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Fourteen years of dreissenid presence in the rocky littoral zone of a large lake: effects on macroinvertebrate abundance and diversity

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Abstract. Establishment of dreissenid mussels in aquatic systems is often accompanied by major changes in the abundance, diversity, and community composition of benthic invertebrates. However, few studies have been published that address the effects of long-term dreissenid presence on the littoral benthos inhabiting hard substrata in lakes. We present the results of a depth-stratified, quantitative survey of littoral benthos conducted at 4 sites in 1993, just before dreissenid invasion, and in 2008, 14 y after the establishment of dreissenids in Lake Simcoe, Ontario. Average densities of nondreissenid invertebrates were 45× greater in 2008 than in 1993. Amphipods, isopods, chironomids and oligochaetes underwent the largest increases in absolute abundance. The taxonomic diversity of the benthic invertebrate community (α diversity) increased significantly. Community structure was more similar within and between depths and sites in 2008 than in 1993, a result implying lower β diversity of the postdreissenid littoral benthos. In addition, fewer differences were found in the densities of organisms between sampling locations in 2008 than in 1993. We suggest that dreissenids increase resource availability to benthic organisms and homogenize the littoral benthos by increasing the evenness of the distribution of food and physical-habitat resources across sites and depths. The transformation of the littoral benthic community of Lake Simcoe reflects a major change in the distribution of energy in the lake and is consistent with a dreissenid-mediated redirection of production from the pelagic to the littoral zone.

Key words: dreissenid mussels, benthic invertebrates, diversity, invasive species, Lake Simcoe.

Almost 25 y have passed since the dreissenid mussels *Dreissena polymorpha* and *Dreissena rostriformis bugensis* invaded North American freshwaters. Colonization of North American aquatic ecosystems by these species has been associated with significant changes to many aspects of the aquatic environment. One of the most ecologically significant effects attributed to dreissenids has been the redirection of primary and secondary production from the pelagic to the littoral zone, a process that has been called *benthification* (Mills et al. 2003), or the *nearshore shunt* (Hecky

et al. 2004). Benthic invertebrate communities have been particularly strongly affected by dreissenids, and most studies have shown increases in abundance and α diversity (taxonomic richness) of the littoral benthos (Stewart and Haynes 1994, Silver Botts et al. 1996, Ricciardi et al. 1997, Bially and MacIsaac 2000, Beekey et al. 2004a, Ward and Ricciardi 2007) and decreases in the abundance of nondreissenid profundal benthos (Lozano et al. 2001, Nalepa et al. 2003, Higgins and Vander Zanden 2010, Jimenez et al. 2011).

Two mechanisms are seen as responsible for the effects of dreissenids on littoral benthic communities. Dreissenid mussels increase the surface area and complexity of hard and soft substrates. These changes create additional habitat and provide refugia from fish

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predation on and between living mussels and in deposits of their empty shells (Silver Botts et al. 1996, Stewart et al. 1998, Beekey et al. 2004b). Dreissenids also increase the amount of food available to benthic consumers by depositing edible organic material in the form of feces and pseudofeces (Izvekova and Lvova-Katchanova 1972, Gergs and Rothhaupt 2008) and possibly by stimulating benthic primary producers though increases in water clarity and nutrient remineralization rates (Mayer et al. 2002, Hecky et al. 2004). Experimental studies have shown that increases in habitat complexity and food availability are both important, with the former probably playing a more important role (Ricciardi et al. 1997, Stewart et al. 1998).

The long-term effects of dreissenid establishment on the benthos of the Hudson River and of profundal areas of lakes have been studied (Lozano et al. 2001, Nalepa et al. 2007, Jimenez et al. 2011, Strayer et al. 2011), but few investigators have focused on the long-term effects of dreissenids on the benthos inhabiting littoral hard substrates, presumably because of the difficulty of sampling these habitats quantitatively (Downing 1984). Much of the information about dreissenid effects on hard-substrate-dwelling littoral benthos comes from short-term studies done with artificial substrates. We are aware of only 1 long-term, quantitative study of dreissenid effects on natural hard substrates, repeated 3 times at 2 adjacent sites in Lake Ontario (Stewart and Haynes 1994, Haynes et al. 1999, 2005). Moreover, most studies of effects of dreissenids in littoral zones have been done on a limited spatial scale (but see Ricciardi et al. 1997), so little is known about the way dreissenids affect the spatial distribution patterns of benthos in littoral zones and whether their effects are site and depth specific.

The objective of our study was to evaluate the effect of long-term dreissenid presence on the benthos of rocky littoral areas in a large, temperate lake. We conducted quantitative, depth-stratified sampling of the benthos at 4 sites in Lake Simcoe, Ontario, just prior to and 14 y after dreissenid establishment in the lake. We describe changes in the density, community composition, and diversity of the benthos and present evidence that long-term *Dreissena* presence has resulted in a more homogenous benthic community in terms of the abundance and community composition of macroinvertebrates across the littoral zone.

Methods

Study site

Lake Simcoe is a large (722 km²), oligomesotrophic lake in a predominantly agricultural (43% of watershed area) watershed in southern Ontario (Fig. 1).

Lake Simcoe has an extensive littoral zone, and ~45 to 55% of the lake bottom area of the main basin is in the euphotic zone (D. O. Evans, Ontario Ministry of Natural Resources, unpublished data). The littoral zone is dominated by hard substrates, such as cobble, pebble, and boulder, with areas of sand and softer sediments in sheltered and deeper areas. Dreissenid veligers were first observed in Lake Simcoe in 1992, but dreissenids were not observed in the benthos until the winter of 1994–1995 and did not become abundant on natural substrates until autumn 1995 (Evans et al. 2011). By 2008, dreissenids were abundant throughout the littoral zone of the lake and had attained a mean biomass of 27.2 g shell-free dry mass/m² in the main basin of the lake, with >80% of the biomass concentrated in the littoral zone (Ozersky et al. 2011).

Four sites were sampled in this study: Sibbald and Blackbird Points in the south-central part of the lake, and Grape and Strawberry Islands in the north (Fig. 1). Substrata at all sites consisted of mixtures of cobble, pebble, and boulder with some patches of sand at 6-m depths in 1993. In 2008, these substrata were covered with living dreissenid mussels, and spaces between rocks were largely filled with empty mussel shells and soft, fine-grained material.

Sampling design

Study sites were sampled at 3 depths (2, 4, and 6 m) between 25 August and 16 September 1993 and on 20–21 September 2008 with airlifts (Barton and Hynes 1978) operated by divers. Airlifts were equipped with 500- μ m Nitex[®] collection bags in 1993 and 375- μ m Nitex[®] collection bags in 2008. The airlifts were supplied with compressed air from the surface in 1993 and from a standard SCUBA tank in 2008. In both years divers systematically vacuumed the substrate within randomly placed sampling quadrats while removing and cleaning rocks by hand or with a scraper to a depth of 20 cm or until the underlying hard substrate was reached. Three or 4 quadrats (0.25 m² in 1993, 0.0625 m² in 2008) were sampled at each depth at each site in both years. Smaller quadrats were used in 2008 because the large amount of mussel-shell material collected would have made preserving, storing, and processing samples from larger quadrats impracticable.

Benthic samples were preserved in the field with 10% buffered formalin. Samples collected in 1993 were stored in formalin until 2008 when they were transferred to ethanol prior to sorting. Samples collected in 2008 were transferred to ethanol within 2 to 4 d of return to the laboratory. Samples were elutriated by repeated washing and decanting to

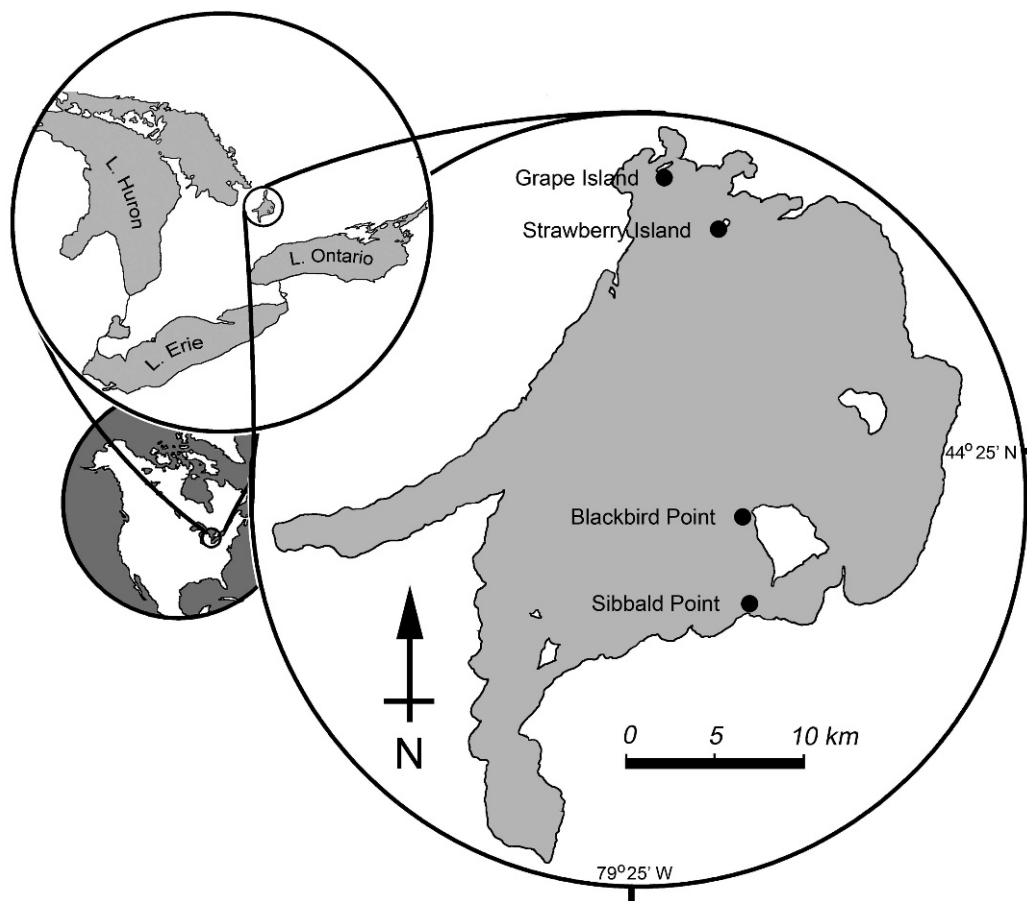


FIG. 1. Map of Lake Simcoe in relation to the Laurentian Great Lakes. Sampling sites are marked with filled circles.

separate lighter organic material from the heavier sand and mussel shells. Macroinvertebrates were sorted from the light and heavy fractions obtained by elutriation with the aid of a dissecting microscope. Some of the 2008 samples were subsampled by spreading the elutriated material evenly on a round dish, subdividing it into 8 even slices and randomly selecting 2 opposite slices to make up a $\frac{1}{4}$ subsample. Benthic invertebrates in 1 replicate from each depth/site combination were identified to the lowest practical level (Appendix 1; available online from: <http://dx.doi.org/10.1899/10-122.1.s1>) and enumerated to assess differences in α diversity (taxonomic richness) between years. Because of financial and time constraints, invertebrates in the remaining replicates were identified to a level between order and species (Table 1, Appendix 2; available online from: <http://dx.doi.org/10.1899/10-122.1.s2>). Although crayfish were frequently collected in 1993 and 2008, they are not included in the results of this study because the smaller quadrat size and subsampling protocol used in 2008 would have made comparisons between 1993 and 2008 difficult for such relatively large and mobile

animals. Oribatid mites were also excluded because the mesh used in 1993 was too coarse to retain them.

Statistical analyses

Mann–Whitney U tests were used to examine changes in the total abundance of macroinvertebrates between 1993 and 2008 across all sites and depths and to compare total and relative abundances of different taxonomic groups across all sites and depths between 1993 and 2008. Only taxa comprising $\geq 3\%$ of any sample were included in these comparisons. Non-parametric Mann–Whitney U tests were used instead of t -tests because data could not be transformed to approximate normal distributions. Changes in taxonomic richness (α diversity) between the 2 years were assessed with an unpaired 2-sample t -test on number of taxa/sample in samples sorted to the lowest practical level. Two-way analyses of variance (ANOVAs) followed by Tukey's post hoc tests were used to examine differences in nondreissenid macroinvertebrate abundance among sites and depths in 1993 and in 2008. Invertebrate abundances from 1993

TABLE 1. Mean (SE) total density and % composition (excluding *Dreissena* spp.) of benthic invertebrates in 1993 and 2008 across all sampling sites ($n = 4$) and depths ($n = 3$). Asterisks represent a significant difference between 1993 and 2008 (Mann–Whitney U tests) and appear beside the significantly larger value. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Taxon	Density (no./m ²)		Relative abundance (%)	
	1993	2008	1993	2008
Amphipoda				
<i>Hyalella azteca</i>	40.3 (12.6)	2740.6 (451.1)***	8.2 (1.3)	16.7 (2)**
<i>Gammarus</i> sp.	5.3 (1.5)	1902.2 (320.6)***	1.1 (0.3)	10.9 (1.1)***
<i>Echinogammarus ischnus</i>	0 (0)	1092.6 (296.9)***	0 (0)	5.1 (1.4)***
<i>Crangonyx</i> sp.	13.8 (4.5)	630.4 (147.8)***	3.9 (0.9)	3.2 (0.5)
Isopoda				
<i>Caecidotea racovitzai</i>	0.2 (0.1)	1614.2 (236.4)***	0.2 (0.2)	10.9 (1.3)***
Gastropoda				
Hydrobiidae	14.4 (3)	254.9 (48.3)***	9.6 (2.4)	1.5 (0.3)
Physidae	7.6 (1.6)	50.5 (10.1)*	2.4 (0.5)**	0.3 (0.1)
Planorbidae	0.1 (0.1)	134.8 (63.7)***	0.1 (0.1)	0.7 (0.3)**
Pleuroceridae	7.6 (2.5)***	0 (0)	2.5 (0.8)***	0 (0)
Ancylidae	0.4 (0.2)	485.7 (101.4)***	0.5 (0.3)	3.4 (0.7)***
Bivalvia				
Sphaeriidae	32.6 (4.6)	91 (18)	13.9 (1.6)***	0.5 (0.1)
<i>Dreissena polymorpha</i>	0 (0)	3322.5 (347.6)***	– (–)	– (–)
<i>D. rostriformis bugensis</i>	0 (0)	100.1 (16.5)***	– (–)	– (–)
Unionidae	0.3 (0.2)	0 (0)	0.5 (0.4)	0 (0)
Insecta				
Chironomidae	106 (28.9)	3338.3 (485.2)***	21.1 (2.6)	20.4 (2.5)
Polycentropodidae	6.7 (1.6)	261 (52.4)***	1.4 (0.3)	2.3 (0.5)
Helicopsychidae	0 (0)	85 (53.3)***	0 (0)	0.3 (0.1)***
Leptoceridae	2 (0.5)	58 (23.2)	1 (0.4)	0.3 (0.1)
Hydroptilidae	0.3 (0.2)	21 (8.2)*	0.2 (0.2)	0.1 (0)
Hydropsychidae	0.6 (0.4)	0.7 (0.5)	0.1 (0.1)	0 (0)
Caenidae	1.6 (0.6)	18.8 (6.6)	0.2 (0.1)	0.1 (0)
Heptageniidae	35.5 (8.8)	55.8 (17.2)	8.5 (1.4)***	0.3 (0.1)
Ephemeroidea	0.7 (0.3)	21.7 (8.1)*	0.2 (0.1)	0.2 (0.1)
Sialidae	0.1 (0.1)	12.4 (3.8)***	0.2 (0.2)**	0.1 (0)
Elmidae	14.5 (4.9)	92.8 (45.1)	3.7 (1.3)	0.6 (0.3)
Psephenidae	0.9 (0.4)*	0 (0)	0.4 (0.2)*	0 (0)
Acari				
Hydracarina	26.4 (14.1)	324.1 (73.1)***	6.6 (1.3)**	1.8 (0.3)
Worms				
Planariidae	0.8 (0.3)	404.3 (85.4)***	0.3 (0.2)	2.3 (0.4)***
Oligochaeta	43.7 (10.7)	2540.8 (309.3)***	11.2 (1.9)	15.4 (1.3)**
Hirudinea	1.5 (0.5)	49.4 (14.6)***	1.4 (1)*	0.3 (0.1)
Nematoda	3 (1.8)	312.2 (75.4)***	0.2 (0.1)	1.8 (0.4)***
Other	1 (0.3)	99.2 (45.5)***	0.2 (0.1)	0.5 (0.2)**
Total	367.7 (71.1)	20115.1 (1713.6)***	100 (0)	100 (0)

were $\log_{10}(x)$ -transformed to meet assumptions of normality, and equal variance and \sqrt{x} -transformation was applied to 2008 densities to meet assumptions of normality. The 2008 data could not be transformed to meet the assumption of equality of variance, but ANOVA was used because it is relatively robust against violation of this assumption, especially when the number of replicates in different treatments is equal or nearly equal (Glass et al. 1972). The use of 2 different transformations for the 1993 and 2008 data

should not present a problem in interpreting the results of ANOVA tests because the results of the statistical tests were compared and not the data themselves. The experimental unit for all statistical tests was macroinvertebrate density from individual replicates.

Changes in community composition of nondreissenid macroinvertebrates were analysed with multivariate methods. The experimental unit for all multivariate tests was macroinvertebrate density from individual

TABLE 2. Results of 2-way analysis of variance to determine the effects of sampling site and depth on the abundance of nondreissenid benthic invertebrates in the littoral zone of Lake Simcoe in 1993, prior to dreissenid invasion, and in 2008, 14 y after dreissenid establishment.

Source	df	F	p
1993			
Site	3	21.34	<0.00001
Depth	2	24.45	<0.00001
Site × depth	6	1.23	0.315
2008			
Site	3	6.62	0.0013
Depth	2	11.57	0.0002
Site × depth	6	3.49	0.0088

replicates. One-way analysis of similarity (ANOSIM) on Bray–Curtis dissimilarities of \sqrt{x} -transformed invertebrate abundances was used to test for differences in community composition between 1993 and 2008, and 2-way ANOSIM was used to test for differences in community composition among sites and depths in 1993 and in 2008. Similarity of percentages (SIMPER) procedure was used to determine the average dissimilarity among and within sites and depths and to identify the taxa contributing most to the dissimilarity (Clarke and Warwick 2001). Average Bray–Curtis dissimilarities determined with SIMPER were used to assess differences in β diversity among and within sites and depths in 1993 and 2008 (e.g., Anderson et al. 2011). Univariate and multivariate analyses were done with SigmaPlot 11 (Systat Software, Chicago, Illinois) and Primer v.6 (PRIMER-E, Plymouth, UK), respectively.

Results

Nondreissenid taxon richness and density

Sixty-one taxa were identified in the 1993 samples sorted to the lowest practical level (Appendix 1), with an average of 17.0 ± 2.1 (SE) taxa/sample. Eighty-five taxa were identified in the 2008 samples sorted to the lowest practical level (Appendix 1), with an average of 31.2 ± 1.9 taxa/sample. Nondreissenid taxon richness differed significantly between 1993 and 2008 (2-sample independent *t*-test, $t_{23} = -5.05$, $p = 0.00004$).

The mean density of nondreissenid benthic macroinvertebrates was significantly lower in 1993 ($367.7 \pm 71.1/\text{m}^2$ [SE]) than in 2008 ($16692.5 \pm 1569.8/\text{m}^2$ (Mann–Whitney *U* test, $T_{42,45} = 903.0$, $p < 0.00001$). Macroinvertebrate densities differed significantly among sites and depths in 1993, and the depth × site interaction was not significant, indicating a consistent pattern of density with depth among sites (Table 2,

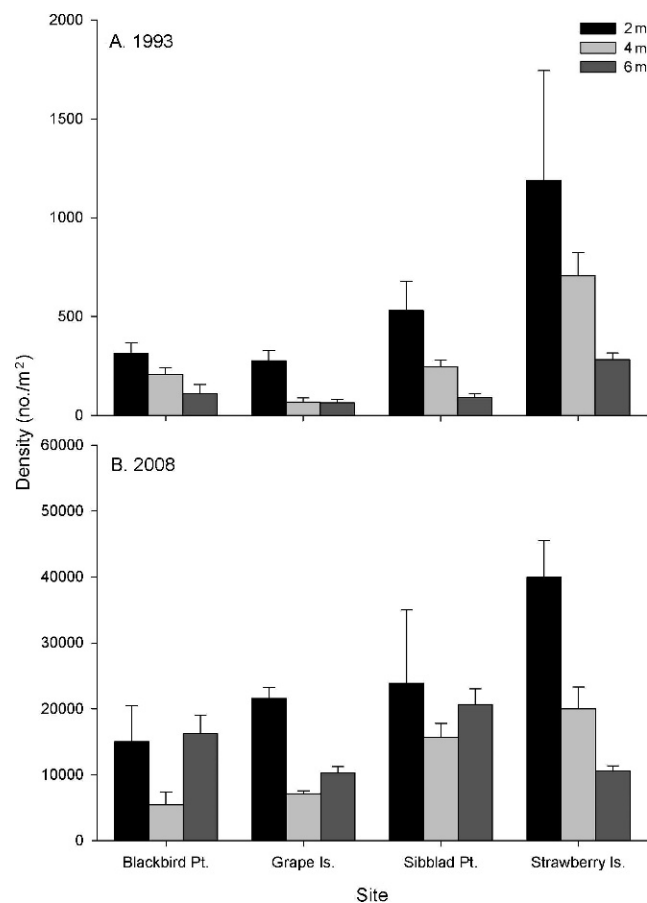


FIG. 2. Mean (± 1 SE) density of benthic macroinvertebrates at 2, 4, and 6 m in 1993 (A) and 2008 (B) at 4 sampling sites. Note different scales of the y-axes. Pt. = Point, Is. = Island.

Fig. 2A). Post hoc tests (Table 3) revealed that macroinvertebrate densities at 6-m depths were significantly lower than densities at 2-m depths at all 4 sites. Macroinvertebrate densities in 2008 varied significantly among depths and sites, and the depth × site interaction was significant (Table 2). The interaction appeared to be a function of the atypical depth distribution of benthos at Strawberry Island (Fig. 2B). The depth × site interaction was not significant when Strawberry Island data were excluded from analysis. Densities at 6-m depths were similar to those at 2-m depths at all sites except Strawberry Island (Tukey's tests; Table 3). Fewer significant differences in macroinvertebrate density were found between sites within depths in 2008 than in 1993, a result suggesting a more even distribution of invertebrate density at different sites in 2008.

Nondreissenid community composition

The benthic macroinvertebrate community across all sites and depths in 1993 was dominated by

TABLE 3. *p*-values from Tukey's pairwise post hoc comparisons of nondreissenid macroinvertebrate abundance in 1993 and 2008. Upper portion of table shows results of comparisons between depths within sites. Lower portion shows results of comparisons between sites within depths. Blk = Blackbird Point, Grp = Grape Island, Sib = Sibbald Point, Str = Strawberry Island. Bold indicates statistically significant values.

Comparison of:	Within	1993				2008			
		Blk	Grp	Sib	Str	Blk	Grp	Sib	Str
Depths	Sites								
2 vs 4 m		0.5756	0.0021	0.1477	0.7553	0.0578	0.0073	0.5724	0.0199
2 vs 6 m		0.0492	0.0006	0.0004	0.0165	0.8601	0.0889	0.9928	0.0003
4 vs 6 m		0.3053	0.9807	0.0341	0.0738	0.0172	0.6877	0.5992	0.1458
Sites	Depths	2 m	4 m	6 m	2 m	4 m	6 m		
Str vs Grp		0.0116	0.0002	0.0017	0.0745	0.0318	0.9999		
Str vs Blk		0.0279	0.0206	0.0364	0.0019	0.0049	0.6333		
Str vs Sib		0.3388	0.0318	0.1508	0.0937	0.8506	0.1752		
Sib vs Grp		0.3758	0.0078	0.5597	0.9999	0.1759	0.2049		
Sib vs Blk		0.5887	0.9781	0.9820	0.4876	0.0367	0.8047		
Blk vs Grp		0.9833	0.0334	0.7237	0.3857	0.8778	0.6456		

Chironomidae (21.1%), Sphaeriidae (13.9%), Oligochaeta (11.2%), Hydrobiidae (9.6%), Heptageniidae (8.5%), and the amphipod *Hyalella azteca* (8.2%). The nondreissenid benthic macroinvertebrate community across all sites and depths in 2008 was dominated by Chironomidae (20.4%), *H. azteca* (16.7%), Oligochaeta (15.4%), *Gammarus* spp. (10.9%), and *Caecidotea racovitzai* (10.9%); the recently introduced Ponto-Caspian amphipod *Echinogammarus ischnus* was relatively abundant (5.1%), especially at shallower sampling locations (Table 1, Appendix 2).

Densities of most taxonomic groups of invertebrates were significantly greater in 2008 than in 1993 (Mann-Whitney *U* test, $\alpha = 0.05$) (Table 1), and the relative abundance of many taxa changed significantly (Mann-Whitney *U* test, $\alpha = 0.05$) (Table 1). The amphipods *H. azteca*, and *Gammarus* spp., the isopod *C. racovitzai*, planorbid snails, Ancylidae, Helicopsychidae, and most worms (Planariidae, Oligochaeta, and Nematoda) increased in relative abundance from 1993 to 2008. In contrast, Physidae, Sphaeriidae, Heptageniidae, Sialidae, Hirudinea, and Hydracarina were relatively less abundant in 2008 than in 1993, and pleurocerid snails and unionid mussels disappeared completely from our samples. Community structure differed significantly between 1993 and 2008 as shown by 1-way ANOSIM on total nondreissenid macroinvertebrate densities across all sites and depths (global $R = 0.92$, $p = 0.001$).

Community composition differed significantly among sites (global $R = 0.722$, $p = 0.001$) and depths (global $R = 0.517$, $p = 0.001$) in 1993 (2-way ANOSIM). The most dissimilar depths were 2 and 6 m, and the most dissimilar sites were Grape Island and Strawberry Island (Table 4). Variations in the abundances of chironomids and oligochaetes contrib-

uted most to the dissimilarity in community composition between sites and depths in 1993 (Appendix 2).

Community composition differed significantly among sites (global $R = 0.79$, $p = 0.001$) and depths (global $R = 0.79$, $p = 0.001$) in 2008 (2-way ANOSIM), but dissimilarities between and within depths and sites were smaller than in 1993 for most comparisons (Table 4). The most dissimilar depths were 2 and 6 m, and the most dissimilar sites were Sibbald Point and Strawberry Island. Variations in the abundances of amphipods and chironomids contributed most to the

TABLE 4. Mean Bray-Curtis % dissimilarity of benthic invertebrate communities within sites and depths and between pairs of depths and sites (SIMPER) for the 1993 benthic community, and the 2008 nondreissenid community. Blk = Blackbird Point, Grp = Grape Island, Sib = Sibbald Point, Str = Strawberry Island.

Comparison	Category	% dissimilarity	
		1993	2008
Within	2 m	33.3	27.5
	4 m	36.5	28.6
	6 m	45.1	19.8
	Blk	35.2	28.5
	Grp	45.8	21.9
	Sib	32.7	28.1
	Str	32.6	22.2
Between	2 vs 4 m	44.7	38.4
	2 vs 6 m	56.1	48.7
	4 vs 6 m	48.3	42.6
	Blk vs Grp	57.3	43.7
	Blk vs Sib	47.6	49.4
	Blk vs Str	54.0	43.9
	Grp vs Sib	57.6	43.9
	Grp vs Str	64.1	44.5
	Sib vs Str	46.6	48.1

dissimilarity between sites and depths in 2008 (Appendix 2).

Dreissena spp.

Dreissena polymorpha made up 19.1% of total macroinvertebrate abundance in 2008, whereas *D. rostriformis bugensis* was less abundant, comprising only 0.6% of the total. Mean densities of *Dreissena* spp. were 2909.3 ± 288.2 (SE), 2888.0 ± 607.6 , 3994.2 ± 1005.5 , and 3945.5 ± 828.4 at Blackbird Point, Grape Island, Sibbald Point, and Strawberry Island, respectively, and 3367.4 ± 688.1 , 3113.0 ± 430.0 , and 3804.3 ± 745.5 at 2-, 4- and 6-m depths, respectively.

Discussion

Our most striking observation was the 45× increased abundance of nondreissenid littoral benthos 14 y after establishment of zebra mussels in Lake Simcoe. This change is considerably larger than that reported in many studies of shorter-term effects of dreissenids on hard-substrate littoral benthos, where increases of up to an order of magnitude are common (Dermott et al. 1993, Stewart and Haynes 1994, Ricciardi et al. 1997, Stewart et al. 1998, Mörtl and Rothhaupt 2003). Our observations also differ from those presented in the only set of studies of the effects of long-term dreissenid presence on hard-substrate littoral benthos. At 2 sites in southwestern Lake Ontario, the densities of nondreissenid invertebrates increased during the first 2 y following dreissenid establishment but then declined to predreissenid densities and remained low 9 y later (Stewart and Haynes 1994, Haynes et al. 1999, 2005). Haynes et al. (2005) attributed this decline to reductions in dreissenid densities and consequent declines in the ability of dreissenids to structure the benthos. We believe that the continued high density of nondreissenid benthos in Lake Simcoe can be ascribed to higher densities of dreissenids than in Lake Ontario and, perhaps more importantly, to the smaller size of Lake Simcoe. The smaller fetch in Lake Simcoe results in lower intensity of disturbance by surface waves than in Lake Ontario. Large quantities of dreissenid shells accumulate in the littoral zone of Lake Simcoe (average ~ 8 L/m²; D. O. Evans, unpublished data), which may not be the case in larger, more hydrodynamically active Lake Ontario. Dreissenid shells provide ideal habitat for benthic invertebrates (e.g., Silver Botts et al. 1996), and the accumulation of this material in the littoral zone of Lake Simcoe, but not in Lake Ontario, may be responsible for the high long-term densities of littoral invertebrates reported in our study.

Qualitative changes to the littoral benthos of Lake Simcoe following establishment of *Dreissena* are similar to those reported in shorter-term studies of dreissenid effects (Dermott et al. 1993, Griffiths 1993, Stewart and Haynes 1994, Ricciardi et al. 1997, Stewart et al. 1998, Mörtl and Rothhaupt 2003, Beekey et al. 2004a). Specifically, the relative abundances of amphipods, isopods, oligochaetes, and some snails increased, whereas native filter-feeding sphaeriid clams declined, and unionid mussels disappeared completely. The qualitative effects of dreissenids on benthos appear to be consistent across systems (Ward and Ricciardi 2007), and our results illustrate that the shorter-term effects of dreissenids on the community composition of littoral benthos can persist through time.

The effects of dreissenids on the diversity of benthic macroinvertebrates in the littoral zone of Lake Simcoe varied with the spatial scale of study. Dreissenids increased the α diversity, or local taxonomic richness (Legendre et al. 2005), of the benthic community (significantly more taxa/sample in 2008 than in 1993). Moreover, sampling-unit area and species richness are positively related, so our decision to use a smaller quadrat in 2008 probably led us to underestimate the positive effect of dreissenids on small-scale α diversity. Whereas α diversity is a measure of the taxonomic richness within a defined area, β diversity is a measure of variation in community composition and reflects the degree of dissimilarity of biotic communities among habitats or along an environmental gradient (Legendre et al. 2005). The most appropriate measure of β diversity is currently under debate (Anderson et al. 2011), but mean Bray–Curtis dissimilarities have been used in the past to examine spatial differences in β diversity (Ellingsen 2001, Hewitt et al. 2005, Anderson et al. 2011). Dreissenid establishment seems to have decreased β diversity of the benthic invertebrate community within and among sites and depths in Lake Simcoe as shown by lower mean Bray–Curtis dissimilarities in 2008 than in 1993. Moreover, invertebrate densities were more similar among depths and sites in 2008 than in 1993.

The increased habitat complexity and physical structure generated by mussels and their shells is thought to increase small-scale habitat heterogeneity, leading to greater local-scale α diversity (Stewart and Haynes 1994, Gutiérrez et al. 2003). We hypothesize that dreissenid establishment decreases β diversity and increases similarity in macroinvertebrate densities throughout the littoral zone by increasing the evenness of resource distribution. In 1993, much of the dissimilarity among communities in shallow and deep portions of the littoral zone was caused by lower densities and species richness of macroinvertebrates

at 6-m sites than at 2- and 4-m sites. Increases in water clarity caused by dreissenids probably resulted in greater benthic primary production in deeper portions of the littoral zone, leading to higher abundances of organisms at our deeper sampling locations (Mayer et al. 2002). Biodeposition of large quantities of edible organic material in the form of feces and pseudofeces (Izvekova and Lvova-Katchanova 1972, Gergs and Rothhaupt 2008, Gergs et al. 2011) throughout the littoral zone also should decrease differences in food availability among depths and sites and should contribute to increased evenness of resource distribution in the littoral zone. Higher densities and α diversity at deeper sites in 2008 than in 1993 are consistent with the hypothesis of increased food availability at deeper sites.

Dreissenid effects on physical habitat structure also might cause reduced β diversity and more homogeneous distribution of benthic invertebrates in the littoral zone. By creating similar types of habitat throughout the lake, dreissenids could moderate the effects on the benthic macroinvertebrate community of environmental factors that may vary within and among sites, such as substrate composition, predation pressure by fish, and exposure to disturbance by waves. Our findings regarding lower β diversity following dreissenid establishment are comparable to those of Pacciardi et al. (2011), who studied the effects of another invasive ecosystem engineer, the marine algae *Caulerpa racemosa*. Pacciardi et al. (2011) found increased α diversity and decreased β diversity of marine benthos in the presence of *C. racemosa*, which they attributed to changes in patterns of resource distribution.

We have attributed the changes that occurred in the benthic community from 1993 to 2008 to the establishment of dreissenids and their effects on physical habitat structure and energy transfer from the pelagic to the littoral zone of the lake. However, other ecological factors that changed between 1993 and 2008 could have affected the littoral benthos of Lake Simcoe. P loading decreased by $\sim 30\%$ from the early 1990s to the late 2000s (Scott et al. 2001, Winter et al. 2007, Young et al. 2010, 2011). During the same period open-lake TP decreased slightly and total N concentrations were essentially unchanged (Young et al. 2010, 2011). Declines in P loadings have the potential to affect benthic consumers through changes in the proportions of planktonic and benthic primary producers in the littoral zone (Blumenshine et al. 1997), but the relatively modest decrease in the nutrient status of the lake is unlikely to account for the magnitude and direction of the changes in the density and community composition of littoral benthos observed in our study. The possible influences of other factors, including

climate change, and food web effects of invasive cladocerans, such *Bythotrephes longimanus*, on resource availability in the littoral zone have yet to be resolved, but are unlikely to explain our results.

Differences in sampling methods between 1993 and 2008 could have affected our results. The finer mesh size used in 2008 could have retained smaller organisms and led to higher perceived abundances and diversity in 2008. This effect is unlikely because most of the organisms captured in 2008 were large enough to have been retained by the 500- μm mesh used in 1993. Slightly different airlift designs were used in 1993 and 2008, but the presence of large pebbles in samples from both years suggests that both designs were similarly powerful and efficient. A smaller quadrat was used in 2008 than in 1993. However, both quadrats were very large compared to the sizes of organisms sampled, so any differences in abundance caused by quadrat size differences should have been small. Differences in diversity caused by smaller quadrat size would, if anything, make our conclusions regarding changes in diversity conservative. We believe that any effect of methodological differences on our results would be minor relative to the magnitude of the observed changes in the benthic community.

To conclude, we found that long-term dreissenid presence in Lake Simcoe has greatly modified the littoral benthos of the lake. Density and α diversity of littoral-zone macroinvertebrates have increased dramatically since the establishment of dreissenids. The more even distribution of individuals and lower β diversity across sites and depths in 2008 than in 1993 suggest that dreissenids have increased the evenness of resource distribution in the littoral zone. Results of our study and recent studies of the phytoplankton, benthic primary producers, and profundal benthos of Lake Simcoe (Eimers et al. 2005, Depew et al. 2011, Jimenez et al. 2011) are consistent with the idea that dreissenids redirect biological production toward the littoral zones of lakes (Mills et al. 2003, Hecky et al. 2004, Higgins and Vander Zanden 2010) and reflect an important redistribution of energy and nutrients in Lake Simcoe.

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ERRATUM

Materials on pages 916 (Table 1), 917 (Table 2, Fig. 2A), 918 (Tables 3, 4), and text on pages 917–919 (**Results: *Nondreissenid* taxon richness and density, *Nondreissenid* community composition**) of the article by Ozersky et al. in the December 2011 issue (J-NABS 30:913–922) should be replaced by the materials below the next paragraph. The material in the **Discussion** presented below should be considered in conjunction with the **Discussion** in the original publication (pp. 919–920).

Correction to Ozersky et al. 2011

We reported on changes to the littoral benthos of a large lake following establishment of invasive dreissenid mussels. We relied on predreissenid benthos samples collected in 1993, just prior to dreissenid establishment, and postdreissenid samples collected at the same sites in 2008, 14 y after dreissenid establishment. Samples from 1993 and 2008 were counted in 2008 at the taxonomic level of family or species for most groups. Recently, we discovered that the 1993 samples were counted to the taxonomic level of order shortly after collection, and the benthos returned to the original sampling jars along with the substrate. Comparison of the original counts of the 1993 samples with counts done in 2008 revealed discrepancies, with total abundance in original counts being on average 46% higher than in counts performed in 2008. We attribute the discrepancy to sample loss caused by the original handling and long storage times. To account for the issue of sample loss, we reanalyzed our data set using the original counts of the 1993 samples at the coarser (order level) taxonomic level of the original counts. Nematodes were not included in the original counting of 1993 samples, so they are excluded from the reanalysis. Below we present corrected versions of Tables 1–4 and of Fig. 2A, summarize the results of the reanalysis, and briefly discuss how the reanalysis affects the interpretation of our study.

TABLE 1. Mean (SE) total density and % composition (excluding *Dreissena* spp.) of benthic invertebrates in 1993 and 2008 across all sampling sites ($n = 4$) and depths ($n = 3$). Asterisks represent a significant difference between 1993 and 2008 (Mann–Whitney U tests) and appear beside the significantly larger value. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Taxon	Density (no./m ²)		Relative abundance (%)	
	1993	2008	1993	2008
Crustacea				
Amphipoda	80.7 (15.3)	6365.9 (936.5)***	13.1 (1.4)	36.6 (2.9)***
Isopoda	0.2 (0.1)	1614.2 (236.4)***	0.2 (0.2)	11.1 (1.4)***
Mollusca				
Gastropoda	58.8 (12.8)	929.1 (122.1)***	17.0 (3.1)*	6.1 (0.7)
Nondreissenid bivalves	43.3 (6.2)	91.0 (18.0)	11.7 (1.5)***	0.5 (0.1)
Dreissenidae	–	3422.6 (356.2)	–	–
Insecta				
Chironomidae	149.2 (43.6)	3338.3 (485.2)***	18.9 (2.1)	20.8 (2.6)
Trichoptera	14.1 (2.52)	433.8 (78.6)***	2.9 (0.4)	3.1 (0.5)
Ephemeroptera	60.7 (13.2)	98.1 (18.1)	10.4 (1.6)***	0.6 (0.1)
Coleoptera	17.7 (6.3)	93.2 (45.0)	3.4 (1.1)	0.6 (0.3)
Acari				
Hydracarina	57.5 (26.4)	324.1 (73.1)**	9.6 (1.5)***	1.8 (0.3)
Worms				
Planariidae	1.1 (0.6)	404.3 (85.4)***	0.3 (0.1)	2.4 (0.4)***
Oligochaeta	68.0 (18.1)	2540.8 (309.3)***	11.3 (1.9)	15.8 (1.4)**
Hirudinea	1.9 (0.5)	49.4 (14.6)***	1.2 (0.8)	0.3 (0.1)
Polychaeta	0.5 (0.3)	62.2 (44.4)	0.1 (0.0)	0.3 (0.2)
Other	1.9 (0.6)	23.5 (5.1)**	0.1 (0.2)	0.2 (0.0)
Total	533.9 (109.1)	19,770.9 (1666.4)***	100 (0)	100 (0)

TABLE 2. Results of 2-way analysis of variance to determine the effects of sampling site and depth on the abundance of nondreissenid benthic invertebrates in the littoral zone of Lake Simcoe in 1993, prior to dreissenid invasion, and in 2008, 14 y after dreissenid establishment.

Source	df	F	p
1993			
Site	3	24.40	<0.001
Depth	2	19.03	<0.001
Site × depth	6	3.45	0.009
2008			
Site	3	6.71	0.001
Depth	2	11.12	<0.001
Site × depth	6	3.38	0.01

Results

Nondreissenid benthos density

Reanalysis of the data showed that density of nondreissenid invertebrates increased significantly (Mann–Whitney U test, $T_{45,45} = 1037.0$, $p = <0.00001$) from 1993 ($533.9 \pm 109.1/\text{m}^2$ [SE]) to 2008 ($16,348.3 \pm 1521.0/\text{m}^2$). This result is congruent with our initial analysis, but the magnitude of the increase is smaller than we initially reported ($30\times$ vs $45\times$). Densities of invertebrates differed significantly among sites and depths in 1993, with a significant site \times depth interaction, indicating an inconsistent pattern of density with depth among sites (Table 2). This result is similar to that of our initial analysis, except that the interaction was previously not significant. Results of post hoc Tukey's tests (Table 3) differ from the initial analysis in that densities are no longer consistently lower at 6-m depths at all sites than at shallower depths. As in our initial analysis, more significant differences in average invertebrate density were found among sites within depths, confirming a more even distribution of invertebrate density at different sites in 2008 than in 1993 (Table 3).

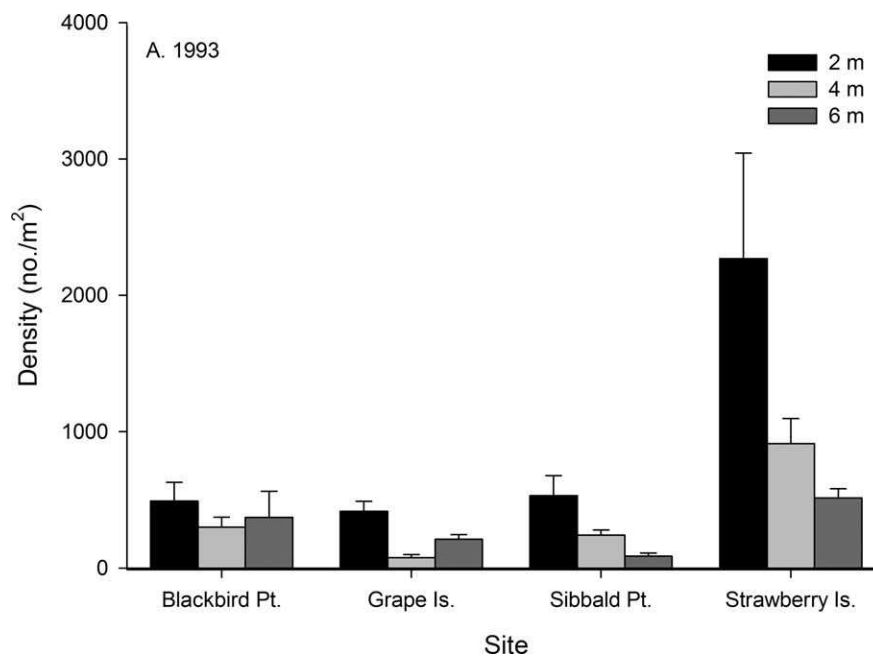


FIG. 2A. Mean (± 1 SE) density of benthic macroinvertebrates at 2, 4, and 6 m in 1993 at 4 sampling sites. Pt. = Point, Is. = Island.

TABLE 3. *p*-values from Tukey's pairwise post hoc comparisons of nondreissenid macroinvertebrate abundance in 1993 and 2008. Upper portion of table shows results of comparisons between depths within sites. Lower portion shows results of comparisons between sites within depths. Blk = Blackbird Point, Grp = Grape Island, Sib = Sibbald Point, Str = Strawberry Island. Statistically significant values are shown in bold font.

Comparison of:		1993				2008			
Depths	Sites	Blk	Grp	Sib	Str	Blk	Grp	Sib	Str
2 vs 4 m		0.5412	0.0002	0.1601	0.0802	0.0566	0.0062	0.6398	0.0280
2 vs 6 m		0.3824	0.1808	0.0004	0.0025	0.9162	0.0799	0.9995	0.0003
4 vs 6 m		0.9640	0.0142	0.0343	0.3390	0.0227	0.6830	0.5735	0.1429
Sites	Depths	2 m	4 m	6 m	2 m	4 m	6 m		
Str vs Grp		0.0010	0.0002	0.0017	0.0947	0.0318	0.9999		
Str vs Blk		0.0018	0.0483	0.0364	0.0025	0.0049	0.6333		
Str vs Sib		0.0031	0.0079	0.1508	0.0947	0.8506	0.1752		
Sib vs Grp		0.9670	0.0097	0.5597	0.9984	0.1759	0.2049		
Sib vs Blk		0.9969	0.9618	0.9820	0.5583	0.0367	0.8047		
Blk vs Grp		0.9941	0.0053	0.7237	0.3909	0.8778	0.6456		

Nondreissenid community composition

Results comparing benthic community composition in 1993 and 2008 at the coarser taxonomic level of the original counts generally agree with results of our initial analysis. The absolute densities of most taxonomic groups increased significantly from the pre- to the postdreissenid period (Table 1), as indicated by Mann-Whitney *U* tests. The relative abundances of snails, nondreissenid bivalves, mayflies, and water mites decreased significantly in the postdreissenid benthos, whereas those of amphipods, isopods, oligochaetes, and flatworms increased. The results of a 1-way ANOSIM test on community composition in 1993 and 2008 showed significant differences between the 2 communities (global $R = 0.934$, $p = 0.001$). Two-way ANOSIM tests on the 1993 benthic community show significant community composition differences between depths (global $R = 0.525$, $p = 0.001$) and sites (global $R = 0.699$, $p = 0.001$). The results of the 1- and 2-way ANOSIM tests are similar to those in the initial analysis. Mean Bray-Curtis % dissimilarity of benthic community composition within and between sites and depths were greater in 1993 than in 2008 (Table 4), which is consistent with initial analysis, although the dissimilarity decreased overall, probably a consequence of using coarser-level taxonomic resolution in the analysis.

TABLE 4. Mean Bray-Curtis % dissimilarity of benthic invertebrate communities within sites and depths and between pairs of depths and sites (SIMPER) for the 1993 benthic community, and the 2008 nondreissenid community. Blk = Blackbird Point, Grp = Grape Island, Sib = Sibbald Point, Str = Strawberry Island.

Comparison	Category	% dissimilarity	
		1993	2008
Within	2 m	22.0	21.0
	4 m	27.0	19.0
	6 m	23.3	13.5
	Blk	27.2	23.7
	Grp	29.4	12.4
	Sib	21.36	20.5
	Str	18.7	13.1
	Between	2 vs 4 m	35.0
	2 vs 6 m	39.3	32.5
	4 vs 6 m	31.9	26.8
	Blk vs Grp	36.9	29.7
	Blk vs Sib	31.8	31.8
	Blk vs Str	40.7	31.7
	Grp vs Sib	36.4	29.4
	Grp vs Str	51.2	28.7
	Sib vs Str	40.1	28.5

Discussion

Reanalysis of our data set using original counts of the predreissenid samples and a lower taxonomic resolution did not change the overall findings of our study. Long-term dreissenid presence was still associated with a large increase in the abundance of nondreissenid littoral benthos. Reanalysis revealed that the increase was not as large as initially reported, but it is still the largest postdreissenid increase in the abundance of benthos described in the literature. Our conclusions about the qualitative effects of dreissenid establishment on the benthic community are consistent with those reported initially, and with those of other studies, showing increases in relative abundance of amphipods, isopods, and oligochaetes, and decreases in relative abundance of nondreissenid bivalves. Our original conclusion of increased α diversity in the postdreissenid benthos is brought into question in light of the reanalysis. Conclusions about the decreased β diversity and increased overall homogeneity of the postdreissenid benthic community may still be valid. Bray–Curtis dissimilarities remained lower for the postdreissenid benthos than the predreissenid benthos upon reanalysis, and fewer differences were found in the total abundance of benthos among sites and depths for the postdreissenid than for the predreissenid benthos.