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Changes in the Freshwater Mussel Community of Lake St. Clair: from Unionidae to *Dreissena polymorpha* in Eight Years

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ABSTRACT. *To determine density changes in both the zebra mussel,* Dreissena polymorpha, *and native mussels, Unionidae, in Lake St. Clair, surveys were conducted in 1990, 1992, and 1994 and compared to a similar survey in 1986 when no* D. polymorpha *was found. Collection methods were the same each year; divers used the quadrat method to collect 10 replicate samples at 29 sites located throughout the lake. The total number of unionids collected declined from 281 in 1986, to 248 in 1990, 99 in 1992, and 6 in 1994, while the number of species collected in each of the four respective years was 18, 17, 12, and 5. The decline in the unionid community occurred gradually over this time period as the* D. polymorpha *population expanded from the southeast region of the lake to the northwest region. Mean density and biomass of* D. polymorpha *throughout the lake was 1,700 m^{-2} and 4.7 gDW m^{-2} in 1990, 1,500 m^{-2} and 3.5 gDW m^{-2} in 1992, and 3,200 m^{-2} and 3.1 gDW m^{-2} in 1994. The density increase can be attributed to the expansion of the population into the northwest region, while the decrease in biomass was mostly a result of a decline in the weight per unit length. Mean biomass of the* D. polymorpha *population in 1994 was actually lower than the mean biomass of unionids in 1986; however, based on literature-derived filtering rates, the filtering capacity of the* D. polymorpha *population in 1994 was 12 times greater than the filtering capacity of the unionid community in 1986. This increase has likely led to reported changes in the Lake St. Clair ecosystem (increased water clarity, increased plant growth, and shifts in fish communities).*

INDEX WORDS: *Unionids, native mussels, zebra mussels, density, biomass, trends, Lake St. Clair.*

INTRODUCTION

The establishment of the zebra mussel, *Dreissena polymorpha*, in North America has caused broad ecological changes in regions where it has become abundant (MacIsaac in press). Because of relatively high filtering rates and often great densities, *D. polymorpha* has the capacity to filter the water column at a rapid rate (MacIsaac *et al.* 1992, Fanslow *et al.* 1995). As a result, energy is shifted from the pelagic to the benthic zones as particles are removed from the water column and deposited on the bottom as unassimilated feces and pseudofeces. In the Great Lakes, phytoplankton populations and primary production in the water column have declined (Holland 1993; Leach 1993; Nicholls and Hopkins 1993; Fahnenstiel *et al.* 1995a, b), while benthic algae and benthic macroinvertebrates have generally increased (Dermott *et al.* 1993, Lowe and Pillsbury 1995, Stewart and Haynes 1994, Skubinna *et al.* 1995) since this mollusk became established. One of the most direct and immediate impacts of *D. polymorpha* is its negative effect on freshwater bivalves of the family Unionidae. Densities of unionids in many regions of the Great Lakes have declined dramatically within just a few years after *D. polymorpha* became established (Nalepa 1994, Schloesser and Nalepa 1994, Gillis and Mackie 1994, Schloesser *et al.* in press). *D. polymorpha* attaches preferentially to the exposed shells of unionids in great numbers and interferes with normal metabolic functions such as feeding and respiration, and with life habits such as burrowing. Unionids in-

fested with *D. polymorpha* show a reduction in fitness and an increase in stress (Haag *et al.* 1993).

Given these ecological impacts and profoundly negative influence on unionids, trends in *D. polymorpha* populations over the long term are of great interest. In suitable habitats, *D. polymorpha* populations increase rapidly during the initial years of the invasion period but, over time, become more stable as food resources become limiting, suitable substrates are colonized, and factors related to density dependent predation limit population growth (Stanczykowska 1977, MacIsaac *et al.* 1991, Stanczykowska and Lewandowski 1993). While a number of studies in North America have examined densities of *D. polymorpha* in both lake and riverine systems and related distributions to specific habitat features (Dermott and Munawar 1993, Mellina and Rasmussen 1994, Stewart and Haynes 1994), there have been few studies that have documented trends in populations over time. In studies that have examined density changes over several years, the population was in the early period of the invasion process and densities varied widely from year-to-year as the population continued to expand (Hebert *et al.* 1991, Marsden *et al.* 1993, Nalepa *et al.* 1995).

In this paper, we summarize trends in populations of both *D. polymorpha* and unionids in Lake St. Clair from 1986 to 1994. *D. polymorpha* was first discovered in North America in southeast Lake St. Clair in 1988 (Hebert *et al.* 1989). Based on the size-frequency distribution of the population at the time, it likely became established in this region in 1986 (Griffiths *et al.* 1991). Thus, populations in the southeast region of Lake St. Clair represent the oldest established population in North America. We conducted surveys of the mussel community in the lake in 1986, 1990, 1992, and 1994. The data presented provide an update of surveys by Hebert *et al.* (1991), who presented initial trends in *D. polymorpha* densities in 1989 and 1990, and by Nalepa (1994), who presented trends in unionid densities between 1986 and 1992. Unionid densities in 1986 were reported by Nalepa and Gauvin (1988); no *D. polymorpha* were found in this 1986 survey.

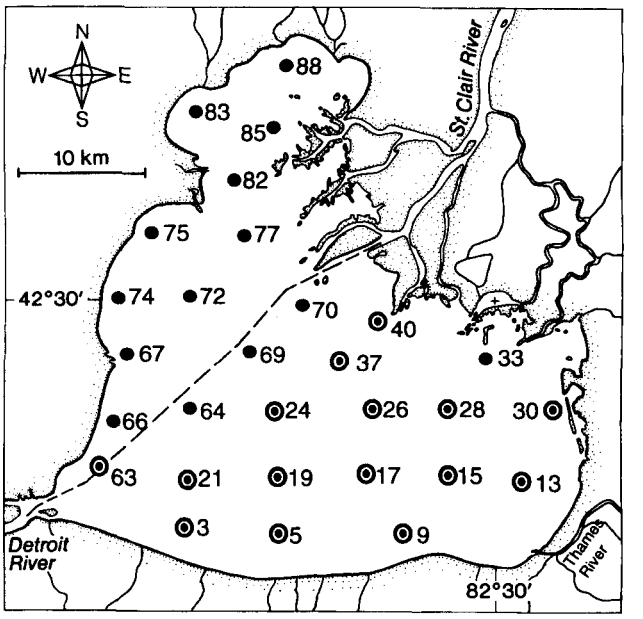

FIG. 1. Location of sampling sites in Lake St. Clair in each of the yearly surveys. Circled sites denote sites where unionids were highly-infested with* D. polymorpha *in 1990 (mean ≥ 55 per unionid). These sites were designated as the southeast region. Uncircled sites denote sites where unionids were lightly infested with* D. polymorpha *in 1990 (mean ≤ 3 per unionid). These sites were designated as the northwest region. Dashed line represents the shipping channel.

METHODS

Sampling sites and methods were the same in each of the four yearly surveys. Twenty nine sites were sampled in the fall of each year (Fig. 1). In 1990, one site (Station 28) was sampled for unionids but not for *D. polymorpha*. Site designations and locations are the same as given in Pugsley *et al.* (1985). Sites were located each year using Loran C. At each site, divers positioned a 0.5 m^2 frame on the bottom and collected all hard material within the frame area to a depth of about 5 cm. Aquatic plants matted on the bottom or extending into the water column within about 0.5 m of the bottom were also sampled, but macrophytes extending into the water column beyond 0.5 m were not sampled. Since newly-settled *D. polymorpha* were found attached to these latter plants in large numbers (diver and personal observations), total numbers of *D. polymorpha* were underestimated. However, since the areal extent of macrophytes in the lake has increased since *D. polymorpha* became established (Griffiths 1993), our sampling protocol minimized the role of macrophytes as a substrate and provided a spatial consistency for assessing trends in *D. polymorpha* over time. Ten replicates were collected at each site with divers moving about 2-3 m between replicates. Only

five replicates for *D. polymorpha* were collected at Station 9 in 1992 and at Station 69 in 1994. Material in each replicate was gently put into a mesh bag (2-mm mesh), supported within a crate, and then brought to the surface. Live unionids were opened and soft tissues placed into preweighed aluminum planchets. *D. polymorpha* attached to unionids were removed, placed into separate containers, and preserved in 5% formalin. All other *D. polymorpha* were removed from substrates (i.e. dead unionid shells, rocks, etc.), rinsed through a 500-μm screen, and preserved. Although another dreissenid species (*D. bugensis*) has been reported from the Great Lakes (May and Marsden 1992), all individuals collected from Lake St. Clair were *D. polymorpha*.

For each individual replicate, up to 500 *D. polymorpha* were counted and measured (shell length); replicates with a greater number of mussels were proportionally split, counted, and measured, and the portion applied to the entire sample. For length-frequency distributions, mussels with a shell length > 5 mm were individually measured using a digitizer pad and placed into size categories of 1-mm intervals. Mussels with a shell length < 5 mm were counted and placed into a single size category. Since these mussels were separated with the naked eye or with a 2× magnifier, some smaller mussels (0.5–1.0 mm) were possibly missed.

Dry weights of unionid soft tissue were obtained directly by drying at 60°C for at least 48 h. To determine dry weights of *D. polymorpha*, individuals were collected monthly from late April to October/November every year for 5 years (1990–94) at two of the sites (Stations 3 and 19; Nalepa *et al.* 1993). These sites represented two different substrate types; substrate at Station 3 consisted of pebbles, gravel, and small rocks, while substrate at Station 19 consisted of silt/mud. The soft tissue of at least five individuals from each of five different size categories was removed from the shell, placed into preweighed aluminum planchets, and dried at 60°C for at least 48 h (Nalepa *et al.* 1993). Shell length of each individual was measured using a digitizer pad. For each sampling date, the relationship between dry weight and shell length (DW:SL) was fit to the general allometric equation $W = aL^b$, where W is the dry weight of soft tissue in mg, and L is the length of the shell in mm.

Dry-weight biomass of *D. polymorpha* in each of the yearly surveys (1990, 1992, and 1994) was determined by first multiplying the number of individuals in each size category by the dry weight of the median length of that size category as calculated from the monthly DW:SL regression nearest the survey date and then adding the products. For purposes of calculation, individuals in the < 5 mm category were assigned a median length of 2.5 mm. Actual dates of the mussel surveys were: 15–22 September 1986 (no *D. polymorpha* found), 12–17 September 1990, 28 September-1 October 1992, and 20–22 September 1994. Dates of DW:SL regressions used to determine *D. polymorpha* biomass were: 11 October 1990, 3 September and 27 October 1992, and 20 September 1994.

Since the initial *D. polymorpha* population in the lake expanded from southeast to northwest between 1988 and 1989 (Hebert *et al.* 1991), sampling sites were divided into a southeast region (n = 15) and a northwest region (n = 14) based on the number of *D. polymorpha* found attached to unionids in 1990, the first year we sampled *D. polymorpha* (Fig. 1; see Nalepa 1994). Unionids at sites in the southeast region were highly infested (mean of ≥ 55 *D. polymorpha* per unionid), while unionids at sites in the northwest region were lightly infested (mean of ≤ 3 *D. polymorpha* per unionid). Although its location is more southeast, Station 33 was included in the northwest region based on the criteria given above.

Bottom substrate at each of the sites in each survey year was recorded from diver observations. Basically, substrates found in later surveys were similar to those in 1986 reported by Nalepa and Gauvin (1988). Exceptions were gravel instead of silt at Station 5, sand/cobble instead of silty sand at Station 74, and sand instead of silty clay at Station 85. Water depths at each site are also given in Nalepa and Gauvin (1988).

Because *D. polymorpha* populations are strongly aggregated (Hunter and Bailey 1992, Mellina and Rasmussen 1994), distribution-free statistics were used to determine significant temporal and spatial differences. Site means were calculated, and the Kruskall-Wallis test was used to test yearly differences for the entire lake and also for the two regions. If differences were significant, post-hoc Tukey-type multiple comparisons were performed (Zar 1984). The Mann-Whitney test was used to test regional differences, and the G-test (log likelihood ratio test; Sokal and Rohlf 1969) was used to test yearly differences in the size-frequency distribution (proportion in each size category) of the population within a given region. Because the G-test does not allow zero values in individual cells, mussels in the southeast region > 29 mm were grouped into one size category; mussels in the northwest region > 23 mm were also grouped.

RESULTS

D. polymorpha

On a lakewide basis, both the density and spatial distribution of *D. polymorpha* increased between 1990 and 1994 (Fig. 2). Mean density at all sites was 1,660 m^{-2}, 1,520 m^{-2}, and 3,240 m^{-2} in 1990, 1992, and 1994, respectively (Table 1). These mean densities were significantly different ($P = 0.003$), with densities significantly higher ($P < 0.05$) in 1994 than in the other 2 years. The lakewide increase in density can be mainly attributed to the expansion of the population from the southeast into the northwest region of the lake between 1992 and 1994. In 1990, mean density at the 14 sites in the northwest region was only 18 m^{-2}, but increased to 190 m^{-2} in 1992, and to 2,050 m^{-2} in 1994 (Table 1). These increases were highly significant ($P < 0.001$). In contrast, yearly mean densities at sites in the southeast region were not significantly different ($P = 0.112$).

An indication of relative changes in the spatial distribution of the population in each of the two regions can be derived from the percentage of individual replicate samples in which *D. polymorpha* was found. In the southeast region, the percentage was quite similar in each of the 3 years—81%, 71%, and 89% of the samples contained *D. polymorpha* in 1990, 1992, and 1994, respectively. However, in the northwest region the percentage increased each year—24%, 75%, and 89% for the 3 years, respectively.

Mean biomass of *D. polymorpha* was 4.67, 3.50, and 3.12 gDW m^{-2} in 1990, 1992, and 1994 (Table 1). These yearly means were significantly different ($P = 0.042$); biomass in 1994 was significantly lower than in 1990 ($P < 0.05$) but not significantly lower than in 1992. Biomass declined 3-fold in the southeast region over this period, but increased 60-fold in the northwest region (Table 1, Fig. 3). The increase in biomass in the northwest region might be expected given the increase in densities over the period, but the decline in biomass in the southeast region occurred despite similar mean densities in each of the 3 years.

To determine if *D. polymorpha* densities in 1994 were dependent upon substrate type, we grouped our sites into three categories based on the dominant substrate (gravel/pebbles/cobble; sand; mud/silt) and compared mean density and biomass (Table 2). Significant differences between the three substrate types were not detected ($P = 0.26$ for density and $P = 0.77$ for biomass). Thus, while densities of *D. polymorpha* generally increase with

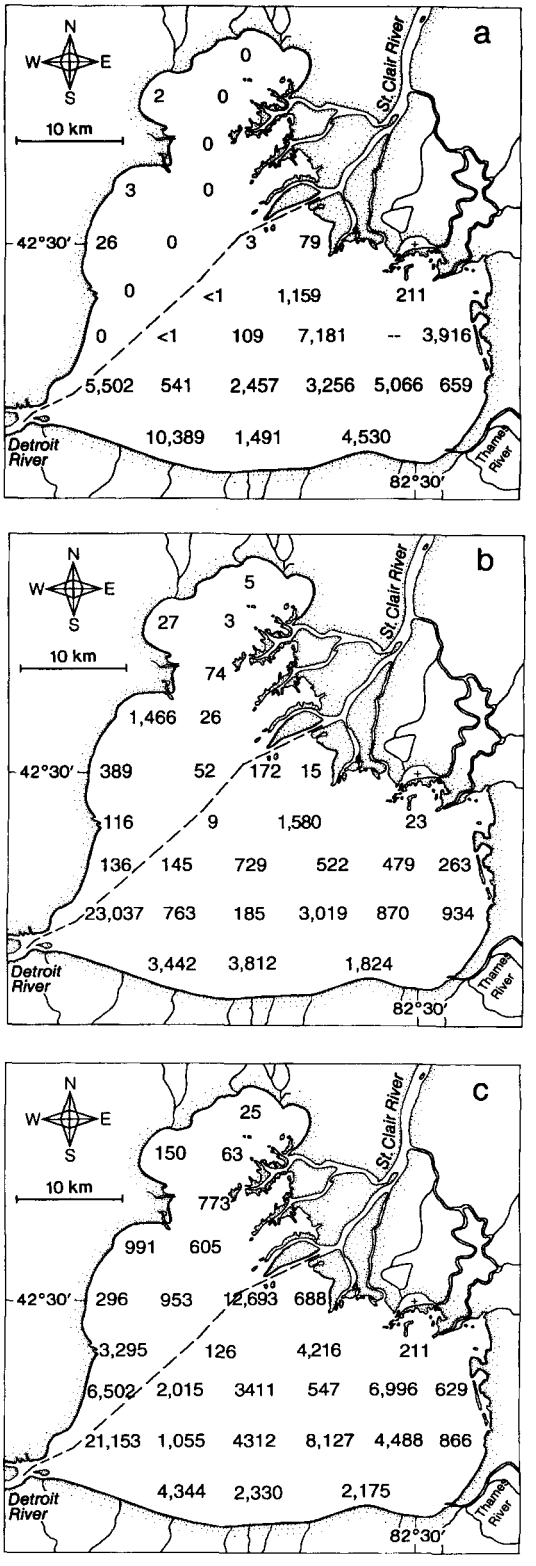

FIG. 2. Mean density (individuals m^{-2}) of* D. polymorpha *at each of the 29 sampling sites in Lake St. Clair in 1990 (a), 1992 (b), and 1994 (c).

TABLE 1. Mean (± SE) density (individuals m^{-2}; upper) and biomass (gDW m^{-2}; lower) of **D. polymorpha** *at all sites, at sites in the southeast region, and at sites in the northwest region of Lake St. Clair in 1990, 1992, and 1994.*

Year	All Sites (n = 29)	Southeast (n = 15)	Northwest (n = 14)
1990	1,663 ± 507	3,310 ± 808	18 ± 15
1992	1,521 ± 793	2,764 ± 1,481	189 ± 102
1994	3,241 ± 844	4,355 ± 1,341	2,047 ± 945
1990	4.67 ± 1.80	9.30 ± 3.19	0.05 ± 0.03
1992	3.50 ± 1.97	6.11 ± 3.74	0.71 ± 0.23
1994	3.12 ± 0.58	3.24 ± 0.73	3.01 ± 0.94

substrate size (Mellina and Rasmussen 1994), densities were not related to substrate type in Lake St. Clair. Soft sediments throughout the lake are scattered with empty unionid shells which provide a hard substrate for *D. polymorpha* attachment. Also, clumps of *D. polymorpha* (druses) are common in areas with soft substrates within the lake (Hunter and Bailey 1992).

All monthly regressions between soft-tissue dry weight and shell length in *D. polymorpha* were significant ($P < 0.001$). To illustrate monthly and yearly trends in DW:SL in 1990-1994, the weight of a standard 15-mm mussel was determined from each monthly regression over the period (Fig. 4). Weights peaked in the spring of each year and then gradually declined through summer and fall. This seasonal pattern is typical and related to the reproductive cycle and to summer stress (Nalepa *et al.* 1993). Of interest are weights in September/October, since regressions from this seasonal period were used to calculate biomass in the surveys. Weights were lowest during this period; thus, given biomass estimates may be considered minimum values. The DW:SL regressions in September/October for the three survey years (1990, 1992, and 1994) are given in Figure 5. In comparing these three regressions, slopes (b) were similar ($P > 0.50$; common slope = 2.576), but intercepts (a) were significantly different ($P < 0.001$) (analysis of covariance; Zar 1984). A Tukey multiple test showed that the intercept of the regression in 1994 was significantly ($P < 0.001$) lower than intercepts in the other 2 years.

Yearly differences in size-frequency distributions were significant for both regions (Fig. 6; southeast

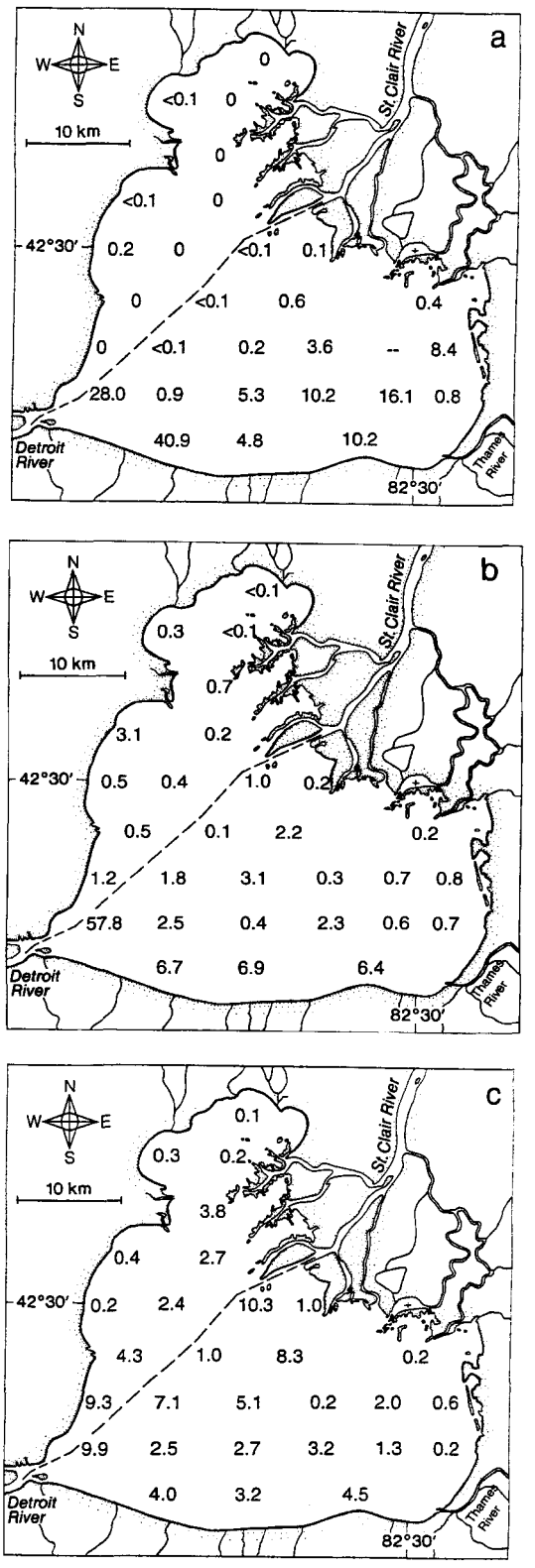

FIG. 3. Mean biomass (gDW m^{-2}) of **D. polymorpha** *at each of the 29 sampling sites in Lake St. Clair in 1990 (a), 1992 (b), and 1994 (c).*

TABLE 2. Mean (± SE) density (individuals m^{-2}) and biomass (gDW m^{-2}) of **D. polymorpha** *at sites with three different substrate types in Lake St. Clair in 1994. Gravel/Pebble/Cobble (n = 4); Sand (n = 7); Silt/Mud (n = 18).*

	Substrate		
	Gravel/ Pebble/Cobble	Sand	Silt/Mud
Density	2,277 ± 835	2,237 ± 1,745	3,846 ± 1,179
Biomass	2.97 ± 0.97	2.67 ± 1.37	3.34 ± 0.77

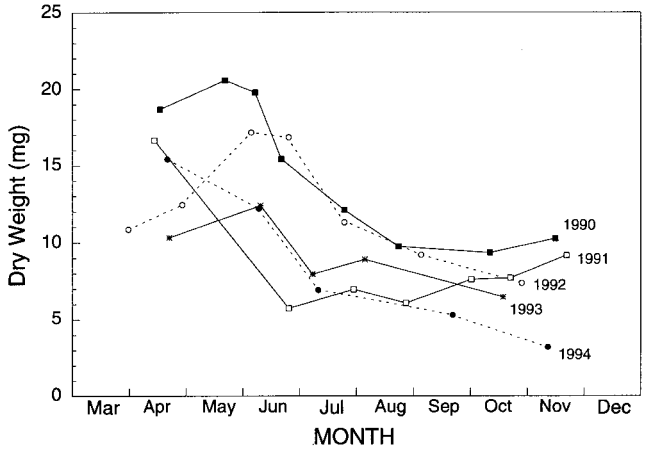

FIG. 4. Seasonal and annual changes in the dry weight of soft tissue of **D. polymorpha** *from two sampling sites in Lake St. Clair in 1990-94. Weights given are for a mussel 15 mm in shell length and were derived from length-weight regressions determined on each sampling date.*

region: G = 628, d.f. = 48, P < 0.001; northwest region: G = 58, d.f. = 34, P < 0.01). In the southeast region, individuals with a shell length < 5 mm dominated the population, accounting for 43.5%, 45.6%, and 47.6% of the population in 1990, 1992, and 1994, respectively. In 1990, there was an apparent modal peak of individuals with a shell length of 16–18 mm, indicating the presence of a cohort older than the 0+ year-class. However, by 1994 no obvious modal peaks of older cohorts were observed and, in general, there were fewer individuals with a shell length greater than about 14 mm. In the northwest region, individuals < 5 mm accounted for only 15.2%, 17.1%, and 21.9% of the population in each of the 3 years, and modal peaks in the size-

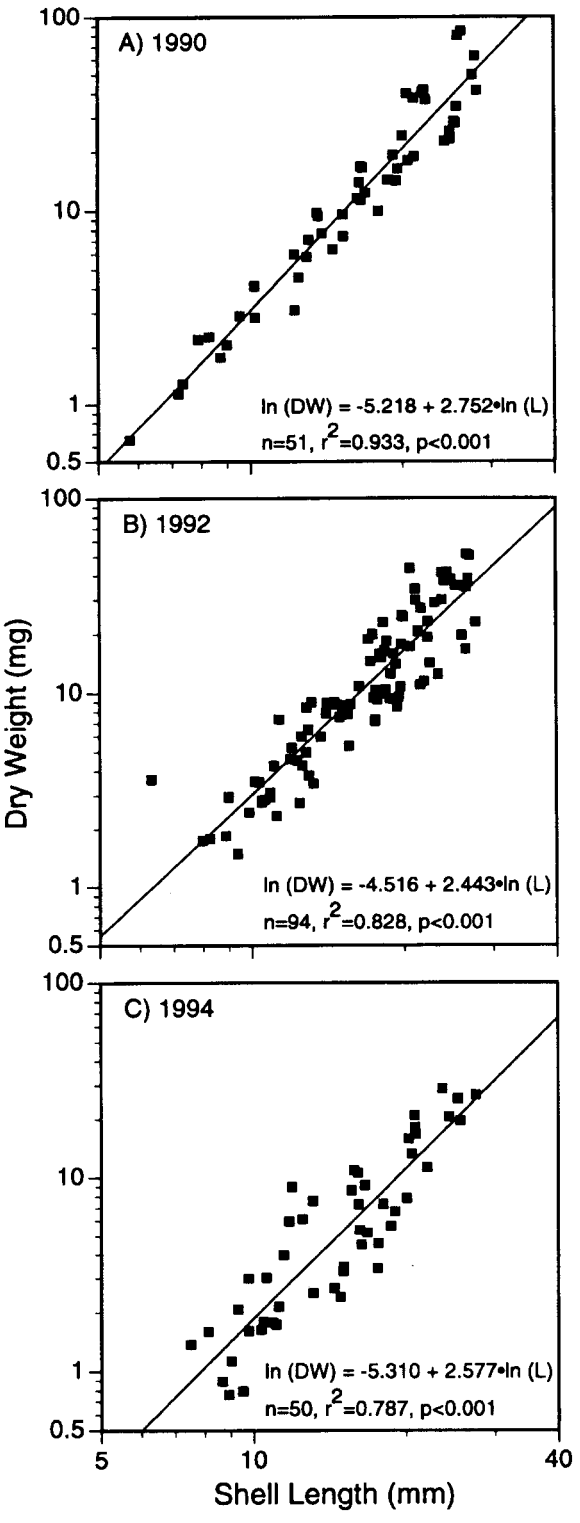

FIG. 5. Relationship between dry weight and shell length of **D. polymorpha** *from two sampling sites in Lake St. Clair in September/October of the 3 years the population survey was conducted, 1990, 1992, and 1994.*

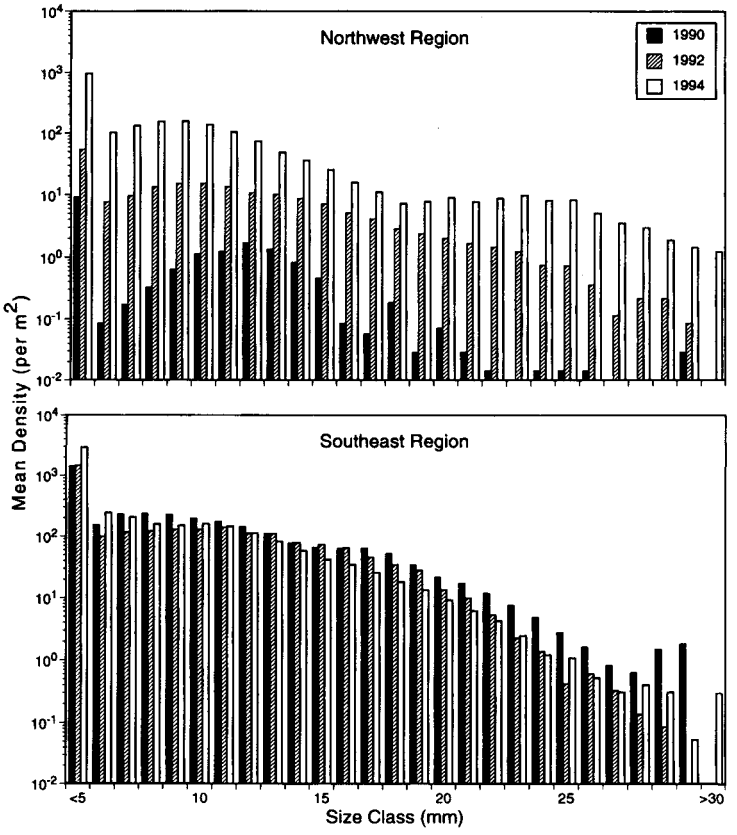

FIG. 6. Yearly trends in the size-frequency distribution of the **D. polymorpha** *population in the southeast region (15 sites) and the northwest region (14 sites) of Lake St. Clair.*

frequency distribution were apparent each year. Modal peaks occurred at 11–13 mm in 1990, at 9–10 mm in 1992, and at 9–10 mm and 23–25 mm in 1994 (Fig. 6). Determining growth rates of individual year classes (cohorts) in this region was not realistic since sampling occurred only every other year. Because of the dominance of mussels < 5 mm, and because the proportion of these small individuals can vary depending on the timing of summer recruitment, yearly differences in size-frequency distributions were also tested with this size category excluded. Differences between years were still significant in the southeast region ($G = 187$, d.f. = 46, $P < 0.001$), but not significant in the northwest region ($G = 34$, d.f. = 32, $P > 0.20$).

As shown, for *D. polymorpha* in the southeast region, both size and dry weight per unit length declined between 1990 and 1994. Thus, both variables contributed to the observed decline in *D. polymorpha* biomass over this period (Table 1). To determine the relative role of these two factors in the biomass decline, the DW:SL regression in fall 1994 was used to calculate biomass from size frequency distributions in 1990. Biomass thus calculated was 5.35 gDW m^{-2}. Given that biomass was 9.30 and 3.24 gDW m^{-2} in 1990 and 1994 respectively, we estimate 65% of the biomass decline between 1990 and 1994 in the southeast region was a result of the decline in dry weight per unit shell length, and 35% a result of a decline in the size of individuals within the population.

In 1994, mean density in the southeast region was significantly higher than mean density in the northwest region ($P = 0.02$), but mean biomass in the two regions was similar ($P = 0.36$). This can be attributed to a difference in the size structure of the population in the two regions ($G = 319$, d.f. = 31, $P < 0.001$). Small individuals (< 7 mm) were more

abundant in the southeast region, while large individuals (> 20 mm) were more abundant in the northwest region (Fig. 6).

Unionidae

Trends in the unionid community in Lake St. Clair between 1986 and 1992 have been documented by Nalepa (1994). During this time period, mean density of the community at all sites decreased from 1.9 m^{-2} in 1986 to 0.7 m^{-2} in 1992. Mean density in the southeast region of the lake declined to 0.0 m^{-2} over this period, while mean density in the northwest region did not change (1.3 m^{-2} in 1986 and 1.4 m^{-2} in 1992). Sampling in 1994 showed that the unionid community declined in the northwest region after 1992, resulting in densities near zero throughout the entire lake in 1994 (Table 3, Fig. 7). In 1986, before *D. polymorpha* became established, the total number of unionids collected was 281, but this number declined to 248 in 1990, 99 in 1992, and 6 in 1994. The number of species declined from 18 in 1986 to 5 in 1994 (Table 4). The spatial pattern of decline was clearly related to the expansion of the *D. polymorpha* population from the southeast to the northwest and an increase in the number of *D. polymorpha* per unionid. In the southeast region, the mean number of *D. polymorpha* per unionid was 300 in 1990, with 97% of all unionids infested (Nalepa 1994). By 1994, no unionids were collected in this region. In the northwest region, the mean number of *D. polymorpha* per unionid was < 1 in 1990 (14% infested), but increased to 32 per unionid in 1992 (97 % infested). By 1994, only 6 unionids were collected in this region, all were infested, and the mean number of *D. polymorpha* per unionid was 190.

Mean unionid biomass gradually declined from 4.44 gDW m^{-2} in 1986 to 0.06 gDW m^{-2} in 1994 (Table 3; Fig. 8). A comparison of relative trends in biomass of unionids and *D. polymorpha* over the study period seems valid since biomass estimates reflect weights in the fall, which is the period just after spawning in both groups. That is, the most abundant unionid species (*Lampsilis siliquoidea*, *Leptodea fragilis*, and *Potamilus alata*) are long-term brooders and release glochidia in late summer (Clarke 1981). Similarly, *D. polymorpha* releases gametes in summer and are spent by fall (Fig. 4). When examining changes in total biomass of the mussel community in the lake, biomass was actually higher in 1986, when the community consisted solely of unionids, than in 1994, when the community was dominated by *D. polymorpha* (Table 5), although the difference between years was not significant ($P = 0.103$). Biomass of both unionids in 1986 and *D. polymorpha* in 1994 was highest at sites near the mouth of the Detroit River (Figs. 3 and 8), but there was no significant correlation between biomass of these two groups when all 29 sites were considered for the 2 years (Pearson correlation; $p > 0.05$).

TABLE 3. Mean density (individuals m^{-2}; upper) and biomass (g DW m^{-2}; lower) of Unionidae at all sites, at sites in the southeast region, and at sites in the northwest region of Lake St. Clair in 1986, 1990, 1992, and 1994.

Year	All Sites (n = 29)	Southeast (n = 15)	Northwest (n = 14)
1986	1.9 ± 0.3	2.5 ± 0.5	1.3 ± 0.3
1990	1.7 ± 0.5	1.8 ± 0.9	1.6 ± 0.4
1992	0.7 ± 0.2	0.0 ± 0.0	1.4 ± 0.4
1994	< 0.1 ± < 0.1	0.0 ± 0.0	< 0.1 ± < 0.1
1986	4.44 ± 0.82	6.00 ± 1.38	2.78 ± 0.60
1990	3.67 ± 1.16	3.54 ± 2.02	3.81 ± 1.16
1992	1.24 ± 0.49	0.0 ± 0.00	2.48 ± 0.90
1994	0.06 ± 0.03	0.0 ± 0.00	0.11 ± 0.06

DISCUSSION

In the period between 1986 and 1994, the unionid community in Lake St. Clair has virtually been extirpated, while the *D. polymorpha* population continued to expand and is now found throughout the lake. These changes occurred gradually over the 8-year time period as *D. polymorpha* extended its range from the southeast region of the lake to the northwest region. As this expansion occurred, unionids were extirpated from the southeast region by 1992, and extirpated from the northwest region by 1994. This pattern of *D. polymorpha* expansion and subsequent decline in unionids can likely be attributed to the distinct water flow patterns within the lake. The high volume of water flowing into the lake from Lake Huron via the St. Clair River creates two distinct water masses (Leach 1972, 1980; Schwab *et al.* 1989). The mass in the northwest region consists mostly of water from the St. Clair River, which rapidly flows through the region (hydraulic residence time 3 days) and exits via the Detroit River. The water mass in the southeast region

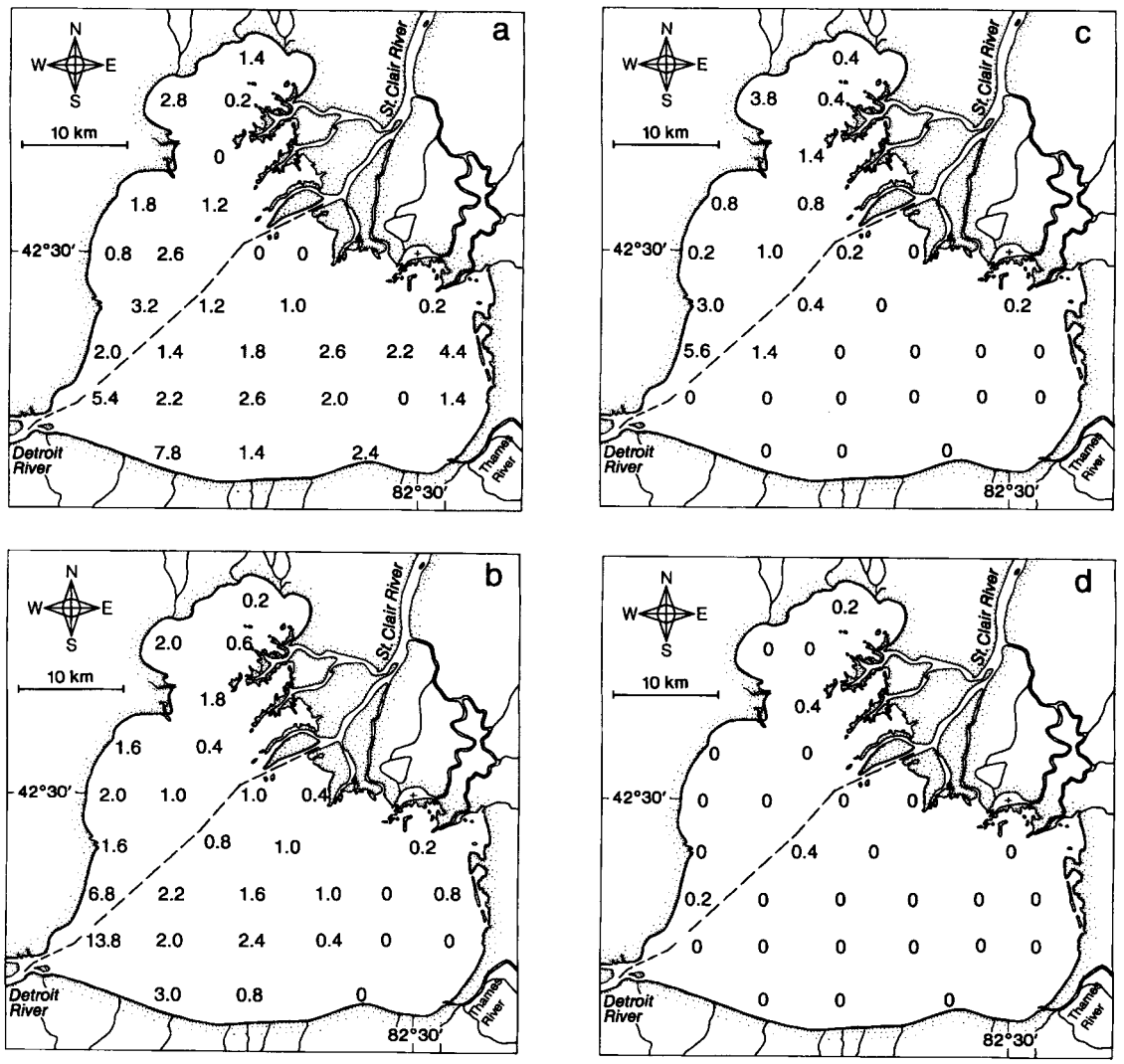

FIG. 7. Mean density (individuals m^{-2}) of Unionidae at each of the 29 sampling sites in Lake St Clair in 1988 (a), 1990 (b), 1992 (c), and 1994 (d).

consists mostly of water from the Thames River and small streams entering along the southern shoreline; this mass is more stagnant (hydraulic residence time 30 days). Although the spatial extent and mixing of the two masses will vary depending on wind speed and direction (Schwab *et al.* 1989), these typical flow patterns likely impeded *D. polymorpha* larvae from easily colonizing the northwest from the southeast. Because of the inflow of cold, nutrient-poor water from Lake Huron, the water mass in the northwest region is less productive than the mass in the southeast region (as measured by chlorophyll, phytoplankton, and zooplankton) (Leach 1972, 1973, 1991; Munawar *et al.* 1991, Sprules and Munawar 1991). Nalepa (1994) thus speculated that *D. polymorpha* may not attain high densities in this region and that unionids therefore may not be heavily colonized. This hypothesis obviously proved to be incorrect.

Because *D. polymorpha* is distributed throughout the lake, of interest is whether the population has peaked and is now more at equilibrium with its surrounding environment. Total biomass was lower in 1994 than in 1990 despite the expansion of the population into the northwest region over the period (Table 1). In the southeast region, mean density and mean biomass were not significantly different in the 3 survey years. Mean biomass actually declined

TABLE 4. Number of individuals of each unionid species collected in Lake St. Clair in 1986, 1990, 1992, and 1994.

Subfamily and Species	Year 1986	1990	1992	1994
Subfamily Ambleminae				
Amplema plicata plicata	6	0	1	1
Elliptio dilatata	20	29	3	0
Fusconaia flava	10	22	1	0
Quadrula quadrula	2	2	0	0
Pleurobema coccineum	1	2	0	0
Subfamily Anodontinae				
Lasmigona complanata complanata	1	1	0	0
Pyganodon grandis	14	11	11	1
Simpsonaias ambigua	0	1	0	0
Strophitus undulatus	1	0	0	0
Subfamily Lampsilinae				
Actinonaias ligamentia	0	1	0	0
Lampsilis cardium	16	16	2	0
Lampsilis fasciola	1	0	0	1
Lampsilis siliquoidea	127	79	45	2
Leptodea fragilis	37	36	5	0
Ligumia nasuta	8	5	5	0
Ligumia recta	3	1	1	0
Obovaria subrotunda	1	2	0	0
Potamilus alatus	29	23	19	1
Truncilla donaciformis	1	12	2	0
Truncilla truncata	3	11	4	0
Total	281	248	99*	6

*Includes one unidentified young-of-the-year

over the period, indicating that at least in this region the population has likely peaked. In the northwest region, both mean density and mean biomass were higher in 1994 than in the previous 2 survey years; however, it seems unlikely that the population will continue to increase to any extent. As noted, the water mass in the northwest region is less productive than the mass in the southeast region. Consequently, while *D. polymorpha* biomass in the two regions was similar in 1994, logically we do not expect biomass in the northwest region to greatly exceed that found in the southeast region. In 1986, unionid biomass was lower by a factor of 2 in the northwest region compared to the southeast region (Table 3). On the other hand, water column productivity may not be a useful predictor of *D. polymorpha* standing stocks. Food quality and temperature can also play a role in *D. polymorpha* growth and survival (Walz 1978d, Schneider 1992, Nalepa *et al.* 1995).

Yearly trends in the size-frequency distribution of *D. polymorpha* in the southeast region showed a decline in the proportion of larger individuals (> 5 mm) over time. Modal peaks clearly distinguishing cohorts older than the 0+ year-class were evident in 1990, but not thereafter. Griffiths *et al.* (1991) distinguished one to two cohorts (in addition to the 0+ year-class) at several sites in the southeast region prior to 1990. Similarly, Hunter and Bailey (1992) reported two to three cohorts at several sites in the southeast region in 1990. Chlorophyll levels in the lake have declined over 4-fold since *D. polymorpha* became established (Nalepa *et al.* 1993), and the loss of distinguishable, older year classes is not atypical in a population exposed to decreased food levels. Since metabolic costs increase with size (Walz 1978b, d), a decrease in available food affects the growth and survival of large individuals more so than small. As a result, young cohorts overgrow older cohorts, and survival in older cohorts is diminished. A size-frequency distribution with no distinguishable older cohorts was observed in inner Saginaw Bay within 2 years of colonization as food levels declined, but older cohorts were still distinguishable in the outer bay where growth conditions were more favorable (Nalepa *et al.* 1995). Older cohorts were still distinguishable in the northwest region of Lake St. Clair in 1994, or 2 years after widespread colonization, so the ultimate size structure of the population in this region is still not clear.

It is unlikely that size-selective predation led to the decline in the proportion of larger *D. polymorpha* in the southeast region between 1990 and 1994. Although Hamilton *et al.* (1994) reported that diving ducks selectively fed on mussels 11-21 mm in a nearshore region of Lake Erie, impacts on the size-frequency distribution of the *D. polymorpha* population were temporary, being observed only in late fall (when ducks were most abundant) and not the following spring. Also, diving ducks were very abundant in their Lake Erie study area. In Lake St. Clair, most migratory duck populations in the fall are found in the delta areas in the northern regions of the lake, and not in the southeast region (Edsall *et al.* 1988). Presently, there is no evidence that fish predation has any impact on *D. polymorpha* populations (Hamilton *et al.* 1994).

The decline in *D. polymorpha* biomass in the southeast region between 1990 and 1994 can be partly attributed to the decrease in mean size of in-

FIG. 8. Mean biomass (gDW m^{-2}) of Unionidae at each of the 29 sampling sites in Lake St. Clair in 1988 (a), 1990 (b), 1992 (c), and 1994 (d).

dividuals in the population, but it was mostly a result of the decrease in weight per unit length. The dry weight of a standard 15-mm mussel was 9.4 g in fall 1990, but only 5.3 g in fall 1994. Fall is the best time to assess changes in baseline weight of *D. polymorpha* since spawning has occurred and weights reflect the impacts of summer stresses (high temperature, low food levels) (Dorgelo and Kraak 1993, Smit and Dudok van Heel 1992). Tissue loss or "degrowth" is common in mollusks when food availability does not meet metabolic demands (Russell-Hunter 1985), and lower weights per unit length in *D. polymorpha* populations have been associated with lower food levels (Stanczykowska 1964, Stanczykowska *et al.* 1975, Nalepa *et al.* 1995). Besides a decline in the minimum weight each year, there was an apparent change in the seasonal pattern of weight gain after the minimum occurred. In 1990 and 1991, an increase in weight occurred in late fall (November), which likely reflected oogenesis and the onset of a new reproductive cycle (Borcherding 1991, Dorgelo and Kraak 1993). Since 1992, however, weight increases in late fall have not been observed. *D. polymorpha* will reabsorb gonadal tissue when conditions are not favorable, particularly when spawning has already occurred (Sprung and Borcherding 1991).

TABLE 5. Mean biomass (gDW m^{-2}) of Unionidae and **D. polymorpha** *in Lake St. Clair in each of the four yearly surveys.*

Year	Unionidae	*Dreissena polymorpha*	Total
1986	4.44	0.00	4.44
1990	3.70	4.67	8.37
1992	1.20	3.50	4.70
1994	0.06	3.12	3.18

Several investigators have made predictions of densities that might eventually be achieved by *D. polymorpha* in Lake St. Clair. Based on density increases between 1988 and 1989, Hebert *et al.* (1991) predicted that densities of over 5,000 m^{-2} would be found throughout the lake within 5 years. Ramcharan *et al.* (1992a) predicted a density of 1,200 m^{-2} in Lake St. Clair based on a model derived from densities and environmental features found in European lakes. With a lakewide density of 3,200 m^{-2} in 1994 and with the assumption that the population is at or near a peak, these predictions were reasonably accurate. While *D. polymorpha* populations can fluctuate widely within a specific lake, varying several orders of magnitude over several decades (Stanczykowska and Lewandowski 1993), models predict that population densities in Great Lakes basins, including Lake St. Clair, should be generally constant over the long term (Ramcharan *et al.* 1992b).

Ricciardi *et al.* (1995) reported a direct correlation between *D. polymorpha* densities, the number of *D. polymorpha* per unionid, and unionid mortality. From regression models derived from various data sets, they showed that unionid mortality increased significantly when *D. polymorpha* density was greater than 1,000 m^{-2}, and predicted that unionid extirpation would occur within a few years at mean densities of over 6,000 m^{-2} and/or 100/unionid. In Lake St. Clair, mean densities of 3,300 m^{-2} and 300/unionid led to extirpation within 2 years (1990–1992) in the southeast region, and mean densities of 189 m^{-2} and 32/unionid led to extirpation in the northwest region, also within 2 years (1992–1994). Densities in the northwest region increased to 2,000 m^{-2} and 190/unionid by 1994. Thus, unionid mortality in both regions appeared to fit model predictions.

With the dramatic decline in unionid density and species richness, the issue of total community loss needs to be considered relative to the constraints of our survey design and sampling effort. As noted by Nalepa (1994), our yearly surveys were designed to assess changes in relative densities and not presence/absence. Given the present rarity of unionids in the lake, future surveys to assess the status of populations will need to examine much larger areas of the bottom by employing such methods as timed searches or transect sampling (Isom and Gooch 1986). Certainly, methods that sample broad areas will be necessary to determine if areas exist where unionids may coexist with *D. polymorpha* within the lake, i.e., unionid "refugia" (Tucker and Atwood 1995, Schloesser *et al.* in press). Recent video footage of large bottom areas in the northwest region of Lake St. Clair taken with a submersible revealed a few living unionids, some without attached *D. polymorpha* (Bob Haas, Michigan Department of Natural Resources, personal communication). In Europe, unionids are still found in many lakes despite the long-term presence of *D. polymorpha* (Lewandowski 1991).

The establishment and increase in *D. polymorpha* has resulted in broad ecological changes within the lake, likely a result of the substantial increase in filtering capacity of *D. polymorpha* compared to unionids. In 1986, mean filtration rate of the most abundant unionid species, *Lampsilis siliquoidea*, was 818 mL gDW^{-1} h^{-1} over the May-October period (Vanderploeg *et al.* 1995). If we assume that all unionid species in the lake had a similar filtration rate, which is a reasonable assumption given the good agreement between this rate and rates for other unionid species (Vanderploeg *et al.* 1995), the filtration capacity of the unionid community in 1986 was 62 L m^{-2} d^{-1} (actual time spent filtering is assumed to be 17 h d^{-1}). To estimate filtration capacity of the *D. polymorpha* population in 1994, the filtration rate of *D. polymorpha* was assumed to be 16 mL $mgAFDW^{-1}$ h^{-1} (Fanslow *et al.* 1995). This rate represents a mean value for rates determined under a wide range of temperature and seston concentrations in Saginaw Bay, Lake Huron over a 2-year period and compares favorably to rates reported for *D. polymorpha* by others (see Table 4, Fanslow *et al.* 1995). If we then further assume that *D. polymorpha* filters 17 h d^{-1} (Walz 1978a) and ash free dry weight is 88% of dry weight (Nalepa *et al.* 1993), the filtration capacity of the *D. polymorpha* population was 747 L m^{-2} d^{-1} in 1994. Thus, between 1986 and 1994, as the suspension-feeding community shifted from unionids to *D. polymorpha*, filtering capacity of the community in-

creased about 12-fold. Since Lake St. Clair has a volume of 3.4 km^3 and an area of 1,110 km^2, the unionid community in 1986 had the capacity of filtering the entire lake volume in 48 days. In contrast, the *D. polymorpha* population in 1994 was capable of filtering the entire lake volume in just 4 days. Given that the flushing rate of the lake is 9 days, water entering the lake will theoretically be filtered 2.3 times by *D. polymorpha* before exiting. In terms of nutrient cycling, Nalepa *et al.* (1991) estimated that the unionid community in 1986 was capable of filtering 0.13 of the lake's total phosphorus load over the May-October period. Over the same seasonal period in 1994, the *D. polymorpha* population was capable of filtering over 1.5 times the phosphorus load.

Increased filtering capacity of the suspension-feeding community has led to dramatic changes in the Lake St. Clair ecosystem. Since *D. polymorpha* became established, water clarity has increased 2-fold (Griffiths 1993), and turbidity levels in the Detroit River, which receives water flowing from the lake, have declined an average of 30% (MacIsaac in press). Increased water clarity has led to increased growth of aquatic plants (Griffiths 1993), and dramatic changes in the fish community. Species associated with plant beds such as smallmouth bass (*Micropterus dolomieu*), largemouth bass (*M. salmoides*), and northern pike (*Esox lucius*) have increased, while other species such as walleye (*Stizostedion vitreum*) have declined (MacIsaac in press).

Both unionids and *D. polymorpha* filter more seston than is actually utilized; this unassimilated material is either rejected before ingestion (pseudofeces), or ingested but not assimilated (feces). The proportion of unassimilated material (relative to that filtered) is comparable in the two mussel groups. For example, in a study to determine phosphorus cycling through the unionid community of Lake St. Clair, Nalepa *et al.* (1991) found that the amount of phosphorus deposited as pseudofeces and feces accounted for 64% of the phosphorus filtered out of the water column. In comparison, *D. polymorpha* biodeposited 59% of phosphorus filtered from the water column in various Polish lakes (Stanczykowska and Planter 1985), and 40% of filtered carbon in laboratory experiments (Walz 1978b). Thus, the increase in biodeposited material in Lake St. Clair between 1986 and 1994 is comparable to the increase in filtering capacity (12-fold). A shift of material from the pelagic to the benthic region has led to an increase in phosphorus concentration of sediments, and to changes in the abundance and composition of the benthic macroinvertebrate community (R. Griffiths, personal communication , Ontario Ministry of the Environment; Griffiths 1993).

Mean biomass of the mussel community in the lake actually declined between 1986 and 1994 as unionids decreased and *D. polymorpha* increased. However, a comparison of typical biomass turnover ratios (P/B) for the two groups indicates a great increase in biomass production. In 1986, the P/B ratio of the unionid community in Lake St. Clair was estimated to be 0.2 (Nalepa and Gauvin 1988). While not measured directly in Lake St. Clair, the P/B for *D. polymorpha* in the nearshore waters of Lake Erie was estimated to be 4.7 (Dermott *et al.* 1993). In European lakes, the P/B ratio for *D. polymorpha* has ranged from 0.4 to 6.8 (Stanczykowska 1976, Walz 1978c). If the Lake Erie estimate is considered reasonable for Lake St. Clair, production of the mussel community within the lake increased 17 fold between 1986 and 1994. This increase is very similar to the independently-derived estimate of the increase in filtration capacity between the two years.

Because of the inflow of high-quality water from Lake Huron and the lake's rapid flushing rate, the Lake St. Clair ecosystem has historically supported a stable and diverse fauna (Leach 1991). Indeed, the unionid community in 1986 appeared little changed from the community described nearly 100 years earlier (Nalepa and Gauvin 1988). Besides the loss of biodiversity and induced ecological changes, the shift from unionids to *D. polymorpha* has implications for the long-term stability of the Lake St. Clair system. The functional mussel community has basically changed from a slow-growing, stable community, with a relatively minor influence on the ecosystem, to a community consisting of a single taxon with a relatively rapid turover rate that strongly affects ecosystem dynamics. Models show that ecosystems strongly influenced by a benthic suspension-feeding component are disproportionately sensitive to fluctuations in that component, and are also more reactive to other perturbations (Herman and Scholten 1990). Long-term monitoring of *D. polymorpha* is therefore essential to understanding any future changes in the lake's ecosystem.

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