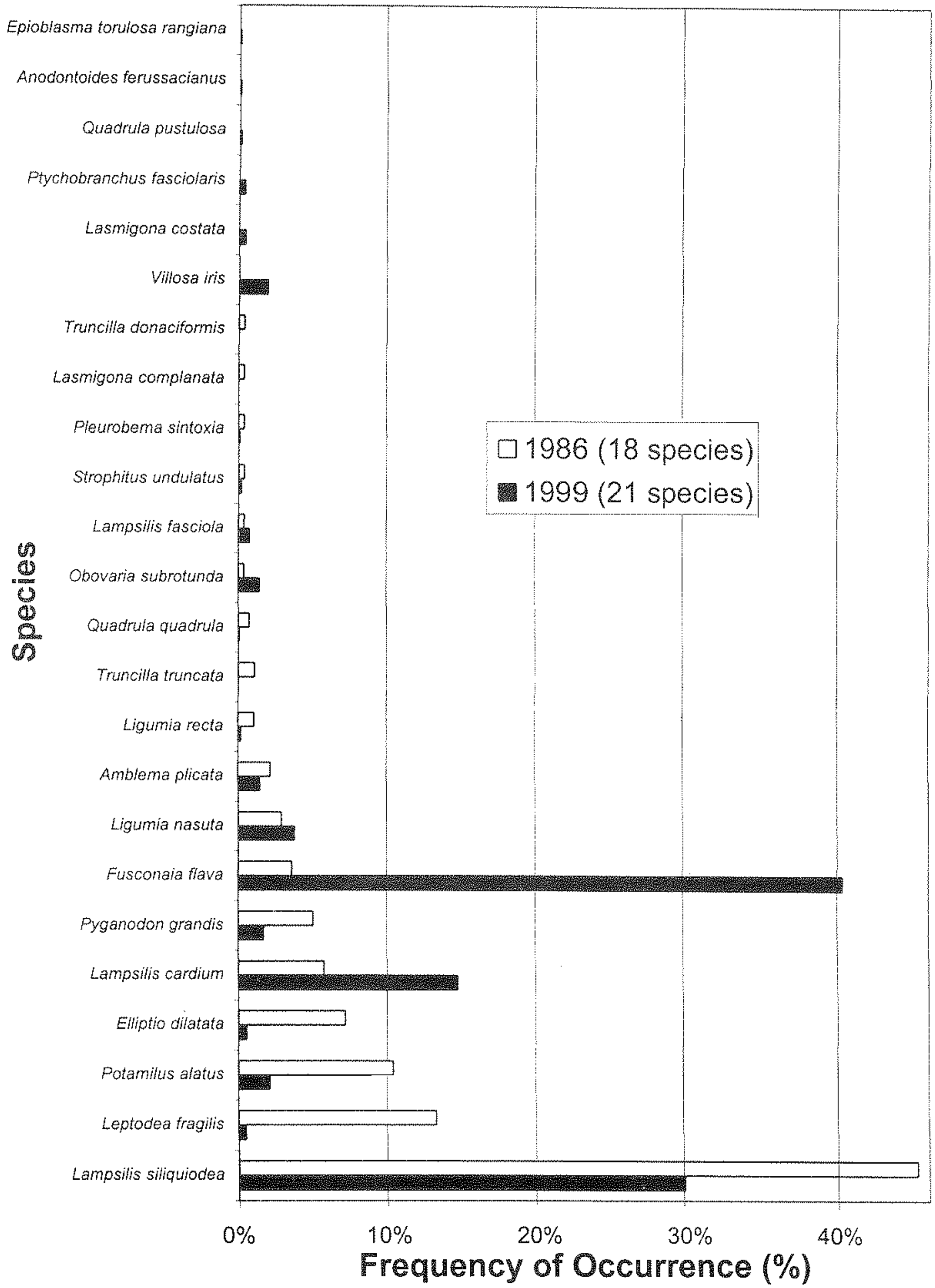


*FIG. 4. Change in frequency of occurrence of unionid species in Lake St. Clair between 1986 (before zebra mussel invasion) and 1999.*

where unionids have also continued to survive (Schloesser *et al.* 1997), the pre-dreissenid community composition of 1983 was somewhat different (43% Lampsilinae, 7% Anodontinae, 49% Ambleminae), but the direction of change was the same (14%, 0, 86%, respectively, in 1993). Even if remnants of the Great Lakes unionid community can withstand the zebra mussel invasion, it is likely that the structure of these communities will be permanently altered.

All of the unionid refuge sites discovered to date in Lake Erie and Lake St. Clair have two things in common, namely, they are very shallow (< 1 to 2 m deep) and they have a high degree of connectivity to the lake. These features appear to combine with other, local factors to discourage the settlement and survival of zebra mussels. For example, Schloesser *et al.* (1997) found that infestation rates at a site on firm, sandy substrates in western Lake Erie were very low (0 and 4/unionid at 1 and 2 m, respectively, vs. 30 to 40/unionid at 4 m), and that zebra mussels colonizing unionids were not more than 2 years old. They believed that zebra mussels were voluntarily releasing from unionids, due perhaps to factors such as wave action, fluctuating water levels, and ice scour.

Another unionid refugium, Metzger Marsh, is a large wetland in western Lake Erie that was historically sheltered by a barrier beach that eventually eroded away. The barrier permitted the accumulation of soft, silt-clay sediments in some areas, and unionids were found in these areas in 1996 (Nichols and Wilcox 1997). Although zebra mussels had been present in the area since 1990, very few unionids were encrusted with dreissenids. Nichols and Wilcox (1997) found that the unionids burrowed 2 to 40 cm into the soft substrates for part of the day during the warm summer months, and observed in experiments that this activity both dislodged and suffocated any attached zebra mussels. The area is also subject to wave action and seiche events from Lake Erie, which further discourages colonization by zebra mussels. If the site were left to nature, however, the soft sediments that sustain the unionids would eventually erode away.

The refuge site in Thompson Bay, the outer harbor of Presque Isle Bay, appears to have been created by a similar set of circumstances. The site is shallow, with silty, sandy sediments and high midday temperatures, and is protected by a low sand bar that is occasionally removed to improve water exchange with Lake Erie (E.C. Masteller, the Pennsylvania State University at Erie, Erie, Pennsylvania, personal communication, December 2001). Unionids at this location are infestation-free (Schloesser and Masteller 1999). Fluctuating water levels and open, exposed conditions in the winter (with ice) are believed to prevent colonization by zebra mussels.

The St. Clair delta refuge site described in this study includes both wave-washed flats with firm sandy substrates and wetland areas with soft, muddy sediments. This variety of habitat types probably explains the great diversity of species found here. Zebra mussel infestation rates were variable and somewhat higher in general than those found in other refugia, but still generally lower than the lethal threshold of 100 dreissenids/unionid as determined by Ricciardi *et al.* (1995). It is possible that the numbers of veligers reaching this site, and/or settling in the area, may vary from year to year depending on wind direction, currents, and water levels. Several studies have shown that temporal variation in densities and colonization rates of zebra mussels can influence zebra mussel-induced mortality of unionids (Schloesser *et al.* 1997).

There is evidence that both Metzger Marsh and Thompson Bay are true refugia - not simply areas where the decline of unionids has been slower than in other areas. Nichols and Amberg (1999) reported that the population dynamics of *L. fragilis*, the dominant unionid in Metzger Marsh, remained unchanged after the zebra mussel invasion. The unionid community in Thompson Bay is being monitored yearly and so far has shown no signs of decline (E.C. Masteller, the Pennsylvania State University at Erie, Erie, Pennsylvania, personal communication, December 2001). The status of the unionids found at the St. Clair delta sites remains unclear at present. Further studies of all refuge sites are needed to better understand the factors responsible for unionid survival. Such information could be used to predict the locations of other natural sanctuaries and to guide their management for the preservation of the Great Lakes unionid fauna.

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