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The Distribution and Abundance of *Dreissena* Species (Dreissenidae) in Lake Erie, 2002

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ABSTRACT. *A lake-wide benthic survey of Lake Erie during summer 2002 indicated that* Dreissena bugensis *is the dominant dreissenid in Lake Erie, especially in the east basin where this species was found at every station but no* Dreissena polymorpha *were collected. Mean (±SD) densities of dreissenid mussels were comparable between the west (601 ± 2,110/m*^{2}*;n = 49) and central (635 ± 1,293/m*^{2}*; n = 41) basins, but were much greater in the east basin (9,480 ± 11,173/m*^{2}*; n = 17). The greater variability in mussel density among stations and replicate samples in the central and west basins than in the east basin is attributable to the preponderance of fine-grained substrata in the nearshore, higher episodic rates of sediment deposition, and periodic hypoxia in bottom waters. Although there was little change in lake-wide mean dreissenid densities between 1992 and 2002 (declining from ca. 2,636 individuals/m2 to 2,025 individuals/m*^{2}*), basin-averaged shell-free dry tissue mass increased by almost four-fold from ca. 6.8 ± 15.6 g /m*^{2} *to 24.7 ± 71.3 g/m*^{2} *in the same interval. Up to 90% of this biomass is in the eastern basin. Other changes in 2002 include the virtual absence of mussels in the 3 to 12 mm size range, probably because of predation by round gobies, and an increase in the average size of mature mussels. The substantial changes observed between 1992 and 2002 suggest that dreissenid populations in Lake Erie were still changing rapidly in abundance and biomass, as well as species composition. The results of this survey suggest that a direct link between* Dreissena *spp. and hypolimnetic hypoxia in the central basin is unlikely.*

INDEX WORDS: *Lake Erie,* Dreissena, *density, biomass, distribution.*

INTRODUCTION

Since their discovery and proliferation in the Laurentian Great Lakes, zebra (*Dreissena polymorpha*) (Hebert *et al.* 1989) and quagga (*Dreissena bugensis*) (May and Marsden 1992) mussels have been implicated as modifiers of nutrient dynamics and biological integrity of lake ecosystems (see reviews in Strayer *et al.* 1999 and Vanderploeg *et al.* 2002). Hecky *et al.* (2004) proposed a conceptual model that describes several mechanisms by which dreissenids reallocate nutrients from the water column to benthic habitats. A fundamental requirement for the accurate assessment of the effects of dreissenids on nutrient cycling is data on the abundance and distribution of mussels. When abundant, dreissenids unquestionably have significant influences on water quality and epibenthic characteristics in shallow water areas (Nicholls and Hopkins 1993, Lowe and Pillsbury 1995, Stewart *et al.* 1998, Vanderploeg *et al.* 2001). Dreissenids had become abundant in the central basin of Lake Erie by 1990. By this time, loadings of total phosphorus to Lake Erie had been reduced to below 11,000 tonnes/y, the level thought to be adequate to improve water quality and reduce the frequency of anoxic events in the central basin (Makarewicz and Bertram 1991). Marked increases in epilimnetic water clarity in the early 1990s (Nicholls and Hopkins 1993)

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and continuing apparent declines in open water total phosphorus concentrations (Millard *et al.* 1999) were ascribed to dreissenid activity. However, more recent evaluations of water quality trends through the 1990s indicate poorer correlations between some of these parameters and the advent of dreissenids. Makarewicz *et al.* (2000) found little difference in nutrient trends in the first 10 y since dreissenids had become established in Lake Erie and the period immediately preceding their arrival. Barbiero and Tuchman (2004) reported that turbidity levels in Lake Erie have tended to increase over the interval during which dreissenids have been present. Nevertheless, when increased total phosphorus concentrations were observed in the central basin during spring monitoring in the late 1990s (Rockwell *et al.* 2005), questions about the role of dreissenids in internal nutrient dynamics and a potential link to hypolimnetic anoxia in the central basin stimulated the coordinated research program reported in this volume (Matisoff and Ciborowski 2005). If dreissenids have a direct effect, there should be a measurable relationship between changing densities of mussels at epilimnetic and metalimnetic depths and temporal patterns of total phosphorus concentrations and frequency of central basin hypolimnetic anoxia.

The biomass of *Dreissena* species in Lake Erie increased between 1992 and 1998 (Jarvis *et al.* 2000), as *D. bugensis* became increasingly abundant relative to *D. polymorpha* in the central and eastern basins (Dermott and Munawar 1993, Mitchell *et al.* 1996, Dermott and Kerec 1997, Mills *et al.* 1999, Jarvis *et al.* 2000, Johannsson *et al.* 2000). Zebra mussels remained dominant in the western basin (Berkman *et al.* 2000, Bially and MacIsaac 2000, Jarvis *et al.* 2000). The two species were originally expected to partition the habitat, with *D. polymorpha* colonizing hard substrates in shallow water, and *D. bugensis* confined to soft sedimentary environments in the colder profundal zone (> 30 m) (Dermott and Munawar 1993). Recent field observations, however, indicate a continued expansion of the quagga mussel into progressively shallower regions as well as soft offshore sediments in Lake Erie (Coakley *et al.* 1997, Berkman *et al.* 1998, Berkman *et al.* 2000, Haltuch *et al.* 2000, Coakley *et al.* 2002).

These observations suggest it is unlikely that recent densities reflect a long-term stabilization of abundance. Therefore, the objective of this study was to describe the distribution, density, and abundance of dreissenid species throughout Lake Erie in 2002, in order to evaluate the potential role of mussels in nutrient dynamics and anoxia, and to document continuing change in the benthic community.

METHODS

From 15 May through 8 September 2002, benthic samples were collected during three surveys that included a total of 107 stations throughout Lake Erie (Fig. 1).

The West Basin Grid survey was conducted between mid-May and mid-August; five petite Ponar (0.0225 m^2) samples were collected from each of 38 stations in the west basin. Station depths ranged from 3.6 to 11.5 m. Secondly, three Petite Ponar samples were collected from each of 17 stations (6.1 to 61.8 m depth) along four transects visited by the U.S.EPA Research Vessel *Lake Guardian* during a cruise from 17 to 21 August 2002 (Guardian survey). (No benthic samples were taken at EPA sites "55" or "Sandusky.") The third survey covered 50 stations along 18 transects perpendicular to the north shore in the west, central and east basins (Northshore survey). Stations were located at depths of 2, 5, and 10 m on most west and central basins transects and 2, 5, 10, and 20 m in the east basin. Three samples were collected at each station during August 2002. A Petite Ponar grab sampler was used at west and central basin sites. Rocky substrata at depths ≤ 10 m in the east basin were sampled with an airlift (0.0314 m^2) by divers. An Ekman grab (0.0225 m^2) was used for the 20-m sites. Hard substrata prevented sampling at two 2-m sites in the west basin (Plum Point, Kingsville). Two 10-m (Comet, Colchester) stations could not be sampled due to poor weather.

All samples were immediately sieved through 250 μm Nitex mesh and the material retained was preserved in 10% buffered formalin. Depth, substrate, and GPS coordinates were recorded at all stations.

Sample Processing

Upon return to the laboratory, the preserved Northshore and Guardian samples were rinsed with water through 250-μm aperture screen and examined under a dissecting microscope. All macroinvertebrates were removed to 70% ethanol. Northshore and Guardian samples that contained very large numbers of animals were subsampled by dividing the residues into eighths and removing organisms from two, nonadjacent subsamples. If the

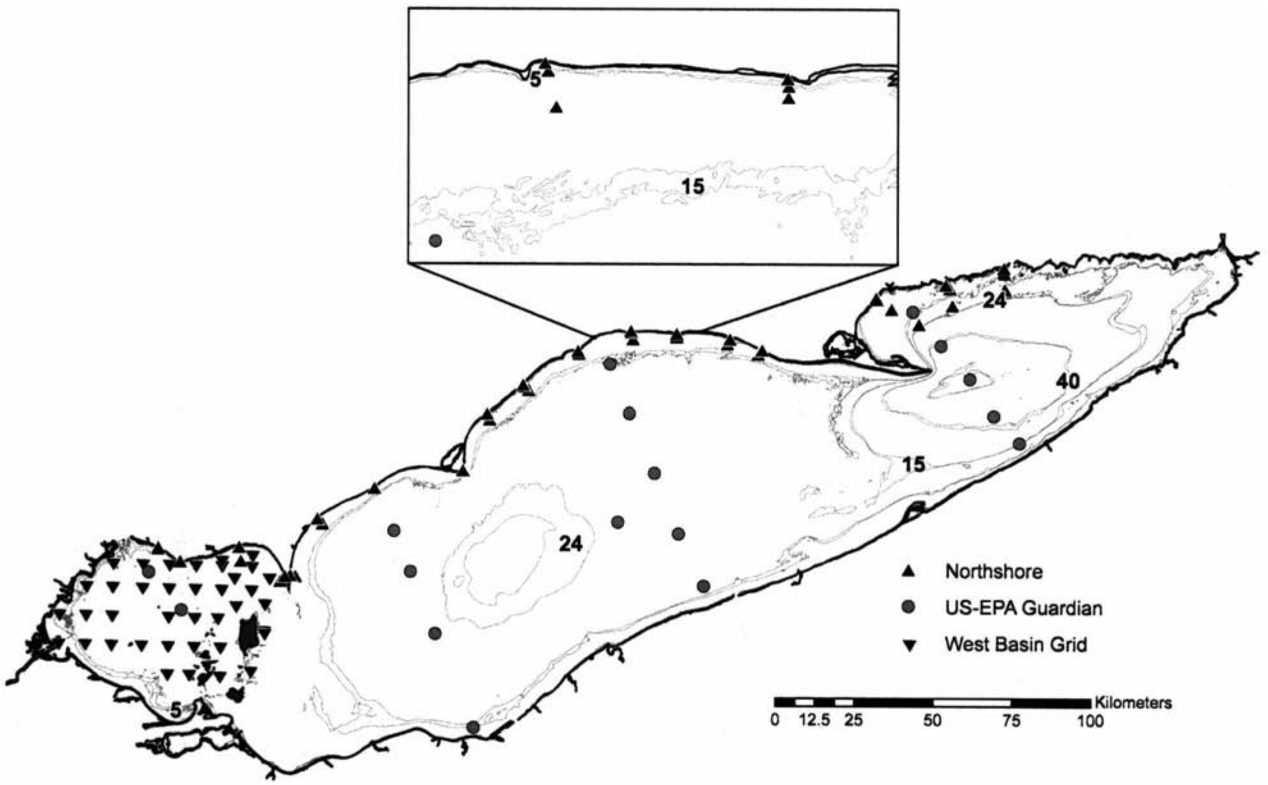

FIG. 1. Lake Erie 2002 **Dreissena** ***survey sample stations. Numbers on isobaths indicate depth in meters.***

numbers of organisms in the eighths differed by > 10%, additional subsamples were sorted. West Basin Grid samples were washed through a set of nested brass sieves (4-mm, 1-mm, 0.5-mm, and 0.25-mm apertures), then dreissenids were counted from each fraction. Large mussels (> 1 mm) were found at only six of the West Basin Grid sites and these dreissenids were identified to species. Nine sites yielded only a few individuals (< 533 mussels/m^2), all of which were too small to be identified reliably; values of density and mass for these nine sites were treated as zeros during subsequent species-specific analyses.

The relationships among shell length, wet (with shell) mass, and shell-free dry tissue mass were determined using dreissenids from one sample from each Guardian and Northshore station. Valve lengths were determined to the nearest 0.01 mm using electronic calipers, and all individuals > 1 mm long were identified to species. Wet mass was determined following the procedures of Jarvis *et al.* (2000), then soft tissue was removed from the shell, dried at 50°C for at least 48 h, and weighted to the nearest 0.01 mg. Mussels < 1 mm were enumerated from all samples, but omitted from further analysis.

Data Analysis

Areal dry mass of *Dreissena* at each sample station was estimated using a regression model of individual shell-free dry tissue mass versus shell length, combined with length-frequency distributions. Mean values for each station were used in a second regression of dry mass against whole wet-mass so that measurements (shell included) reported in previous studies of Lake Erie (Jarvis *et al.* 2000) could be converted to shell-free dry mass. The whole-lake 1992–1998 survey of Jarvis *et al.* (2000) was used for historical comparison with *Dreissena* abundance and dry biomass distribution in our study.

All mass and density data were log-transformed prior to analysis of patterns of distribution relative to basin, depth, and substrate type. The unit of replication was a sampling site, and the variates consisted of the mean values of the three or five samples collected at each site. Two statistical analyses were performed. One incorporated the entire data set (all three surveys) using a multiple regression approach to test for differences among basins, and among classes of depth and substrate type, all treated as dummy variables. The second analysis evaluated variation in dreissenid abundance and mass among depths within Northshore transects. Analyses were performed using Statistica® Version 5.8 (Statsoft Inc. 2000).

Because the numbers of sites sampled throughout the lake varied disproportionately among basins, depth classes, and substrate classes, multiple regression analysis was used to determine how dreissenid density and mass differed among locations. Classes of the independent variables depth (< 4 m, 4–8 m, > 8–15 m, > 15–24 m, and > 24 m), basin (east, central, west), and substrate (mud, sand/silt, sand, coarse material, hard) were treated as binary dummy variables against which densities and mass of each dreissenid species were regressed. Thus, a total of four regression analyses was performed. Both Northshore and offshore data were combined for these analyses.

The Northshore collections alone were analyzed by treating each transect as a block and performing randomized block ANOVA to evaluate the significance of overall differences among depths (2, 5, 10 m) blocked by transect. We substituted Ponar grab sample values collected from the nearest Western Basin Grid station for two western basin transects where the 10-m depth had not been sampled. Data for one missing 2-m station were replaced by a value of zero (equivalent to values at the 2-m depth of adjacent transects on either side). A planned comparison test was performed to determine whether expected differences between the shallow vs. deeper sites (2 m vs. 5 and 10 m) were statistically significant.

RESULTS

Of the 1,100 specimens of *Dreissena* used to describe the relationship between shell length and tissue dry mass, only 28 were *D. polymorpha*. Removal of these individuals from the analysis made no difference to the to the pooled regression results ($p > 0.05$), so they were omitted from analysis. Valve length of mussels used for allometric models ranged from 4.9 mm to 38.5 mm, however no mussels collected from the west basin from either the Northshore or Guardian surveys were large enough to allow direct biomass measurements. Relationships between dry tissue mass (g) and shell length (mm) for mussels from the central and western basins at each depth class revealed three distinct groups: central basin, east basin 2–20 m, and east basin > 20 m. When coefficient a was constrained to be shared among these three groups, coefficient b differed significantly between regression equations for mussels collected from the three locations, so that each is described by a different regression equation ($F_{2,1069} = 290.9$, $p < 0.0001$, Bonferroni, $p < 0.001$). Therefore, three separate regression models were used to estimate dry tissue mass from shell length for individual mussels collected from these areas of the lake (Patterson M.W.R. and Barton, D.R, unpublished data). The allometric equations for central basin dreissenids were applied to west basin mussels because too few mussels large enough for biomass measurement were found at the west basin Northshore and Guardian survey sites.

$$\text{dry tissue mass (g)} = 1.659 \times 10^{-5}(\text{shell length (mm)})^{2.463}\ (R^2 = 0.82).$$

This equation was used to estimate dry tissue mass from shell length distributions for all samples collected in 2002.

We used the following relationship between site mean dry tissue weight and site mean whole wet weight of dreissenids to convert values of mass (as wet weights with shell) reported by Jarvis *et al.* (2000) from surveys done from 1992 through 1998 to dry mass (tissue only) for comparison with our data:

$$\text{shell-free dry mass (g)} = 0.0265 * \text{whole wet mass (g)}\ (R^2 = 0.96).$$

2002 Dreissenid Distribution

Dreissenids were present at 57 of the 107 sites surveyed in 2002 (Table 1, Fig. 2), including all of the 17 stations in the east basin and about 44% of the stations in the central and west basins. The mean (±standard deviation) lake-wide density and dry mass of *Dreissena* spp. were 2,025±5,665 individuals/m^2 and 24.7±71.3 g dry tissue/m^2 (Table 1). Numerical densities did not differ significantly between the west (601.1 mussels/m^2) and central (635 mussels/m^2) basins, but were an order of magnitude greater in the east basin (9,481 mussels/m^2) (Table 2).

Dreissena bugensis was the dominant species in Lake Erie (Table 1), accounting for approximately

TABLE 1. 2002 Lake Erie **Dreissena** ***mean density (individuals m^{-2} ± standard deviation) and mean dry tissue biomass (g m^{-2} ± standard deviation) by basin and depth (m). N = no. of sites sampled, f = frequency of occurrence.***

			D. bugensis Density			*D. polymorpha* Density			Total Density			Total Dry Biomass (g m^{-2})	
Basin	Depth (m)	N	f	Mean	±S.D.	f	Mean	±S.D.	f	Mean	±S.D.	Mean	±S.D.
West	0–4	4	2	153.3	250.9	1	257.8	515.6	2	180.0	303.6	2.4	4.8
	4–8	15	8	548.2	1,378.5	7	588.2	1,402.9	11	1,253.2	3,564.2	11.1	28.2
	8–15	30	4	126.7	485.5	2	112.3	510.3	10	331.2	953.7	3.6	14.4
	15–24		—	—	—	—	—	—	—	—	—	—	—
	> 24		—	—	—	—	—	—	—	—	—	—	—
	Total	49	14	257.9	859.4	10	269.9	891.8	23	601.1	2,110.4	5.8	19.3
Central	0–4	10	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0	0.0
	4–8	11	4	960.2	1,587.6	3	22.9	50.2	4	983.1	1,628.4	18.8	34.5
	8–15	13	8	1,038.1	1,610.5	4	9.1	17.7	8	1,047.2	1,613.6	28.6	48.8
	15–24	7	5	163.0	216.4	4	67.7	141.5	5	230.7	249.5	0.7	1.3
	> 24		—	—	—	—	—	—	—	—	—	—	—
	Total	41	17	614.6	1,279.3	11	20.6	65.3	17	635.2	1,292.8	14.2	34.2
East	0–4	3	3	11,002.6	4,309.1	0	0.0	0.0	3	11,002.6	4,309.1	58.1	44.1
	4–8	3	3	3,816.1	1,103.4	0	0.0	0.0	3	3,816.1	1,103.4	37.4	24.9
	8–15	4	4	8,218.9	8,471.6	0	0.0	0.0	4	8,218.9	8,471.6	108.3	128.3
	15–24	4	4	17,835.3	20,375.1	0	0.0	0.0	4	17,835.3	20,375.1	233.9	250.2
	> 24	3	3	4,167.5	3,438.8	0	0.0	0.0	3	4,167.5	3,438.8	38.6	29.9
	Total	17	17	9,480.9	11,173.1	0	0.0	0.0	17	9,480.9	11,173.1	104.2	146.6
Total	0–4	17	5	1,977.7	4,569.6	1	60.7	250.1	5	1,984.0	4,567.5	10.8	27.5
	4–8	29	15	1,042.5	1,701.5	10	312.9	1,034.0	18	1,415.9	2,844.4	16.8	30.5
	8–15	47	16	1,067.5	3,245.0	6	74.2	408.5	22	1,200.5	3,273.5	19.4	52.0
	15–24	11	9	6,589.2	14,285.2	4	43.1	114.8	9	6,632.3	14,264.3	85.5	180.6
	> 24	3	3	4,167.5	3,438.8	0	0.0	0.0	3	4,167.5	3,438.8	38.6	29.9
	Total	107	48	1,859.9	5,558.5	21	131.5	614.9	57	2,025.0	5,664.9	24.7	71.3

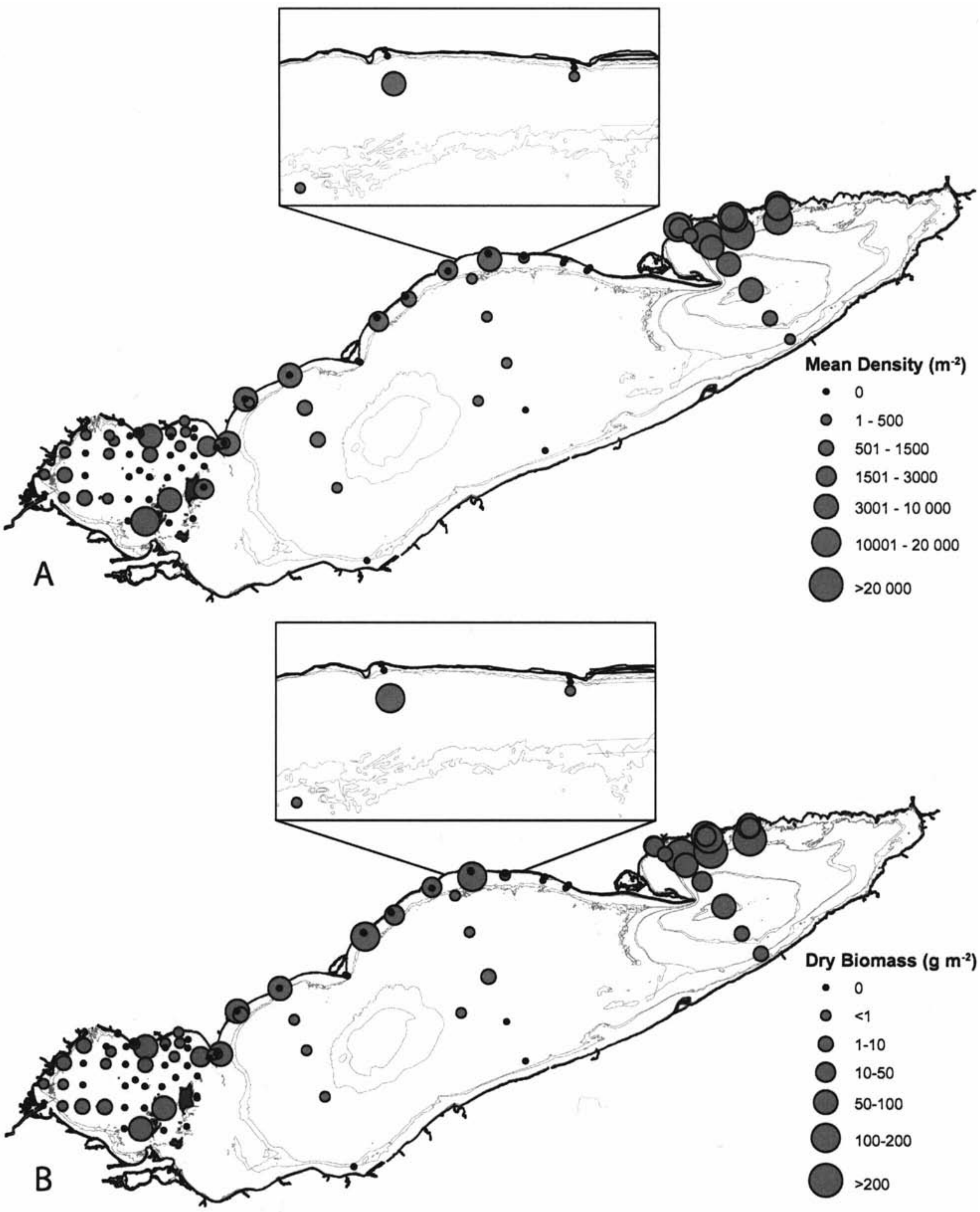

FIG. 2. The distribution of **Dreissena** *in Lake Erie, 2002: A) mean density (individuals/m^2) and B) dry tissue mass (g/m^2) distribution.*

TABLE 2. Regression coefficients for dummy variables relating classes of depth, basin and substrate texture to density of Dreissena bugensis (cumulative $R^2 = 0.56$ $F_{[10,97]} = 12.48$, $p < 0.001$), and D. polymorpha (cumulative $R^2 = 0.15$, $F_{[10,98]} = 1.75$, $p = 0.08$). Regression coefficient values for depth, basin, and substrate class are expressed relative to < 4 m, eastern basin and mud, respectively. + $p < 0.10$ (not significant), * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Dreissena bugensis		*Dreissena polymorpha*	
Variable	Reg. Coeff.±SE	t-value	Reg. Coeff.±SE	t-value
Intercept	1.907 ± 0.630	3.03	–0.836 ± 0.495	–1.69
Depth > 4–8 m	0.656 ± 0.357	1.84+	0.442 ± 0.280	1.58
Depth > 8–15 m	0.337 ± 0.368	0.91	–0.022 ± 0.289	–0.07
Depth > 15–24 m	0.951 ± 0.570	1.67+	0.652 ± 0.448	1.46
Depth > 24 m	0.805 ± 0.867	0.93	0.512 ± 0.681	0.75
West Basin	–1.821 ± 0.515	3.54***	1.161 ± 0.405	2.87**
Central Basin	–1.881 ± 0.409	4.60***	0.747 ± 0.321	2.32*
Sand/Silt	0.753 ± 0.393	1.91+	0.324 ± 0.309	1.05
Sand	0.054 ± 0.404	0.13	0.142 ± 0.317	0.45
Coarse	1.224 ± 0.566	2.16*	0.181 ± 0.445	0.41
Hard	1.713 ± 0.535	3.20**	0.693 ± 0.421	1.65

TABLE 3. Regression coefficients for dummy variables relating classes of depth, basin and substrate texture to biomass of Dreissena bugensis (cumulative $R^2 = 0.55$ $F_{[10,94]} = 11.53$, $p < 0.001$), and D. polymorpha (cumulative $R^2 = 0.09$, $F_{[10,98]} = 0.96$, $p = 0.56$). Regression coefficient values for depth, basin, and substrate class are expressed relative to < 4 m, eastern basin, and mud, respectively. + $p < 0.10$ (not significant), * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Dreissena bugensis		*Dreissena polymorpha*	
Variable	Reg. Coeff.± SE	t-value	Reg. Coeff.± SE	t-value
Intercept	2.066 ± 0.737		–0.111 ± 0.341	
Depth > 4–8 m	0.800 ± 0.417	1.92+	0.120 ± 0.198	0.61
Depth > 8–15 m	0.831 ± 0.430	1.93+	–0.061 ± 0.203	0.30
Depth > 15–24 m	1.125 ± 0.680	1.65	0.316 ± 0.315	1.01
Depth > 24 m	1.109 ± 1.007	1.10	0.205 ± 0.466	0.44
West Basin	–2.574 ± 0.602	4.28***	0.395 ± 0.283	1.40
Central Basin	–2.364 ± 0.477	4.96***	0.066 ± 0.227	0.29
Sand/Silt	0.166 ± 0.467	0.36	–0.094 ± 0.211	0.45
Sand	0.197 ± 0.466	0.42	0.141 ± 0.216	0.65
Coarse	0.868 ± 0.655	1.33	–0.035 ± 0.303	0.12
Hard	1.767 ± 0.622	2.84**	0.072 ± 0.294	0.24

87% of the mussels identified from all three surveys, and was significantly more abundant in the east basin than in the west or central basins (density: $p < 0.001$, Table 2; biomass: $p < 0.001$, Table 3). Both the density and biomass of *D. polymorpha* declined from west to east ($p < 0.05$, Table 2): zebra mussels accounted for 45%, 3%, and 0% of mean *Dreissena* density in the west, central, and east basins, respectively. Mean zebra mussel dry mass calculated using all samples from the three surveys was only 0.80 g /m^2, compared to 23.43 g/m^2 for quagga mussels.

Densities of zebra mussels were greatest at depths of 4–8 m lake-wide. In contrast, maximum densities and biomass of quagga mussels occurred at depths of 15–24 m (Table 2). Differences in density among depth intervals were not significant for either species for the combined surveys (Tables 2 and 3), except that *D. polymorpha* was almost completely restricted to the shallow western basin.

TABLE 4. Analyses of variance of density and biomass of Dreissena bugensis and D. polymorpha distribution at depths of 2, 5, and 10 m along transects from the Canadian side of Lake Erie.

Density

		Dreissena bugensis			*Dreissena polymorpha*		
	DF	MS	F	*p*	MS	F	*p*
Transect	17	4.5370	2.677	0.007	0.6173	1.292	0.255
Depth	2	5.7935	3.418	0.044	1.5338	3.211	0.053
[2 vs. (5+10)]	1	11.1545	6.581	0.015	2.5571	5.353	0.027
Discrepance	34	1.6949			0.4777		
Total	53						

Biomass

		Dreissena bugensis			*Dreissena polymorpha*		
	DF	MS	F	*p*	MS	F	*p*
Transect	17	0.9757	2.435	0.013	0.00012	0.995	0.486
Depth	2	0.8871	2.214	0.125	0.00025	2.137	0.134
[2 vs. (5+10)]	1	1.5450	3.856	0.058	0.00013	1.116	0.298
Discrepance	34	0.4007			0.00012		
Total	53						

However, analysis of the transect-specific Northshore data indicated that both species were significantly more abundant at depths of 5 and 10 m than at 2 m ($p < 0.05$; Table 4). The distribution of mussel mass exhibited the same pattern. Mass of *D. bugensis* was lowest in the shallowest depth class (< 4 m) and greatest biomass occurred in the 15–24-m depth class of the eastern basin (Table 1). Because biomass was highly variable among samples, the difference in biomass relative to the shallowest depths only approached (but didn't achieve) statistical significance for the 8–15 m depth class ($p < 0.08$, Table 3).

Part of the difference in mussel abundance among basins is due to differences in substratum. All sites sampled in the east basin at depths ≤ 10 m were on bedrock, boulders, or cobbles; airlift samples yielded 6,334 ± 4,441 quagga mussels/m^2 (Fig. 3). Similar hard substrata in the western basin were not sampled as efficiently with the Ponar grab used for the West Basin Grid. Fine-grained sediments (mud, silt, sandy silt) were sampled effectively by the grab in all basins and supported high densities of mussels (1,599 ± 5,937/m^2), but numbers of individuals were extremely variable both among stations and among replicate samples at most stations. This was especially true in the west basin where the mean density of dreissenids was 601 ± 2,110/m^2, and the maximum was 13,822/m^2. Densities of *D. bugensis* on coarse and hard substrates were significantly greater than on mud ($p < 0.05$, and $p < 0.01$, respectively, Table 2). There were no significant differences in density of *D. polymorpha* with respect to substrate texture (Table 2). *Dreissena bugensis* biomass was significantly greater on hard (bedrock) substrate than on mud ($p < 0.01$; Table 3). Although greater mass also occurred on coarse substrate than on mud, that difference was not statistically significant. Mass of *D. polymorpha* did

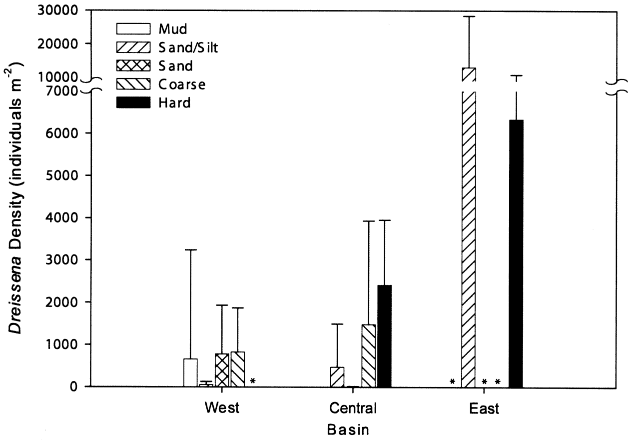

FIG. 3. Mean density (individuals/m^2) of* Dreissena *in Lake Erie during 2002, by basin and substrate. Error bars indicate 1 standard deviation. * = category not sampled.

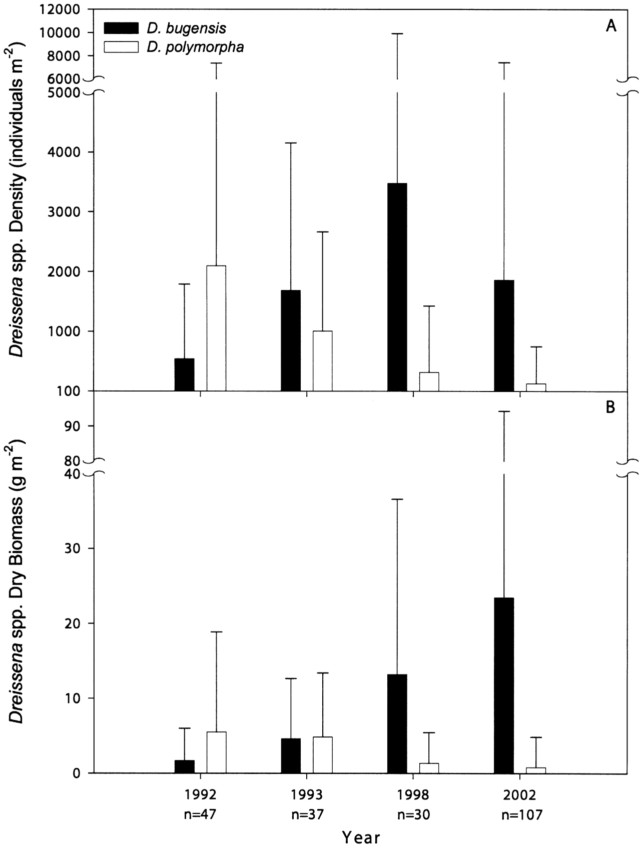

FIG. 4. Mean density (individuals/m^2) (A) and mean dry tissue mass (g/m^2) (B) of* D. bugensis *and* D. polymorpha *from all sites surveyed during the years 1992, 1993, 1998 (data from Jarvis* et al. *2000) and 2002. n = number of sites surveyed each year. Error bars indicate 1 standard deviation.

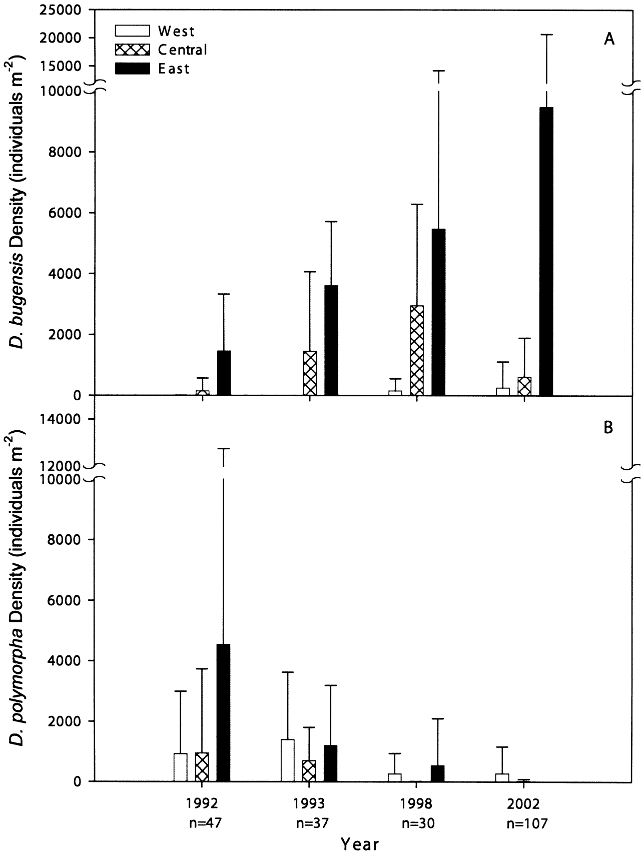

FIG. 5. Mean density (individuals/m^2) of* D. bugensis *(A) and* D. polymorpha *(B) by basin and year for all sites surveyed during the years 1992, 1993, 1998 (data from Jarvis* et al. *2000), and 2002. Error bars indicate 1 standard deviation.

not vary significantly among substrate classes (Table 3).

Changes in *Dreissena* spp. Distribution: 1992–2002

The lakewide mean density of *Dreissena* spp. in 2002 (2,025/m^2) was 53% lower than in 1998 (3,791/m^2), but dry mass was 1.7 times as great (24.6 g/m^2 vs. 14.5 g/m^2) (Fig. 4). Neither of these differences was statistically significant ($p > 0.05$) because of the large variability among stations and replicates in both years. The change in biomass was attributable to quagga mussels, whose mean areal mass increased significantly ($p < 0.01$) from ca. 1.7 g/m^2 in 1992, to 13.2 g/m^2 in 1998, and 23.4 g/m^2 in 2002, despite a decrease from 3,478 to 1,860 individuals/m^2 from 1998 to 2002 (Figs. 5A, 6A).

The change in zebra mussel abundance in the same period was also not statistically significant ($p > 0.05$), even though mean lake-wide zebra mussel density decreased from ~2,096 individuals (5.5 g)/m^2 in 1992, to 131 individuals (0.8 g)/m^2 in 2002 (Figs. 5B, 6B). *Dreissena bugensis* dry mass was consistently greatest in the eastern basin across all years. However, mass and density increased disproportionately through time in the eastern basin, whereas decreases have occurred in the western and central basins (Figs. 5, 6). Dry mass of *D. bugensis* increased from 13.2 g/m^2 in 1998, to 23.4 g/m^2 in 2002, but increased from 17.8 g/m^2 to 104.2 g/m^2 within the eastern basin considered alone. The overall decline in density of quagga mussels while total mass increased from 1998 to 2002 is attributable to a change in the size frequency distribution of mussels. For example, stations E3 and 933 from Jarvis

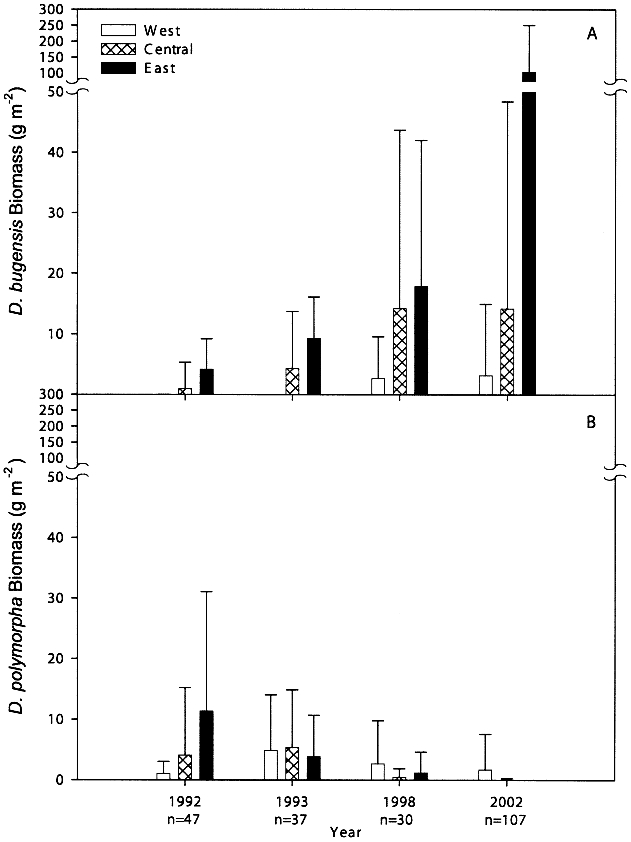

FIG. 6. Mean dry tissue mass (g/m²) of* D. bugensis *(A) and* D. polymorpha *(B) by basin and year for all sites surveyed during the years 1992, 1993, 1998 (data from Jarvis* et al. *2000), and 2002. Error bars indicate 1 standard deviation.

et al. (2000) correspond very closely to our Port Ryerse 10-m and Evans Point 20-m stations. The virtual absence of individuals between 3 and 12 mm in length (Fig. 7) at these stations in 2002, was typical of stations throughout Lake Erie.

DISCUSSION

1992–2002 Distribution

The results of benthic surveys in 2002 suggest that the distribution and size structure of dreissenid populations in Lake Erie is still evolving. After initially appearing on softer, offshore sediments (Dermott and Munawar 1993, Mills *et al.* 1993, Mills *et al.* 1996, Jarvis *et al.* 2000, Martel *et al.* 2001), *D. bugensis* has become increasingly dominant throughout Lake Erie, completely displacing *D. polymorpha* in the eastern basin, and accounting for 43% of the mussels in samples from the west basin as of 2002. The total density of dreissenids appears to have decreased slightly, while mass has increased.

This shift in dominance from *D. polymorpha* to *D. bugensis* likely reflects differences in assimilation efficiency and respiration rates which make the quagga mussel a superior competitor at high densities and low food concentrations (Baldwin *et al.* 2002, Stoeckmann 2003). The early success of quagga mussels in deeper water is thought to reflect higher growth rates at low food concentrations (Diggins 2001, Baldwin *et al.* 2002) and a lower tolerance of high temperatures (Domm *et al.* 1993, Spidle *et al.* 1995, Thorp *et al.* 1998). Both food availability and temperature should be higher in shallow, more turbulent waters, and *D. polymorpha* is still common in the western basin of Lake Erie. However, water temperatures in the western basin rarely approach the upper lethal limits for either *Dreissena* species. Food concentrations in the nearshore of the eastern basin (0.5–4.0 µg Chl *a*/L; Depew 2003) are within the range known to favour quagga over zebra mussels (Baldwin *et al.* 2002), and are somewhat higher in the western basin (MacDougall *et al.* 2001). Perhaps even more significantly, mussels have limited access to the water column during much of the summer in the shallow (≤ 6 m) nearshore zone of the eastern basin because of the dense growths of *Cladophora glomerata* that completely blanket all hard substrates from May through mid-August (Higgins *et al.* 2005). *Cladophora* coverage is less extensive in the west and central basins because of the limited availability of hard substrates and the higher turbidity caused by resuspension of sediments during strong winds. We suggest that the complete replacement of *D. polymorpha* by *D. bugensis* in the eastern basin has been facilitated by the combination of low concentrations of phytoplankton and a luxuriant carpet of benthic algae. These conditions are themselves a result of the establishment of dreissenids in Lake Erie, and their subsequent effects on the distribution of nutrients (Hecky *et al.* 2004).

Given the general west to east decline in primary production in Lake Erie (MacDougall *et al.* 2001), it is somewhat surprising that the abundance of *Dreissena* spp. now increases from west to east. Some of this pattern is directly attributable to the high densities of quagga mussels we collected in airlift samples from the extensive areas of rocky substrata along the north shore of the east basin. MacIsaac *et al.* (1992) reported very high densities

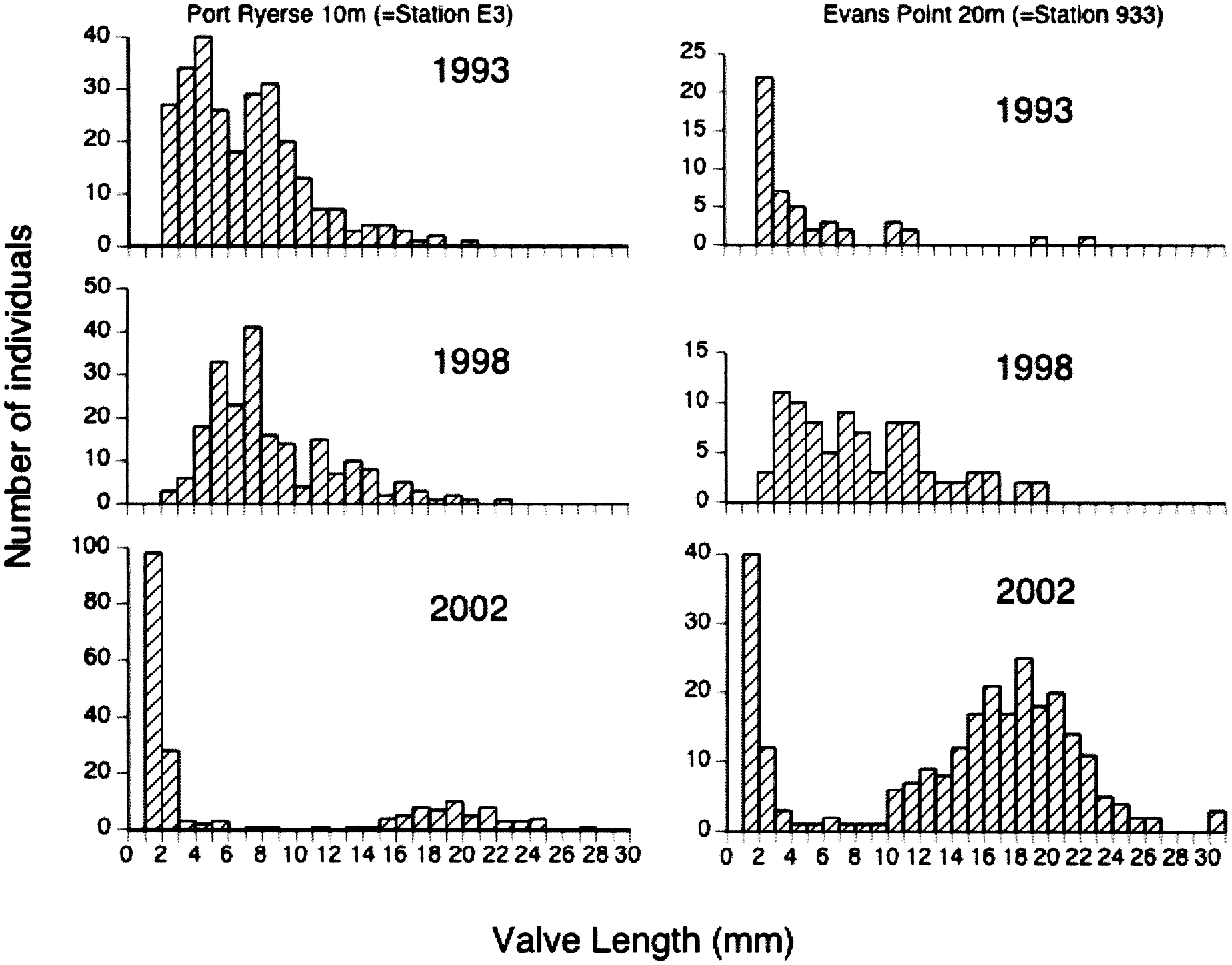

FIG. 7. Length-frequency distributions of* Dreissena *spp. from stations E3 and 933 during 1993 and 1998 from Jarvis* et al. *(2000) and corresponding stations sampled in 2002 (Port Ryerse 10 m and Evans Point 20 m).

of *D. polymorpha* (ca. 250,000/m^2), most of which were ≤ 5 mm in length, on rocks in western Lake Erie in 1991, but methodological differences preclude direct comparison with our results. Hard substrates account for about 15% of the bottom of the west basin (Coakley *et al.* 1997), but grab samplers are ineffective on rock so the densities of mussels on this substrate in 2002 are unknown.

All other sampling sites visited by the Northshore survey in the west and central basins had substrata consisting of fine gravel or sand at depths ≤ 5 m (Coakley 1972, Gelinas and Quigley 1973, Thomas *et al.* 1976), and finer-grained sediments in deeper water. Frequent disturbance by wave action strongly limits the abundance of mussels on sand and gravel in shallow water, and the few mussels collected in these samples were almost all < 6 mm in length, suggesting they had settled recently. Colonization of softer sediments in deeper water largely depends on the availability of larger particles to which initial colonists can attach (Coakley *et al.* 1997, Berkman *et al.* 1998, Berkman *et al.* 2000, Haltuch *et al.* 2000, Coakley *et al.* 2002). Long-term survival of mussels in such habitats can be limited by episodic anoxia of the bottom waters and deposition of sediment (Dermott and Munawar 1993, Coakley *et al.* 1997, Bially and MacIsaac 2000), both of which are common in the central and west basins. Hypolimnetic anoxia has not been recorded in the much deeper eastern basin. Sediment inputs to the east basin are also proportionally less because of the rocky shoreline, which limits shore erosion (Quigley and Tutt 1968), and the small number of tributary streams. Consequently, the colonization of softer, offshore sediments has been uninterrupted in the east basin, resulting in high densities of mussels. The impacts of episodic anoxia and sediment deposition are evident in the lower and more variable densities of mussels on soft sediments in the west and central basins.

The apparent decline in the lake-wide density of *Dreissena* spp. between 1998 and 2002 is consistent with frequently observed population dynamics of invasive species (Sakai *et al.* 2001). The increase in biomass during that time interval, however, suggests that the dreissenid populations in Lake Erie are still in a state of flux. When the size-frequency distributions of mussels collected in 2002 are compared with those from previous surveys (e.g., Dermott and Munawar 1993, MacIsaac 1996, Coakley *et al.* 1997, Jarvis *et al.* 2000), the disappearance of animals in the 3 to 12 mm size classes is striking. This is the size range preferred by round gobies (Ray and Corkum 1997). The average size and proportion of adult quagga mussels appears to have increased over time, but especially since 1998, and this is the interval during which round gobies invaded eastern Lake Erie. These observations suggest that predation by gobies is having a strong impact on the recruitment of mussels to the juvenile and adult stages (Barton *et al.* 2005). Quagga mussels that have achieved a shell length > 12 mm may be largely free of goby predation. The consequences of this are difficult to predict without information about round goby abundance and the longevity of quagga mussels once they have reached adult size.

While our observation of replacement of zebra mussels by quagga mussels is not novel, the marked increase in mean areal dry mass, especially in the eastern basin over the last decade, is. Increased biomass and filtering capacity by dreissenids stimulates nutrient cycling and storage through benthic habitats (Arnott and Vanni 1996, Dobson and Mackie 1998, Ackerman 1999, Covich *et al.* 1999, Strayer *et al.* 1999, Ackerman *et al.* 2001, Conroy *et al.* 2005) driving strong benthic-pelagic linkages (Schindler and Scheuerell 2002). While *D. bugensis* has been shown to remove and retain phosphorus from the water column more efficiently than does *D. polymorpha* (Conroy *et al.* 2005), internal loading and cycling of phosphorus will be intensified with greater densities of mussels of either species. Hecky *et al.* (2004) hypothesized that dreissenids are re-engineering the nearshore environment; the high densities of mussels in the profundal zone of eastern Lake Erie suggest these effects may not be limited just to the nearshore.

The biomass of *D. bugensis* increased substantially in the east basin of Lake Erie between 1992 and 2002, but it is not clear that this trend can be expected to continue. Obviously, there must be an upper limit set by the total energy inputs to Lake Erie, but in the shorter term, the absence of mussels in the 3–12 mm length class suggests that predation is limiting recruitment to the adult population at depths ≤ 20 m. Whether or not this intensity of predation will continue also remains to be seen but seems unlikely based on the observations reported by Barton *et al.* (2005).

The estimates of abundance of dreissenids reported here are summaries of the samples collected in 2002. If we weight and sum our estimates for each basin according to the relative area of depths and types of substratum available, almost 90% of the total mass of mussels in Lake Erie in 2002 occurred in the east basin (Ciborowski, Barton, and Krieger, unpublished data). This is inconsistent with conjectures that the recent increase in frequency and severity of hypoxia in the central basin (Charlton *et al.* 1999, Rockwell *et al.* 2005) is a direct consequence of the establishment of *Dreissena* species, because most of the mussels are presently downstream of the central basin. Therefore, if there are direct links among dreissenid activity, altered nutrient dynamics, and central basin hypoxia, either eastern basin quagga mussels are influencing central basin processes (gyres can theoretically circulate water from the eastern to the central basin (León *et al.* 2005), or there must be a substantial time lag between the (past) influence of dreissenids on particle and nutrient dynamics and biological oxygen demand in the hypolimnion of the central basin.

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