

Long-term Trends in Benthic Macroinvertebrate Populations in Lake Huron over the Past Four Decades

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ABSTRACT. Surveys of the benthic macroinvertebrate community were conducted in the main basin of Lake Huron in 2000 and 2003, and in Georgian Bay and North Channel in 2002. Results were compared to surveys conducted in the 1960s and early 1970s. Although data of earlier surveys were inconsistent, our best estimates suggest that total density of the four major benthic taxa (*Diporeia* spp., *Oligochaeta*, *Sphaeriidae*, and *Chironomidae*) in the main basin declined dramatically between the early 1970s and 2000. Populations of all major taxa continued to decline between 2000 and 2003, particularly *Diporeia* and *Sphaeriidae*. *Diporeia* was rare or absent in the southern end of the lake and in some nearshore areas in 2000, and by 2003 was not found at depths < 50 m except in the far northeastern end of the lake. Densities of the major taxa in Georgian Bay and North Channel in 2002 were not different from densities in 1973 despite differences in survey methods. A limited study in southern Georgian Bay, however, found that densities of both *Diporeia* and *Sphaeriidae* declined to zero at most sites between 2000 and 2004. The population of *Dreissena polymorpha* was stable in all lake areas, but *Dreissena bugensis* increased, particularly at the 31–50 m depth interval in the main basin. Since there were no extensive surveys in Lake Huron in the period between nutrient abatement (late 1970s) and the establishment of *Dreissena* (early 1990s), it is difficult to determine relative roles of these events on observed declines. However, since phosphorus loads have been stable since the early 1980s, declines between 2000 and 2003 can likely be attributed to *Dreissena*.

INDEX WORDS: Zoobenthos, Georgian Bay, North Channel, *Diporeia*, density changes.

INTRODUCTION

Benthic macroinvertebrate communities in the Great Lakes are currently undergoing broad changes that are unprecedented in both spatial extent and temporal scale. Some taxa considered to play important roles in Great Lakes ecosystems are declining in abundance, or becoming totally lost from the system (Nalepa *et al.* 1996, Dermott and Kerec 1997, Nalepa *et al.* 1998), while others are increasing or have returned after decades-long absences (Kreiger

and Ross 1993, Schloesser *et al.* 2000, Haynes *et al.* 2005). Evidence suggests that two factors are the primary cause of these community changes: phosphorus abatement programs initiated in the late 1970s, and the introduction and spread of *Dreissena polymorpha* (zebra mussel) and *Dreissena bugensis* (quagga mussel) in the late 1980s. Less phosphorus leads to decreased pelagic productivity and less organic material settling to the benthic region. Consequently, most major macroinvertebrate taxa may be expected to decrease since, in deep lake systems, these taxa are dependent on settled organic material

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as a source of food (Saether 1980). The benthic community has also been greatly affected by the establishment and spread of *Dreissena*. Through their filtering activities, dreissenids alter food pathways and serve as competitors to other benthic taxa for settling organic material. In addition, *Dreissena* beds increase structural complexity of the substrate, enhancing the retention of mussel biodeposits that can be used as a food resource, and providing some species refuge from fish predation (Gonzalez and Downing 1999, Bailley and MacIsaac 2000). Overall, responses to *Dreissena* are complex and varied, depending upon the particular habitat and taxa (Strayer and Smith 2001, Nalepa et al. 2003), and also upon the time period since initial colonization (Haynes et al. 2005).

In terms of assessing long-term trends in the macroinvertebrate community, Lake Huron has been the least studied of all the Great Lakes. While recent trends have been documented in Saginaw Bay (Nalepa et al. 2003), in South Bay located on the northeast shoreline (McNickel et al. 2006), and in the shallow, nearshore zone (< 2 m) (Barton 2004), trends in the open waters of the main basin, Georgian Bay, and North Channel remain largely unknown. Several benthic surveys were conducted in these areas in the early 1970s (Schelske and Roth 1973, Shrivastava 1974, Loveridge and Cook 1976; Great Lakes Research Division [GLRD]-University of Michigan, unpublished data), but no wide-scale surveys have been conducted since this time period.

In this paper, we present results of surveys conducted in the main basin of Lake Huron in 2000 and 2003, and in Georgian Bay and North Channel in 2002. We assess long-term trends by comparing our results to results of surveys conducted in the 1960s and early 1970s. Of particular interest were trends in the benthic amphipod *Diporeia*. This organism has declined in Lakes Michigan, Erie, and Ontario, and is now absent from large areas of these lakes (Nalepa et al. 2006a). *Diporeia* plays a major role in the cycling of energy between lower and upper trophic levels (Gardner et al. 1990), and the decline of this organism has affected many fish species, including lake whitefish, alewife, and sculpin (Hondorp et al. 2005, Mohr and Nalepa 2005, Madenjian et al. 2006).

METHODS

Recent Surveys

In the main basin, samples were collected at 65 sites in July/August 2000, and at 85 sites in

July/August 2003, while in Georgian Bay and North Channel samples were collected at 15 and 13 sites, respectively, in August 2002 (Fig. 1). In addition, samples were also collected at five sites along a depth gradient (20 m, 40 m, 60 m, 80 m, and 93 m) off Cape Rich in southern Georgian Bay (Fig. 1). These Cape Rich sites were sampled yearly in late summer 2000-2004 by the Ontario Ministry of Natural Resources as part of their monitoring program.

Except for sites sampled off Cape Rich, triplicate samples were taken at each site with a Ponar grab (area = 0.047 m²) and then washed into an elutriation device fitted with a nitex sleeve having 0.5-mm openings. Retained material was immediately preserved in 5% buffered formalin containing rose bengal stain. Duplicate samples were taken at the Cape Rich sites with a Ponar grab and washed through a 0.50-mm mesh screen.

Besides the 85 sites sampled in the main basin in 2003, an additional 23 sites were sampled in the northeastern portion of the lake at depths < 35 m. These samples were taken and provided to us by the National Water Research Institute, Canada. The samples were collected in duplicate with a Ponar grab and washed through a screen with 0.5 mm mesh openings. Only *Diporeia* and *Dreissena* were counted in these samples. These additional data were used to better define spatial distributions in 2003, but were excluded from any statistical analysis when examining temporal trends.

In the laboratory, retained residue was placed in a white enamel pan and organisms were picked, counted, and sorted into major taxonomic groups (Amphipoda, Oligochaeta, Chironomidae, *Dreissena*, Sphaeriidae, and other) under a low-power magnifier lamp (1.5 x). All organisms collected in the main basin in 2000, and in Georgian Bay/North Channel in 2002, were identified to the lowest practical taxonomic level. For oligochaetes, between 75 and 100 individuals in a replicate (proportionately split with a Folsom plankton splitter when numbers were high) were cleared in lacto-nophenol before identification. Only oligochaetes with a prostomium were included in abundance estimates. In 2003, oligochaetes and chironomids were not identified beyond the group level. Since oligochaete fragments (without prostomium) can only be recognized during the process of species identification and not when counted and sorted, the total number of oligochaetes at each site in 2003 was corrected based on the mean proportion of fragments found at the same site in 2000 (see Nalepa et al. 1998). For

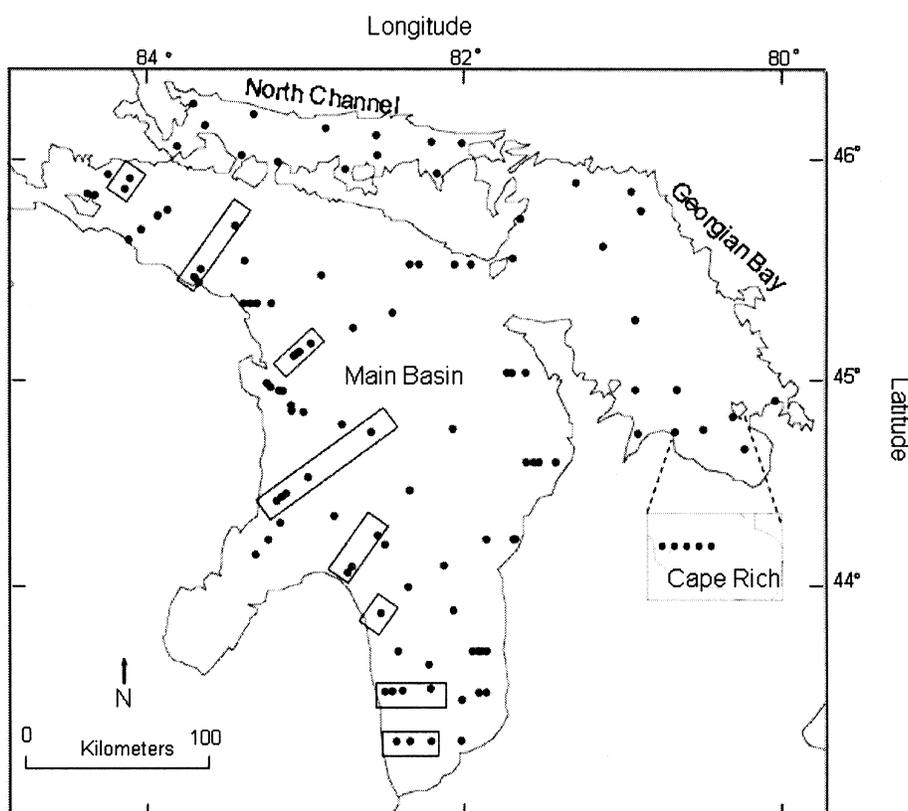


FIG. 1. Sites sampled in the main basin of Lake Huron in 2000 and 2003, and sites sampled in North Channel and Georgian Bay in 2002. Sites within the boxes were sampled in 1972 by the Great Lakes Research Division, University of Michigan. The insert shows location of transect sites sampled off Cape Rich, Georgian Bay in 2000–2004.

the 20 sites sampled in 2003 and not in 2000, a mean proportion for all sites in the same depth interval was used as the oligochaete correction factor. A similar by-depth correction was applied to the Cape Rich samples. The number of each species found in each replicate at all the sites sampled in the 2000–2003 surveys, along with site coordinates, are given in Nalepa *et al.* (2007).

Historic Comparisons

To assess long term changes in the main basin, we compared our 2000–2003 data to data reported in three separate surveys conducted in the early 1970s. In July 1970, Schelske and Roth (1973) took single samples at 19 sites on the west side of the lake with a Ponar grab and washed the samples through a screen with 0.760-mm openings. Based on proximate location and depth, we matched eight of the sites sampled in 2000 to sites sampled in

1970, and densities at only these sites were compared. Another survey was conducted in the main basin in April–June 1971 (Shrivastava 1974). Single samples were collected at 52 sites throughout the lake with a Ponar grab and washed through a screen with 0.5-mm openings. Lastly, in early September 1972 a survey was conducted at 50 sites on the west side of the lake by the Great Lakes Research [GLRD], University of Michigan (unpublished). Samples were taken in triplicate with a Ponar grab and washed through a screen with 0.5 mm openings. Of sites in the 1972 survey, 25 were re-sampled (at the same coordinates) in 2000 and 2003. The sites were located on the west side of the lake along eight transects (Fig. 1). Organisms collected in 1972 were identified to the species level, and abundances were available on a per replicate basis. Basic data (taxa abundance per replicate) and site coordinates for the 1972 survey are given in Nalepa *et al.* (2007).

Trends in Georgian Bay/North Channel were examined by comparing 2002 data to data reported in a 1973 survey by Loveridge and Cook (1976). A large number of sites was sampled in 1973, and all sites sampled in 2002 were matched, though not exactly, to 1973 sites by depth and location. In the 1973 survey, one replicate sample per site was taken with a Ponar grab, and washed through a screen with 0.1 mm openings. In the laboratory, samples were further washed through a 0.1 mm screen using a bubble-flow elutriator. Organisms were picked and sorted using a low-power dissecting microscope and identified to the lowest practical taxonomic level. Although these methods differed from ours, no other early data were available for Georgian Bay/North Channel.

Finally, 2003 densities were compared to densities found in a lake-wide survey in 1963–1964 (Barton 1986). Samples in 1963–1964 were collected with a Franklin-Anderson grab and washed through a 0.5–0.6 mm screen. This grab is effective in hard substrates (sand), but grossly underestimates all benthic groups in soft substrates (mud, silt) (Flannagan 1970). Thus, 1963–1964 densities were likely accurate in shallow areas (sand-dominated), but were severely underestimated in deep regions (silt-dominated) (Barton 1986). A single grab sample was taken at each of up to 61 sites on 13 sampling dates in 1963–1964; not all sites were sampled on each date.

Before data were compared, sites were divided into four depth intervals: 18–30 m, 31–50 m, 51–90 m, and > 90 m. These depth intervals are consistent with prior characterization of depth-macroinvertebrate associations in the Great Lakes (Nalepa 1987). The exception was the matched 1970 and 2000 sites, which were divided into 18–32 m and 50–60 m intervals. Since the 2000 and 2003 surveys did not sample at any sites < 18 m, nor at any sites in inner Saginaw Bay, similar sites in the historic surveys were not included in the analysis. Density differences between most yearly comparisons (1971 vs. 2000, 1972 vs. 2000, 1973 vs. 2002, 2000 vs. 2003) for the major taxonomic groups were tested using a two-way ANOVA (year x interval) after $\ln + 1$ transformation to homogenize variances. Some taxonomic groups did not meet the parametric assumption of variance homogeneity but, as noted by McNickle *et al.* (2006), ANOVA is a robust test, and large departures from parametric assumptions have little impact on outcomes. Station means were treated as the source of variation within intervals. Differences between 1970 and 2000, and

between 1963–1964 and 2003 were tested using paired t-test and t-test, respectively, after $\ln + 1$ transformation. Unequal variances were assumed (SYSTAT 11.0). For the comparison between 1963–1964 and 2003 only sites in the 18–30 m interval were considered since, as noted, densities at deeper depths in 1963–1964 were underestimated. Station means in 1963–1964 were determined from sampling dates and then treated as the source of variation within the interval.

Changes in oligochaete community structure were examined using the oligochaete trophic index (Howmiller and Scott 1977) as modified by Milbrink (1983). The index is determined by placing species (excluding Naididae and Enchytraidae) into four categories based on its relative tolerance to organic enrichment. Values of each category range from 0 (intolerant of enrichment; found mostly in oligotrophic conditions) to 3 (tolerant of enrichment; found in highly eutrophic conditions). The assigned category of each species follows that of Milbrink (1983) and Lauritsen *et al.* (1985). To obtain the index, the number of individuals in each category is multiplied by the category value (species in category 0 are assigned a value of 0.5). The products are then summed and divided by the total number of individuals in all categories. We did not apply a density factor to the index as did Milbrink (1983). Between-year differences in relative frequencies within each category were tested using the G-test (log-likelihood ratio).

RESULTS

Main Basin: 1970, 1971, and 1972 vs. 2000

Systematic comparisons between densities in 2000 and the three 1970s surveys gave markedly different results. For the eight matched sites in 1970 and 2000, there were no significant differences (paired t-test; $P > 0.05$) for the four major taxa (*Diporeia*, Oligochaeta, Sphaeriidae, and Chironomidae) at each depth interval (Table 1). In contrast, densities of all the major taxa except *Diporeia* were significantly higher ($P < 0.05$) in 2000 when compared to densities reported in the 1971 survey (Table 2). Year x interval interactions were not significant ($P > 0.05$), indicating these density differences occurred across all depth intervals. Mean densities of the four major taxa in 2000 were either similar to or greater than mean densities reported in 1971 at each interval (Table 2). On the other hand, when densities in 2000 were compared to densities reported in the 1972 survey, densities of each of the

TABLE 1. Mean (\pm SE) density (No. per m^2) of the major macroinvertebrate taxa found at two depth intervals in Lake Huron in 1970 and 2000. The 1970 data are from Schelske and Roth (1973). Standard errors based on station means. Stations in 1970 and 2000 were matched based on depth and spatial proximity. $n = 5$ and $n = 3$ for the 18–32 m and 50–60 m intervals, respectively. Differences between years tested using paired t -test were not significant (ns) at 0.05 level.

Taxa	18–32 m		50–60 m	
	1970	2000	1970	2000
<i>Diporeia</i> spp.	1,220 \pm 841	80 \pm 75 ^{ns}	1,630 \pm 664	2,655 \pm 520 ^{ns}
Oligochaeta	80 \pm 75	1,417 \pm 339 ^{ns}	691 \pm 352	1,140 \pm 245 ^{ns}
Sphaeriidae	76 \pm 48	315 \pm 159 ^{ns}	167 \pm 52	366 \pm 162 ^{ns}
Chironomidae	171 \pm 130	173 \pm 86 ^{ns}	171 \pm 129	173 \pm 66 ^{ns}

major taxa except Chironomidae were significantly lower in 2000 compared to 1972 ($P < 0.05$) (Table 3). Overall declines were 78.4%, 57.1%, 74.2%, and 29.8% for each taxon, respectively. The year \times depth-interval interaction was significant only for *Diporeia* and Chironomidae ($P < 0.05$); these two taxa declined to the greatest extent in the shallowest depth interval (< 30 m).

Like our 2000 survey, organisms in the 1972 survey were identified to species, and there was a difference in species composition of the oligochaete community between years. The frequency of individuals in each of the four trophic categories (relative to the total in all categories) was significantly different at the < 30 m and 31–50 m intervals (G-Test; $P < 0.05$) (Table 4). The density and relative proportion of Type 0 individuals, basically all *Styrodrius heringianus* (97.8%), were lower in 2000 compared to 1972, while the relative proportion of Type 1 individuals was higher. Of Type 1 individuals, the only species that increased to any extent was *Potamothenis vejovskyi*. As a result, the oligochaete trophic index increased from 0.86 to 0.99 at the < 30 m interval, and from 0.57 to 0.71 at the 31–50 m interval.

Relatively minor changes occurred in the chironomid community between 1972 and 2000. The dominant chironomids in 1972 were *Heterotrissocladius oliveri* and *Micropsectra* sp. in the < 30 m and 31–50 m intervals (together 72% of all chironomids at each interval), while *H. oliveri* was dominant in the 51–90 m interval (93%). In comparison, the dominant taxa in the < 30 m interval in 2000 were *Parcladopelma winnelli* (59%) and *Heterotrissocladius changi* (38%), and the dominant taxa in the 31–50 m interval remained *H. oliveri* and *Micropsectra* sp. (67% together). Also, *H. oliveri* remained dominant at the 51–90 m interval (99%). All the species mentioned above are considered to be oligotrophic indicators (Winnell and White 1985).

Main Basin: 2000 vs. 2003

Densities of the four major taxa were each significantly lower ($P < 0.05$) in 2003 compared to 2000, and year \times interval interactions were not significant ($P > 0.05$) (Table 5, Fig. 2). Overall, declines were greatest for *Diporeia* and Sphaeriidae, with lakewide declines of 57% and 74% over the 3-year

TABLE 2. Mean (\pm SE) density (No. per m^2) of the major macroinvertebrate taxa found at four depth intervals in Lake Huron in 1971 and 2000. The 1971 data are from Shrivastava (1974). Standard errors based on station means. The number of stations per depth interval and year is given in parenthesis. $Y =$ year, $I =$ depth interval, P values are from two-way ANOVA. *Variance is not homogeneous between years.

Taxa	18–30 m		31–50 m		51–90 m		> 90 m		P-Value	
	1971 (11)	2000 (10)	1971 (9)	2000 (19)	1971 (16)	2000 (28)	1971 (16)	2000 (8)	Y	Y \times I
<i>Diporeia</i>	223 \pm 100	244 \pm 237	492 \pm 208	876 \pm 287	539 \pm 87	1,918 \pm 177	480 \pm 82	1,646 \pm 254	0.650*	0.014
Oligochaeta	491 \pm 171	1,648 \pm 410	509 \pm 166	1,196 \pm 314	314 \pm 54	792 \pm 87	212 \pm 64	661 \pm 69	$< 0.001^*$	0.389
Sphaeriidae	451 \pm 219	457 \pm 196	164 \pm 52	237 \pm 37	340 \pm 251	323 \pm 44	33 \pm 16	104 \pm 35	0.007*	0.172
Chironomidae	53 \pm 14	883 \pm 451	29 \pm 12	379 \pm 1402	29 \pm 8	73 \pm 11	11 \pm 4	53 \pm 12	< 0.001	0.460

TABLE 3. Mean (\pm SE) density (No. per m^2) of the major macroinvertebrate taxa found at three depth intervals in Lake Huron in 1972 and 2000. The 1972 data are from Great Lakes Research Division, University of Michigan (unpublished). Standard errors based on station means. $n = 5, 11,$ and 9 for the 18–30 m, 31–50 m, and 51–90-m intervals, respectively, in both years. $Y =$ year, $I =$ depth interval, P values are from two-way ANOVA. *Variance is not homogeneous between years.

Taxa	18–30 m		31–50 m		51–90 m		P-Value	
	1972	2000	1972	2000	1972	2000	Y	Y x I
<i>Diporeia</i>	1,896 \pm 1,008	3 \pm 2	5,892 \pm 750	592 \pm 394	4,867 \pm 551	2,332 \pm 365	< 0.001*	< 0.001
Oligochaeta	2,664 \pm 919	1,493 \pm 259	2,831 \pm 414	1,029 \pm 292	1,545 \pm 475	723 \pm 173	0.003	0.267
Sphaeriidae	609 \pm 402	187 \pm 147	1,275 \pm 210	233 \pm 44	462 \pm 104	243 \pm 70	0.002	0.802
Chironomidae	419 \pm 149	121 \pm 45	134 \pm 28	146 \pm 55	65 \pm 14	75 \pm 9	0.054	0.025

period, respectively. In 2000, *Diporeia* was rare in the southern portion of the main basin, in outer Saginaw Bay, and in the northwestern portion of the lake (Fig. 2). By 2003, few or no *Diporeia* were found at sites < 50 m around the entire lake except for the northeast portion. Of the sites sampled in both 2000 and 2003, the number of sites where *Diporeia* was not found increased from 6 to 12 over the 3-year period.

In contrast to the other taxa, the dreissenid population expanded in 2003 compared to 2000, mainly a result of the great increase in densities of *D. bugensis* (Table 5, Fig. 3). The mean lakewide density of *D. bugensis* was $< 1 \pm < 1/m^2$ in 2000, but increased to $560 \pm 253/m^2$ in 2003, and this difference was significant ($F_{[1,143]} = 20.18, P < 0.001$). The year x interval interaction was also significant ($F_{[3,143]} = 4.11, P = 0.009$) as the greatest increase occurred at the 31–50 m interval. On the other hand, densities of *D. polymorpha* in 2003 were not significantly different from densities in 2000 ($F_{[1,143]} = 0.54, P = 0.47$).

Main Basin: 1963–1964 vs. 2003

Mean densities (\pm SE) of *Diporeia*, Oligochaeta, Sphaeriidae, and Chironomidae at sites in the 18–30 m interval ($n = 11$) in 1963–1964 were $818 \pm 256/m^2, 577 \pm 161/m^2, 192 \pm 87/m^2,$ and $87 \pm 21/m^2,$ respectively. When densities in 1963–1964 and 2003 were compared, densities of *Diporeia* and Sphaeriidae in 2003 were significantly lower ($t_{[11, 17]} = 5.03, P < 0.001$ and $t_{[11, 17]} = 2.58, P = 0.018$) than in 1963–1964, whereas densities of Oligochaeta and Chironomidae were significantly higher ($t_{[11, 17]} = 2.23, P = 0.045$ and $t_{[11, 17]} = 2.38, P = 0.030$).

Georgian Bay and North Channel: 1973 vs. 2002, and Georgian Bay (Cape Rich): 2000–2004

In both Georgian Bay and North Channel, differences between years were non-significant ($P > 0.05$) for each taxon (Table 6). Mean total densities in 1973 and 2002 were remarkably similar in both areas. At the 12 sites in Georgian Bay, total densities of the four taxa were $2,736 \pm 436/m^2$ in 1973 and $2,962 \pm 474/m^2$ in 2002, while respective total densities at the 13 sites in North Channel were $3,262 \pm 637/m^2$ and $3,032 \pm 553/m^2$. As in the main basin, the oligochaete community shifted from oligotrophic-indicator taxa (Type 0) to more eutrophic forms (mostly Type 1) between 1973 and 2002 in both locations, and differences were significant (G-test; $P < 0.05$). The mean percentage of Type 0 forms declined from 97.4% to 81.2% in Georgian Bay and from 82.9% to 36.5% in North Channel. The mean oligochaete index in Georgian Bay was 1.00 and 1.09 in 1973 and 2002, respectively, and the index in North Channel was 0.96 and 1.11.

For sites sampled yearly off Cape Rich between 2000 and 2004, temporal trends were apparent only for *Diporeia*, Sphaeriidae, and *D. bugensis* (Table 7). Over the 4-year time period, the former two taxa declined, while the latter increased. For *Diporeia*, density exceeded $1,000/m^2$ at four of the five sites in 2000, but was $0/m^2$ at all sites by 2004.

DISCUSSION

In the main basin, comparisons between densities in our 2000 survey and densities in surveys in the early 1970s failed to provide consistent differences. Densities of all major taxa in 2000 were either similar to, greater than, or lower than densities reported in surveys independently conducted in 1970 (Schelske and Roth 1973), 1971 (Shrivastava

TABLE 4. Mean density (No. per m²) of the major oligochaete taxa at the 18–30 m, 31–50 m, and 51–90 m intervals in 1972 and 2000. The trophic type (Milbrink 1983, Lauritsen et al. 1985) is given in parenthesis next to each species.

Taxa	Year:	Depth Interval					
		18–30 m		31–50 m		51–90 m	
		1972	2000	1972	2000	1972	2000
Enchytraeidae		109	26	743	65	421	201
Lumbriculidae							
<i>Stylodrilus heringianus</i> (0)		534	197	1,683	473	1,104	436
Tubificidae							
<i>Aulodrilus americanus</i> (1)		37	0	0	0	0	0
<i>A. limnobioides</i> (1)		6	6	0	0	0	0
<i>A. pigueti</i> (1)		6	0	0	0	0	0
<i>A. plurisetus</i> (1)		370	6	< 1	26	0	0
<i>Ilyocryptus freyi</i> (1)		< 1	3	0	0	0	0
<i>I. tempeltoni</i> (1)		0	1	0	< 1	0	0
<i>Limnodrilus claparedeianus</i> (3)		1	1	0	0	0	0
<i>L. hoffmeisteri</i> (2)		69	87	8	8	0	2
<i>L. profundicola</i> (0)		1	0	1	0	1	4
<i>L. spiralis</i> (2)		1	0	0	0	0	0
<i>L. udekemianus</i> (2)		0	0	1	0	0	0
<i>Potamothenis moldaviensis</i> (1)		0	27	0	3	0	0
<i>P. vejdovskyi</i> (1)		34	137	2	249	0	0
<i>Rhyacodrilus coccineus</i> (1)		3	0	3	5	0	0
<i>R. montana</i> (0)		0	0	1	0	2	0
<i>Spirosperma ferox</i> (1)		303	306	240	48	3	0
<i>S. nikolskyi</i> (0)		0	0	48	20	17	2
<i>T. tubifex</i> (3)		0	0	0	1	5	10
<i>T. superiorensis</i> (0)		1	1	0	1	0	1
<i>Varietochaeatidrilus augustipenis</i> (2)		0	3	0	0	1	0
Immatures without hair setae		900	248	107	41	18	11
Immatures with hair setae		201	56	49	96	4	29
Naididae*		74	314	16	43	4	0
Type 0		540	198	1,736	498	1,124	442
Type 1		760	558	243	327	3	0
Type 2		70	90	9	8	1	2
Type 3		1	1	0	1	5	10
Total Oligochaeta Typed		1,371	848	1,988	834	1,133	453
Total Oligochaeta		2,655	1,492	2,904	1,079	1,580	693

*1972: *Arcteonais lomondi*, *Chaetogaster* sp., *Piguetiella michiganensis*, *Pristina osborni*, *Slavina appendiculata*, *Specaria josinae*, *Uncinaiis uncinata*, *Vejdovskyella comata*, *Vejdovskyella intermedia*

2000: *Arcteonais lomondi*, *Chaetogaster* sp., *Nais simplex*, *Piguetiella michiganensis*, *Specaria josinae*, *Stylaria lacustris*, *Uncinaiis uncinata*

1974), and 1972 (GLRD unpublished), respectively. These inconsistencies are directly related to the dramatic differences in densities reported in these three earlier surveys (Fig. 4). For instance, total densities in the 1972 survey were 5.3–8.3 times greater than densities in the 1971 survey over all depth intervals. Since density differences were apparent even at the deeper intervals where populations are generally stable and changes tend to occur only over long time periods, survey differences were not likely a

result of normal year-to-year variation. Whereas it is difficult to reconcile how densities may have been overestimated in the 1972 survey, features of both the 1970 and 1971 surveys may have led to density underestimates. Samples in the 1970 survey were washed through a screen with 0.76-mm openings, which may have allowed some organisms to be lost compared to the 0.5-mm openings used in the other surveys. Densities in the 1971 survey were much lower than in either 1970 or 1972. Oth-

TABLE 5. Mean (\pm SE) density (No. per m^2) of the major macroinvertebrate taxa found at four depth intervals in Lake Huron in 2000 and 2003. Standard errors based on station means. $n = 10, 19, 28,$ and 8 for the 18–30 m, 31–50 m, 51–90 m, and > 90 m depth intervals in 2000, respectively and $n = 17, 27, 33,$ and 8 for the same intervals in 2003. Y = year, I = depth interval, P values are from two-way ANOVA. *Variance is not homogeneous between years.

Taxa	Year	Depth Interval								P Value	
		18-30 m		31-50 m		51-90 m		> 90 m		Y	Y x I
		2000	2003	2000	2003	2000	2003	2000	2003		
<i>Diporeia</i>		244 \pm 237	97 \pm 92	876 \pm 287	248 \pm 103	1,918 \pm 177	900 \pm 130	1,646 \pm 254	984 \pm 65	0.002	0.304
Oligochaeta		1,648 \pm 410	1,783 \pm 417	1,196 \pm 314	1,460 \pm 368	792 \pm 87	374 \pm 41	661 \pm 69	443 \pm 74	0.036*	0.107
Sphaeriidae		457 \pm 196	47 \pm 21	237 \pm 37	67 \pm 13	323 \pm 44	106 \pm 17	104 \pm 35	80 \pm 42	< 0.001	0.703
Chironomidae		883 \pm 451	238 \pm 55	379 \pm 140	62 \pm 14	73 \pm 11	27 \pm 5	53 \pm 12	17 \pm 5	< 0.001	0.432
<i>Dreissena</i>											
<i>polymorpha</i>		386 \pm 342	297 \pm 209	6 \pm 2	7 \pm 4	0 \pm 0	18 \pm 17	0 \pm 0	0 \pm 0	0.374	0.412
<i>Dreissena</i>											
<i>bugensis</i>		3 \pm 2	297 \pm 180	2 \pm 1	1,469 \pm 757	0 \pm 0	70 \pm 44	0 \pm 0	1 \pm 1	< 0.001*	0.011

ers have also noted that densities reported in this survey were atypically low (Cook and Johnson 1974, Barton 1986). Total densities in 1971 were even lower than densities reported in a 1950s survey in Lake Huron by Teter (1960). Teter used a Peterson grab, a sampling device that underestimates some major benthic taxa by 2–4 times compared to the Ponar (Nalepa *et al.* 2002). One theory for low densities in the 1971 survey argues that, by sampling only in the spring, the survey missed young *Diporeia* because these small, spring-hatched individuals might pass through the mesh size used (Cook and Johnson 1974). Regardless, vast differences in the three surveys conducted in Lake Huron in the early 1970s illustrate the difficulties when comparing densities from one-year surveys conducted by different entities separated by a long period of time (Barton 1989). Yet despite these inconsistencies, we suggest that comparative differences between the 1972 survey and 2000 best represent benthic trends in the lake over this period of time. Collection methods in the two surveys were exactly the same (three replicates per site using the same sampler type and mesh size), stations were at the same locations, and sampling was conducted about the same time of year (August–September).

The time between the 1960s and late 1970s/early 1980s was a period of marked increases in benthic densities in the Great Lakes (Johnson and McNeil 1986, Nalepa 1987). Nutrient loads had increased for several decades, productivity was at a peak, and benthic populations had not yet fully responded to nutrient abatement programs initiated in the late 1970s. Fully aware of the shortcomings of pre-

vious surveys and excluding the problematic 1971 survey, total densities at all sites sampled in Lake Huron at the shallowest depth interval were 1,674/ m^2 in 1963–1964, 2,213/ m^2 in 1970 (likely an underestimate), and 5,902/ m^2 in 1972. This is a 3.5-fold increase in 9 years. For perspective, we compared density trends in Lake Huron to those in Lake Michigan over the same general time period. In Lake Michigan, densities increased from 4,400/ m^2 in 1964–1966 to 16,400/ m^2 in 1980–1981 at the 18–30 m interval (Nalepa 1987). When calculated on an annual basis, the rate of change was generally similar in the two lakes; the increase in total density was 0.39 fold per year in Lake Huron compared to 0.26 fold per year in Lake Michigan. Considering that the 1980–1981 sampling date in Lake Michigan was just after phosphorus abatement and the 1972 sampling date in Lake Huron was just before, rates of change in the two lakes would probably be even more similar if sampling dates matched more closely.

Phosphorus loads in Lake Huron declined from 5.1 million kg/year in 1978 to below target levels of 4.3 million kg/year in 1981, and have generally remained below these levels ever since (Beeton *et al.* 1999). Phytoplankton biomass also generally declined (Dobiesz *et al.* 2005). Because there were no surveys conducted in the main basin in the period between when loads declined and when *Dreissena* became established, it is not possible to differentiate the relative influences of these two events on apparent trends between 1972 and 2000. After abatement but before *Dreissena* in Lake Michigan, densities of *Diporeia*, Oligochaeta, and Sphaeriidae

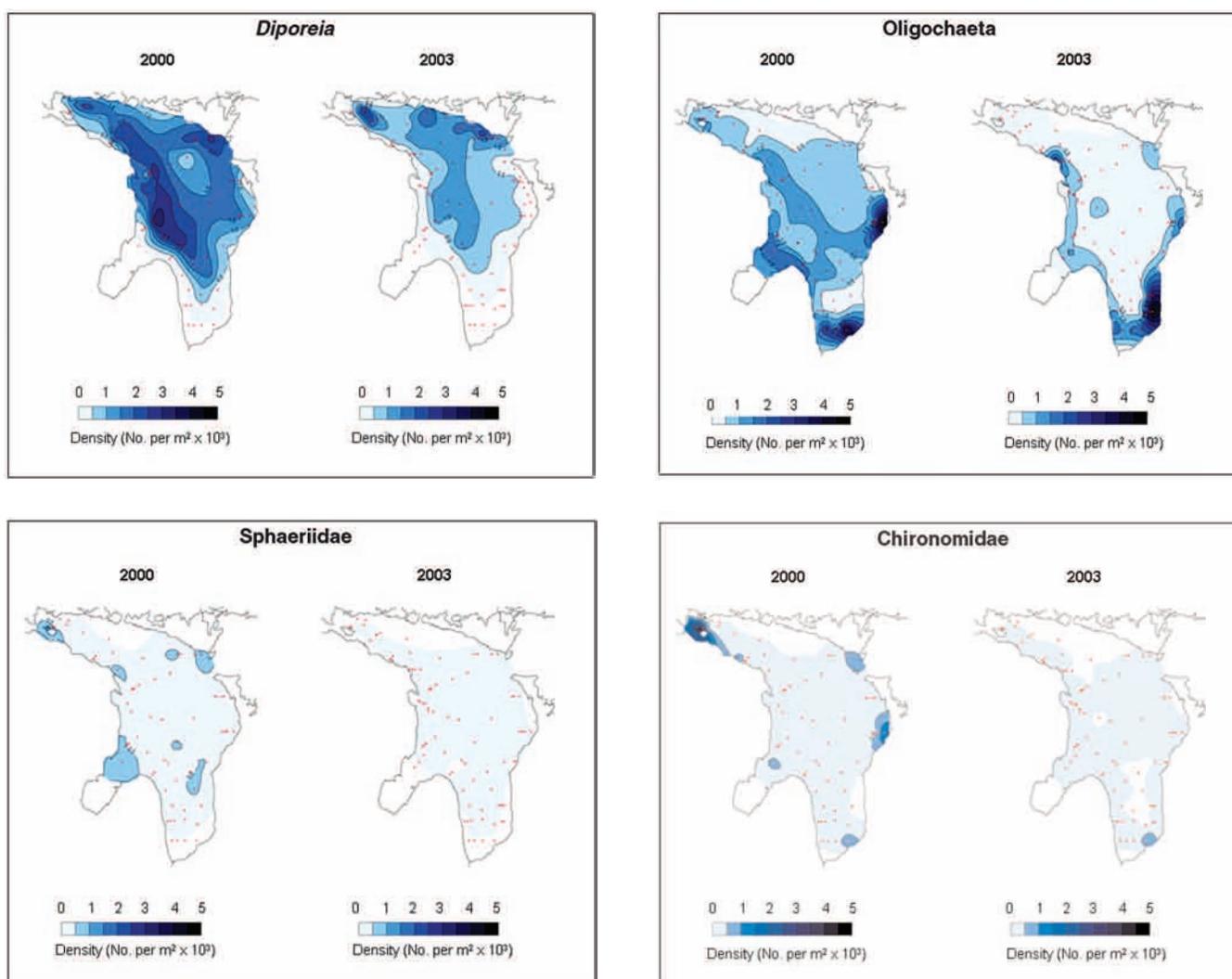


FIG. 2. Mean density (No. per m² × 10³) of the major macroinvertebrate groups (*Diporeia*, *Oligochaeta*, *Sphaeriidae*, *Chironomidae*) in Lake Huron in 2000 and 2003. Small crosses denote sampling sites. Values on isopleths correspond to values on the given density scale.

declined at a rate of 2.6% to 8.2% per year at sites 18–30 m, and 0.7% to 2.9% per year at sites 31–50 m (Nalepa *et al.* 1998). Declines were minimal at depths > 50 m. We can only speculate on what the benthic response to abatement was in Lake Huron, but rates and depth-specific decline patterns were probably similar to those in Lake Michigan.

Although densities of the four major taxa apparently declined in the main basin, similar declines were not evident in Georgian Bay and North Channel. Densities of all four taxa in 2002 were similar to densities found in 1973 despite the use of a much finer screen size (0.1 mm) in the earlier survey that would have retained more organisms than the 0.5

mm size used in 2002. The lack of density differences suggests that increased productivity resulting from nutrient enrichment was not an issue in either area over the period, or perhaps productivity increased but then declined to 1973 levels by 2002. Regardless, recent changes in the southern portion of Georgian Bay (off Cape Rich) such as the loss of *Diporeia* and *Sphaeriidae* can likely be attributed to *Dreissena*. Interestingly, although declines in these taxa were clearly evident by 2002 at the Cape Rich sites, similar declines were not evident at sites sampled over the entire bay in the wider survey of 2002. Possibly, this difference may be related to greater densities of *Dreissena* found at the Cape

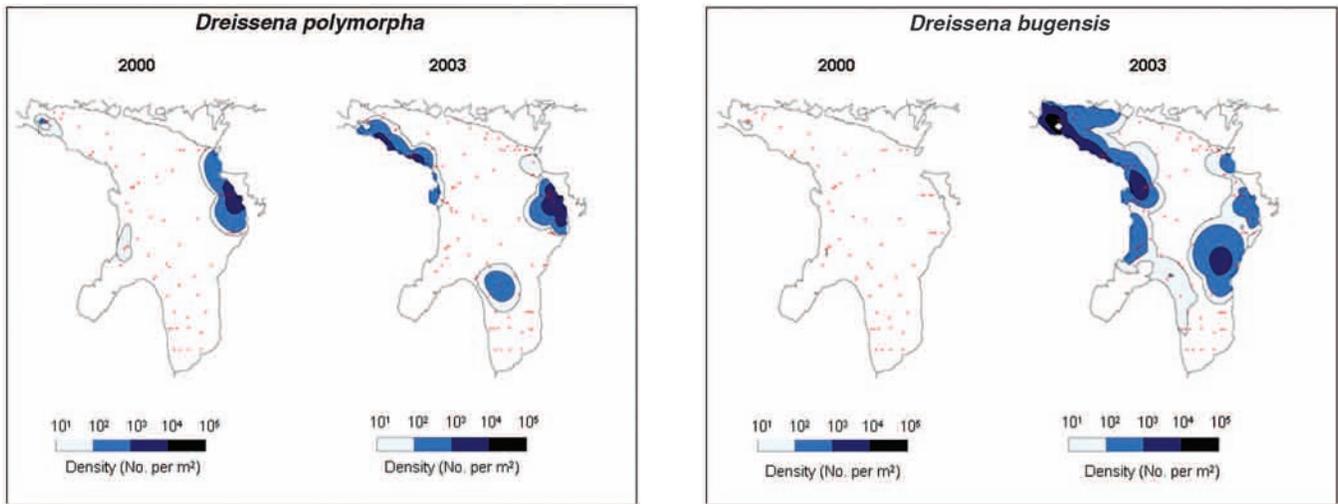


FIG. 3. Mean density (No. per m^2) of *Dreissena polymorpha* and *Dreissena bugensis* in Lake Huron in 2000 and 2003. Small crosses denote sampling sites. Values on isopleths correspond to values on the given density scale.

Rich sites. At the shallowest site off Cape Rich (20 m), mean density of *Dreissena* was $1,700\ m^{-2}$ in 2002 compared to a mean of only $86\ m^{-2}$ at the $< 30\ m$ interval in the 2002 survey.

In a study of benthic community changes between 1980–81 and 2002–2003 in South Bay, Lake Huron, all major taxa except oligochaetes declined (McNickel *et al.* 2006). Oligochaetes actually increased, and this increase was attributed to the availability of dreissenid biodeposits as a food source. In other studies, the response of oligochaetes to the presence of dreissenids has varied, with both increases (Howell *et al.* 1996, Botts *et al.* 1996, Bailley and MacIsaac 2000) and decreases (Lozano *et al.* 2001, Strayer and Smith 2001, Nalepa *et al.* 2003) reported. It is apparent that response in oligochaetes is variable and more a function of spatial scale. In general, positive responses are local and confined to areas in close proximity to mussel beds, whereas negative responses are more system-wide and a function of resource diversion by the mussels. In inner Saginaw Bay, oligochaetes did not decline in shallow areas of the bay where *Dreissena* was present, but did decline in deeper areas where *Dreissena* was absent (Nalepa *et al.* 2003). Similarly, in the main basin between 2000 and 2003, oligochaete densities were the same or higher in the nearshore ($< 50\ m$) where *Dreissena* was most abundant, but were lower in the offshore where *Dreissena* was rare. This pattern

is consistent with the nearshore “shunt” hypothesis which states that *Dreissena*, through filtering and biodeposition, retains nutrients and organic material in nearshore areas while diverting resources from offshore areas (Hecky *et al.* 2004). As infaunal detritivores, oligochaetes are the benthic group most likely to reflect these resource shifts. McNickle *et al.* (2006) suggested that positive impacts of dreissenids on oligochaetes can best be detected where phosphorus levels/organic enrichment are not strongly influenced by anthropogenic sources, such as in their South Bay study area. We found that in areas like inner Saginaw Bay or the main basin where anthropogenic sources were present, oligochaetes did not increase, but were less prone to decline compared to other taxa. The Cape Rich sites were not likely influenced by anthropogenic sources, but oligochaete densities were highly variable and trends over the 4-year period in this limited area were not apparent. With dreissenids now expanding in Georgian Bay, further sampling throughout the bay may provide further insights into oligochaete response patterns.

Species composition of the oligochaete community changes predictably with nutrient abatement as eutrophic and mesotrophic species become less dominant, and oligotrophic species increase (Johnson and McNeil 1986, Nalepa *et al.* 1998). Seemingly inconsistent with the premise that nutrient abatement played some role in decreased

TABLE 6. Mean (\pm SE) density (No. per m^2) of the major macroinvertebrate taxa found at three depth intervals in Georgian Bay and North Channel, Lake Huron in 1973 and 2002. $n = 3, 5,$ and 9 for the 18–30 m, 31–50 m, and 51–90 m intervals in Georgian Bay; $n = 5, 6,$ and 2 for the < 30 m, 31–50 m, and 51–90-m intervals in North Channel. $Y =$ year, $I =$ depth interval, P values are from two-way ANOVA. *Variance is not homogeneous between years.

Taxa	18–30 m		31–50 m		51–90 m		P-Value	
	1973	2002	1973	2002	1973	2002	Y	Y x I
Georgian Bay								
<i>Diporeia</i>	2,117 \pm 661	1,687 \pm 830	1,603 \pm 665	1,457 \pm 596	1,507 \pm 354	1,684 \pm 306	0.306*	0.652
Oligochaeta	781 \pm 628	707 \pm 344	522 \pm 307	767 \pm 293	270 \pm 239	413 \pm 144	0.066*	0.784
Sphaeriidae	302 \pm 189	1,814 \pm 526	806 \pm 383	853 \pm 214	389 \pm 203	175 \pm 58	0.107	0.508
Chironomidae	57 \pm 19	162 \pm 34	200 \pm 141	94 \pm 26	35 \pm 10	44 \pm 11	0.225	0.844
<i>D. polymorpha</i>	—	19 \pm 10	—	24 \pm 23	—	2 \pm 2		
<i>D. bugensis</i>	—	0 \pm 0	—	36 \pm 34	—	0 \pm 0		
North Channel								
<i>Diporeia</i>	1,369 \pm 471	2,046 \pm 705	1,520 \pm 96	896 \pm 401	3,441 \pm 1,663	3,349 \pm 43	0.501*	0.473
Oligochaeta	952 \pm 592	653 \pm 269	205 \pm 51	322 \pm 163	29 \pm 10	1,174 \pm 232	0.134	0.104
Sphaeriidae	983 \pm 384	875 \pm 280	780 \pm 236	357 \pm 163	898 \pm 236	635 \pm 200	0.488	0.510
Chironomidae	231 \pm 57	99 \pm 22	126 \pm 53	198 \pm 57	104 \pm 85	54 \pm 25	0.618	0.218
<i>D. polymorpha</i>	—	1 \pm 1	—	0 \pm 0	—	0 \pm 0		
<i>D. bugensis</i>	—	0 \pm 0	—	0 \pm 0	—	0 \pm 0		

oligochaete densities in the main basin between 1972 and 2000 was the observed shift in species composition. A lower proportion of oligotrophic indicator species and a higher proportion of mesotrophic indicator species suggests nutrient abatement had little or no effect. The paradox of having a decrease in densities along with a shift to species less indicative of oligotrophic conditions may possibly be explained by the response of species considered to be oligotrophic indicators such as *Stylogdrilus heringianus*. When nutrients increase in oligotrophic systems, these species can initially increase in abundance relative to other indicator species, leading to a decrease in index values (Milbrink 1983). Logically then, densities of oligotrophic species will decrease relative to other indicator species when nutrient abatement occurs. As evidence, *S. heringianus* decreased to a greater extent than most other indicator species in the main basin between 1972 and 2000. Yet as evidenced in Georgian Bay and North Channel, a shift to more mesotrophic species can apparently occur with no change in density.

As noted, phosphorus loads in Lake Huron have generally remained below target levels since the early 1980s, yet all the major taxa declined significantly between 2000 and 2003. We suggest that these changes were likely related to the introduction and expansion of dreissenids. Declines in the main

basin and at the Cape Rich sites were most pronounced for *Diporeia* and Sphaeriidae, and other studies in the Great Lakes have shown that these taxa are highly impacted by *Dreissena* (Dermott and Kerec 1997, Nalepa *et al.* 1998, Lauer and McComish 2001). Whereas *Diporeia* was already gone or rare in many areas (i.e., southern end of the lake) when our sampling was initiated in 2000, declines likely paralleled the spread of *Dreissena*. The decline of *Diporeia* in outer Saginaw Bay was well-documented and occurred in the mid-1990s, just a few years after *Dreissena* became established (Nalepa *et al.* 2003). This close temporal relationship between *Diporeia* declines and dreissenid expansion is typical for other regions of the Great Lakes (Nalepa *et al.* 2006a). Based on distributions of the two taxa, the negative response of *Diporeia* to *Dreissena* in Lake Huron was far-reaching. For instance, *Diporeia* was least abundant in the southern end of the lake in 2000, and yet *Dreissena* was rare or absent in this portion of the lake, at least at the sites sampled. Between 2000 and 2003, the general decline of *Diporeia* was spatially systematic; that is, lower densities observed in some nearshore areas in 2000 expanded to offshore areas by 2003. This pattern is similar to that found in both Lakes Michigan and Ontario where the loss of *Diporeia* in offshore areas (> 50 m) preceded the expansion of *Dreissena* from nearshore areas (Dermott 2001,

TABLE 7. Mean (\pm SE) density (No. per m^2) of the major macroinvertebrate taxa found at different depths off Cape Rich, Georgian Bay in 2000–2004.

Depth/Year	Taxa					
	<i>Diporeia</i>	Oligochaeta	Sphaeriidae	Chironomidae	<i>D. polymorpha</i>	<i>D. bugensis</i>
20 m						
2000	315 \pm 105	1,411 \pm 698	486 \pm 219	210 \pm 38	2,240 \pm 1,897	0 \pm 0
2001	38 \pm 19	303 \pm 14	286 \pm 133	181 \pm 67	191 \pm 114	0 \pm 0
2002	19 \pm 19	347 \pm 77	67 \pm 10	114 \pm 38	1,649 \pm 219	48 \pm 29
2003	0 \pm 0	226 \pm 34	45 \pm 10	610 \pm 76	534 \pm 343	95 \pm 95
2004	0 \pm 0	925 \pm 857	0 \pm 0	143 \pm 143	4,176 \pm 934	458 \pm 114
40 m						
2000	1,144 \pm 153	226 \pm 23	153 \pm 153	67 \pm 48	0 \pm 0	0 \pm 0
2001	1,516 \pm 105	134 \pm 51	372 \pm 86	219 \pm 29	10 \pm 10	0 \pm 0
2002	524 \pm 181	231 \pm 74	572 \pm 19	67 \pm 10	10 \pm 10	0 \pm 0
2003	496 \pm 0	148 \pm 60	610 \pm 381	10 \pm 10	0 \pm 0	0 \pm 0
2004	0 \pm 0	936 \pm 180	0 \pm 0	10 \pm 10	0 \pm 0	0 \pm 0
60 m						
2000	2,174 \pm 591	886 \pm 166	0 \pm 0	105 \pm 29	10 \pm 10	0 \pm 0
2001	791 \pm 10	218 \pm 4	10 \pm 10	0 \pm 0	0 \pm 0	0 \pm 0
2002	48 \pm 10	218 \pm 12	19 \pm 19	38 \pm 0	0 \pm 0	0 \pm 0
2003	0 \pm 0	47 \pm 32	38 \pm 38	210 \pm 210	0 \pm 0	0 \pm 0
2004	0 \pm 0	431 \pm 91	0 \pm 0	10 \pm 10	0 \pm 0	67 \pm 67
80 m						
2000	1,802 \pm 181	412 \pm 16	0 \pm 0	219 \pm 10	0 \pm 0	0 \pm 0
2001	1,468 \pm 191	36 \pm 4	124 \pm 29	67 \pm 29	0 \pm 0	0 \pm 0
2002	86 \pm 29	135 \pm 8	86 \pm 10	29 \pm 10	0 \pm 0	0 \pm 0
2003	0 \pm 0	71 \pm 24	86 \pm 10	29 \pm 29	0 \pm 0	10 \pm 10
2004	0 \pm 0	131 \pm 123	10 \pm 10	0 \pm 0	0 \pm 0	19 \pm 19
92 m						
2000	1,707 \pm 620	283 \pm 99	76 \pm 57	249 \pm 172	0 \pm 0	0 \pm 0
2001	1,182 \pm 19	287 \pm 59	343 \pm 38	67 \pm 10	0 \pm 0	0 \pm 0
2002	114 \pm 0	346 \pm 88	143 \pm 86	0 \pm 0	0 \pm 0	0 \pm 0
2003	0 \pm 0	210 \pm 85	420 \pm 38	10 \pm 10	0 \pm 0	0 \pm 0
2004	0 \pm 0	471 \pm 81	0 \pm 0	48 \pm 48	0 \pm 0	0 \pm 0

Nalepa *et al.* 2006b). The remote influence of *Dreissena* on *Diporeia* was very evident at the Cape Rich sites and contrasted to the depth-progressive decline observed in the main basin. Over the 5-year sampling period, decline rates at the shallowest (20 m) and deepest (92 m) sites off Cape Rich were the same despite *Dreissena* being present only at the former depth. While the loss of *Diporeia* typically occurred in areas far-removed from *Dreissena*, the continued presence of *Diporeia* in some areas seemed to correspond to the relative absence of *Dreissena*. For instance, in 2003 *Diporeia* was present at depths < 50 m only in the northeast portion of the lake, and this was the only lake area where *Dreissena* was rare. This inconsistent spatial pattern between abundances of *Diporeia* and *Dreissena* in Lake Huron was similar to that found in Lake

Michigan where the loss of *Diporeia* was closely associated with the presence/increase of *Dreissena* at some locations but not at others (Nalepa *et al.* 2006b).

A lake wide survey of *Diporeia* and *Dreissena* was conducted in Lake Michigan in 2000 (Nalepa *et al.* 2006b), the same year as our Lake Huron survey. When densities of *Diporeia* in the two lakes were compared, densities in Lake Michigan were 2.8, 1.9, 1.6, and 1.3 times greater than densities in Lake Huron at the 18–30 m, 31–50 m, 51–90 m, and > 90 m intervals, respectively (Fig. 5). When the same comparison was made for *Diporeia* in the mid-1960s at the shallowest interval, densities were 2.6 times greater in Lake Michigan. The ratio in the two lakes has thus apparently not changed between the mid-1960s and 2000, indicating declines in *Di-*

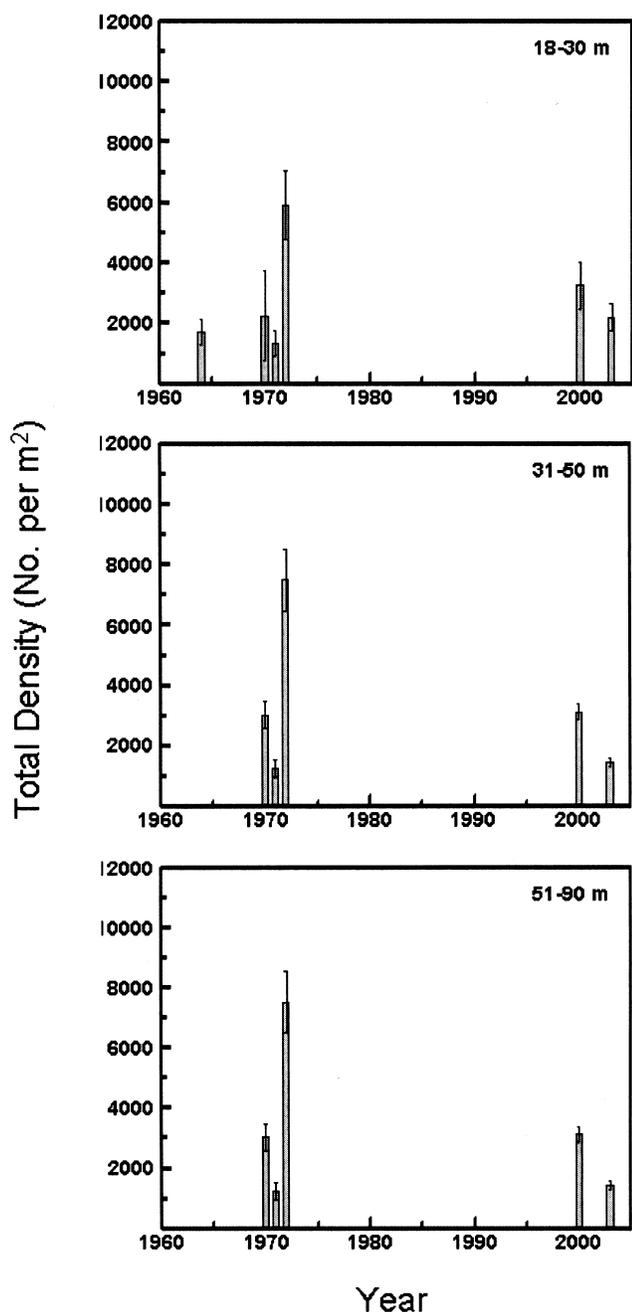


FIG. 4. Mean (\pm SE) total density (No. per m^2) of the four major benthic macroinvertebrate groups (*Diporeia*, *Oligochaeta*, *Sphaeriidae*, *Chironomidae*) at three depth intervals in the main basin of Lake Huron between 1963 and 2003. All sites included except those in inner Saginaw Bay, Georgian Bay, and North Channel. Years: 1963-1964 (Barton 1986), 1970 (Schelske and Roth (1973), 1971 (Shrivastava 1974), 1972 (GLRD unpublished), and 2000 and 2003 (this study).

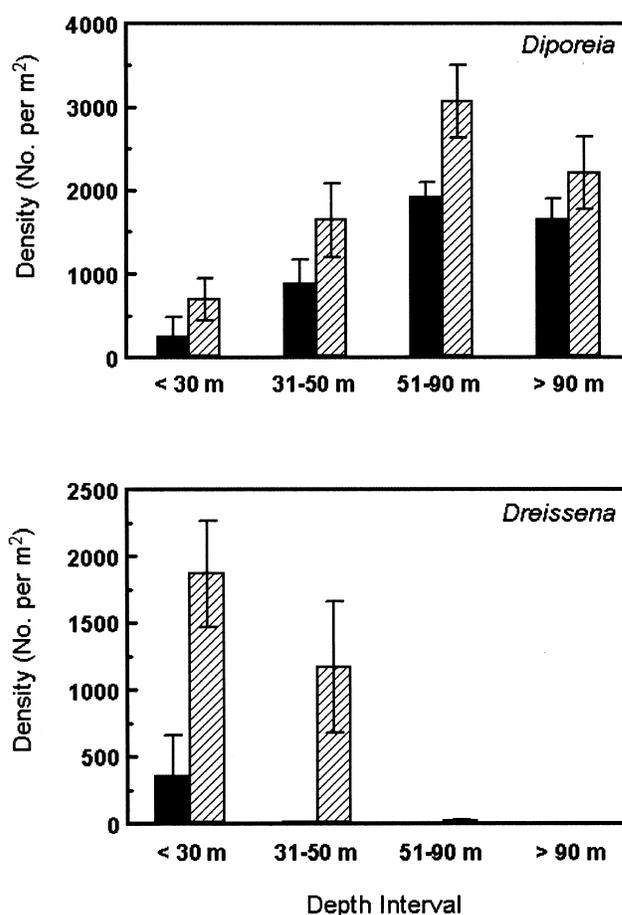


FIG. 5. Mean (\pm SE) density (No. per m^2) of *Diporeia* (top) and *Dreissena* (bottom) at four depth intervals in Lake Huron (solid) and Lake Michigan (hatched). Densities based on lakewide surveys in 2000 in both Lake Michigan (Nalepa et al. 2006a) and Lake Huron (this study).

poreia appear to be similar in the two lakes despite far lower densities of *Dreissena* in Lake Huron (Fig. 5).

Densities of *D. polymorpha* were stable in the main basin between our two sampling periods, but densities of *D. bugensis* increased, particularly in the 31–50 m depth interval. *D. bugensis* was first found in Lake Huron in the Straits of Mackinac region in 1997 (Nalepa et al. 2001). Over time, we expect *D. bugensis* to continue to increase in deeper regions (> 50 m), and also to replace *D. polymorpha* in shallow regions (< 50 m), as it has done in Lake Ontario (Mills et al. 1999). As the *D. bugensis* population continues to expand, we also expect that *Diporeia* and other major taxa will continue to

decline. A functional food web shift from *Diporeia* to *Dreissena* will have strong consequences to other components of the Lake Huron food web, particularly fish species that rely on *Diporeia* as a major source of food. Because of the continued loss of *Diporeia*, lake whitefish in Lake Huron have switched to other diet items such as *Dreissena*, zooplankton, and chironomids (Pothoven and Nalepa 2006). These other food items have a lower energy density than *Diporeia* and, as a consequence, energy intake of lake whitefish was estimated to be less than one-half the intake prior to *Diporeia*'s decline (McNickle et al. 2006). Growth and condition of whitefish in Lake Huron have decreased, similar to decreases noted in the other Great Lakes where *Diporeia* have disappeared (Mohr and Nalepa 2005). Further, alewife populations in Lake Huron have recently collapsed (Roseman et al. 2006) and, while exact reasons are still unclear, the collapse was temporally coincident with the loss of *Diporeia* and the expansion of *D. bugensis*. In Lake Michigan, declines in abundance and/or energy density of alewife have been linked to the decline of *Diporeia* (Hondorp et al. 2005, Madenjian et al. 2006). Integrated monitoring of all food web components including the benthic macroinvertebrate community will provide further insights into the changing nature of the Lake Huron ecosystem.

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REFERENCES

- Bailly, A., and MacIssac, H.J. 2000. Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. *Freshwater Biol.* 43:85–97.
- Barton, D.R. 1986. *Benthic fauna from Great Lakes Institute cruises on Lake Huron and Georgian Bay 1963 and 1964*. Can. Tech. Rep. Fish. Aquat. Sci. 1487.
- . 1989. Some problems affecting the assessment of Great Lakes water quality using benthic macroinvertebrates. *J. Great Lakes Res.* 15:611–622.
- . 2004. Differences in wave-zone benthic invertebrate communities in Lake Huron and Georgian Bay, 1974–2003. *J. Great Lakes Res.* 30:508–518.
- Beeton, A.M., Sellinger, C.E., and Reid, D.F. 1999. An introduction to the *Great Lakes ecosystem*. In *Great Lakes Fisheries Policy and Management: a Binational Perspective*, W.W. Taylor and C.P. Ferreri, eds., pp. 3–54. Michigan State University Press, East Lansing, MI.
- Botts, P.S., Patterson, B.A., and Schloesser, D.W. 1996. Zebra mussel effects on benthic invertebrates: physical or biotic? *J. N. Amer. Benthol. Soc.* 15:179–184.
- Cook, D.G., and Johnson, M.G. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. *J. Fish. Res. Board Can.* 31: 763–782.
- Dermott, R. 2001. Sudden disappearance of the amphipod *Diporeia* from eastern Lake Ontario, 1993–1995. *J. Great Lakes Res.* 27: 423–433.
- , and Kerec, D. 1997. Changes to the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. *Can. J. Fish. Aquat. Sci.* 54: 922–930.
- Dobiesz, N.E., McLeish, D.A., Eshenroder, R.L., Bence, J.R., Mohr, L.C., Henderson, B.A., Ebener, M.P., Nalepa, T.F., Wolft, A.P., Johnson, J.E., Argyle, R.L., and Makarewicz, J.C. 2005. Ecology of the Lake Huron Fish Community 1970–1999. *Can. J. Fish. Aquat. Sci.* 62:1432–1451.
- Flannagan, J. F. 1970. Efficiencies of various grabs and corers in sampling freshwater benthos. *J. Fish. Res. Board Can.* 27:1691–1700.
- Gardner, W.S., Quigley, M.A., Fahnenstiel, G.L., Scavia, D., and Frez, W. A. 1990. *Pontoporeia hoyi*—a direct trophic link between spring diatoms and fish in Lake Michigan. In *Large Lakes Ecological Structure and Function*. M.M. Tilzer and C. Serruya, eds. New York: Springer-Verlag.
- Gonzalez, M.J., and Downing, A. 1999. Mechanisms underlying amphipod responses to zebra mussel (*Dreissena polymorpha*) invasion and implications for fish-amphipod interactions. *Can. J. Fish. Aquat. Sci.* 56:679–685.
- Haynes, J.M., Tisch, N.A., Mayer, C.M., and Rhyne, R.S. 2005. Benthic macroinvertebrate communities in southwestern Lake Ontario following invasion of *Dreissena* and *Echinogammarus*: 1993 to 2000. *J. N. Amer. Benthol. Soc.* 24:148–167.
- Hecky, R.E., Smith, R.E.H., Barton, D.R., Guilford, S.J., Taylor, W.D., Charlton, M.N., and Howell, T. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurent-

- ian Great Lakes. *Can. J. Fish. Aquat. Sci.* 61: 1285–1293.
- Hondorp, D.W., Pothoven, S.A., and Brandt, S.B. 2005. Influence of *Diporeia* density on the diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. *Trans. Am. Fish. Soc.* 134:588–601.
- Howell, E.T., Marvin, C.H., Bilyea, R.W., Kauss, P.B., and Somers, K. 1996. Changes in environmental conditions during *Dreissena* colonization of a monitoring station in eastern Lake Erie. *J. Great Lakes Res.* 22:744–756.
- Howmiller, R.P., and Scott, M.A. 1977. An environmental index based on relative abundance of oligochaete species. *J. Water Pollut. Cont. Fed.* 49:809–815.
- Johnson, M. G., and McNeil, O. C. 1986. Changes in abundance and species composition in benthic macroinvertebrate communities of the Bay of Quinte, 1966–1984. In: Project Quinte: *point source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario*. C.K. Minns, D.A. Hurley, and K.H. Nicholls, eds. Can. Spec. Publ. Fish. Aquat. Sci. No. 86.
- Kreiger, K.A., and Ross, L.S. 1993. Changes in the benthic macroinvertebrate community of the Cleveland Harbor area of Lake Erie from 1978 to 1989. *J. Great Lakes Res.* 19:237–249.
- Lauer, T.E., and McComish, T.S. 2001. Impact of zebra mussels (*Dreissena polymorpha*) on fingernail clams (Sphaeriidae) in extreme southern Lake Michigan. *J. Great Lakes Res.* 27:230–238.
- Lauritsen, D.D., Mozley, S.C., and White, D.S. 1985. Distribution of oligochaetes in Lake Michigan and comments on their use as indices of pollution. *J. Great Lakes Res.* 11:67–76.
- Loveridge, C.C., and Cook, D.G. 1976. *A preliminary report on the benthic invertebrates of Georgian Bay and North Channel*. Can. Dept. Environ. Fish. Mar. Serv., Tech. Rep. 610.
- Lozano, S.J., Scharold, J.V., and Nalepa, T.F. 2001. Recent declines in benthic macroinvertebrate densities in Lake Ontario. *Can. J. Fish. Aquat. Sci.* 58: 518–529.
- Madenjian, C.P., Pothoven, S.A., Dettmers, J.M., and Holuszko, J.D. 2006. Changes in seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels. *Can. J. Fish. Aquat. Sci.* 63:891–902.
- McNickle, G.G., Rennie, M.D., and Sprules, W.G. 2006. Changes in benthic invertebrate communities of South Bay, Lake Huron following invasion by zebra mussels (*Dreissena polymorpha*), and potential effects on Lake Whitefish (*Coregonus clupeaformis*) diet and growth. *J. Great Lakes Res.* 32:180–193.
- Milbrink, G. 1983. An improved environmental index based on the relative abundance of oligochaete species. *Hydrobiologia* 102:89–97.
- Mills, E.L., Chrisman, J.R., Balswin, B., Owens, R.W., O’Gorman, R.O., Howell, T., Roseman, E.F., and Raths, M.K. 1999. Changes in the dreissenid community in the lower Great Lakes with emphasis on southern Lake Ontario. *J. Great Lakes Res.* 25:187–197.
- Mohr, L.C., and Nalepa, T.F. 2005. *Proceedings of a Workshop on the Dynamics of Lake Whitefish (Coregonus clupeaformis) and the Amphipod Diporeia spp. in the Great Lakes*. Technical Report 66. Great Lakes Fishery Commission, Ann Arbor, MI.
- Nalepa, T.F. 1987. Long term changes in the macrobenthos of southern Lake Michigan. *Can. J. Fish. Aquat. Sci.* 44:515–524.
- , Hartson, D.J., Gostenik, G.W., Fanslow, D.L., and Lang, G.A. 1996. Changes in the freshwater mussel community of Lake St. Clair: from Unionidae to *Dreissena polymorpha* in eight years. *J. Great Lakes Res.* 22:354–369.
- , Hartson, D.J., Fanslow, D.L., Lang, G.A., and Lozano, S.J. 1998. Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980–1993. *Can. J. Fish. Aquat. Sci.* 55:2402–2413.
- , Schloesser, D.W., Pothoven, S.A., Hondorp, D.W., Fanslow, D.L., Tuchman, M.L., and Fleischer, G.W. 2001. First finding of the amphipod *Echinogammarus ischnus* and the mussel *Dreissena bugensis* in Lake Michigan. *J. Great Lakes Res.* 27: 384–391.
- , Fanslow, D.L., Lansing, M.B., Lang, G.A., Ford, M., Gostenik, G.W., and Hartson, D.J. 2002. *Abundance, biomass, and species composition of benthic macroinvertebrate populations in Saginaw Bay, Lake Huron, 1987–96*. NOAA Technical Memorandum GLERL-122, Great Lakes Environmental Research Laboratory, Ann Arbor, MI.
- , Fanslow, D.L., Lansing, M.B., and Lang, G.A. 2003. Trends in the benthic macroinvertebrate community of Saginaw Bay, Lake Huron, 1987 to 1996: responses to phosphorus abatement and the zebra mussel, *Dreissena polymorpha*. *J. Great Lakes Res.* 29:14–33.
- , Rockwell, D.C., and Schloesser, D. W. 2006a. *Disappearance of the amphipod Diporeia spp. in the Great Lakes: Workshop summary, discussion, and recommendations*. NOAA Technical Memorandum GLERL-136. NOAA, Great Lakes Environmental Research Laboratory, Ann Arbor, MI.
- , Fanslow, D.L., Foley, A.J., III, Lang, G.A., Eadie, B.J., and Quigley, M.A. 2006b. Continued disappearance of the benthic amphipod *Diporeia* spp. in Lake Michigan: is there evidence for food limitation? *Can. J. Fish. Aquat. Sci.* 63:872–890.
- , Fanslow, D.L., Pothoven, S.A., Foley, A.J., III, Lang, G.A., Mozley, S.C., and Winnell, M.W. 2007. *Abundance and distribution of benthic macroinvertebrate populations in Lake Huron in 1972 and*

- 2000–2003. NOAA Technical Memorandum GLERL-140. NOAA, Great Lakes Environmental Research Laboratory, Ann Arbor, MI.
- Pothoven, S.A., and Nalepa T.F. 2006. Feeding ecology of lake whitefish in Lake Huron. *J. Great Lakes Res.* 32:489–501.
- Roseman, E.F., Schaeffer, J.S., French J.R.P., III, O'Brien, T.P., and Faul, C.S. 2006. *Status and trends of the Lake Huron deepwater demersal fish community, 2005*. Report to the Great Lakes Fishery Commission, Upper Lakes Meetings, Ypsilanti, MI, March, 2006.
- Saether, O.A. 1980. The influence of eutrophication on deep lake benthic invertebrate communities. *Prog. Water Technol.* 12:161–180.
- Schelske, C.L., and Roth, J.C. 1973. *Limnological survey of Lakes Michigan, Superior, Huron, and Erie*. Great Lakes Research Division Publ. No. 17, University of Michigan, Ann Arbor, MI.
- Schloesser, D.W., Kreiger, K.A., Ciborowski, J.J.H., and Corkum, L.D. 2000. Recolonization and possible recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: *Hexagenia* spp.) in Lake Erie of the Laurentian Great Lakes. *J. Aquat. Ecosys. Stress. Recov.* 8:125–141.
- Shrivistava, H. 1974. *Macrobenthos of Lake Huron*. Fish. Res. Bd. Canada, Tech. Rep. 449.
- Strayer, D.L., and Smith, L.C. 2001. The zoobenthos of the freshwater tidal Hudson River and its response to the zebra mussel (*Dreissena polymorpha*) invasion. *Arch. Hydrobiol. Suppl.* 139:1–52.
- Teter, H.E. 1960. The benthic fauna of Lake Huron. *Trans. Am. Fish. Soc.* 89:1983–197.
- Winnell, M.H., and White, D.S. 1985. Trophic status of southeastern Lake Michigan based on the Chironomidae (Diptera). *J. Great Lakes Res.* 11:540–548.

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