Recent declines in benthic macroinvertebrate densities in Lake Ontario[1]

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Abstract: Surveys of benthic macroinvertebrates conducted in Lake Ontario during 1994 and 1997 revealed recent declines in populations of three major taxonomic groups: Oligochaeta, Sphaeriidae, and *Diporeia* spp. (Amphipoda), with the most drastic reductions occurring in the latter. Results from sediment measurements were used to classify deepwater sediments into three habitat zones. Densities of all three taxa declined in the shallowest (12–88 m) of the sediment zones between 1994 and 1997; the greatest changes in density were observed for *Diporeia*, which declined from 3011 to 145 individuals·m^{-2}, and for total benthic macroinvertebrates, which declined from 5831 to 1376 individuals·m^{-2}. Mean densities of *Dreissena* spp. in 1997 were highest in the shallowest zone, and the areas of greatest densities corresponded to areas of largest reductions in *Diporeia* populations. We believe that dreissenids are competing with *Diporeia* by intercepting the supply of fresh algae essential for *Diporeia* survival. A decline in macroinvertebrate densities, especially populations of an important food item such as *Diporeia*, in Lake Ontario sediments at depths of 12–88 m may have a detrimental impact on the benthic food web.

Résumé : Des inventaires des macroinvertébrés benthiques du lac Ontario en 1994 et 1997 ont révélé des déclins récents dans les peuplements de trois importants groupes taxonomiques, les oligochètes, les sphaeriidés et, de façon encore plus marquée, les amphipodes *Diporeia* spp. Des analyses de sédiments ont permis de classifier les substrats de la zone profonde en trois types d'habitats. Les densités des trois taxons ont diminué dans la zone la moins profonde (12–88 m) de 1994 à 1997; les déclins les plus importants se sont manifestés chez les *Diporeia*, don't les densités sont passées de 3011 à 145 individus·m^{-2}, et dans le peuplement total de macroinvertébrés qui a baissé de 5831 à 1376 individus·m^{-2}. Les densités moyennes les plus élevées de *Dreissena* spp. en 1997 ont été retrouvées dans la zone la moins profonde, leurs densités maximales correspondant aux régions des plus forts déclins des peuplements de *Diporeia*. Nous croyons que les dreissénidés font compétition aux *Diporeia* en leur bloquant l'accès aux algues fraîches nécessaires à leur survie. Un déclin des densités des macroinvertébrés, particulièrement celui d'une ressource alimentaire importante comme les peuplements de *Diporeia*, dans les sédiments du lac Ontario aux profondeurs 12–88 m peut avoir un effet néfaste sur le réseau alimentaire benthique.

[Traduit par la Rédaction]

Introduction

The deepwater, benthic macroinvertebrate community of the Great Lakes is dominated by a few species of organisms. The cold–stenotherm association includes Oligochaeta, Sphaeriidae, and *Diporeia* spp. (Cook and Johnson 1974). Two species of oligochaetes, *Stylodrilus heringianus* and *Limnodrilus hoffmeisteri,* are found throughout the offshore regions and may account for 10–20% of the total benthic population density (Mozley and Howmiller 1977). Members of the bivalve family Sphaeriidae are usually found in waters less than 90 m deep and account for 5–15% of the total benthic population density. The amphipod *Diporeia* spp. (for-merly *Pontoporeia hoyi*) is the most abundant macro-invertebrate (Mozley and Howmiller 1977; Nalepa 1991) in the Great Lakes. In deeper water habitats, it accounts for 40–70% of the total density of benthic organisms (Nalepa 1991), reaching greatest densities at depths below the summer thermocline in waters 30–60 m deep.

In the Great Lakes, *Diporeia* is found in greatest numbers in soft or fine sediments and in sand overlain with a thin layer of detritus (Marzolf 1965). An important source of food for *Diporeia* arrives in the spring and fall when water conditions favor diatom blooms and subsequent settling of diatoms onto the sediments (Saether 1980). *Diporeia* depends on settling algae for growth and reproduction, storing

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Fig. 1. Location of sampling stations in Lake Ontario in (*a*) 1994 and (*b*) 1997.
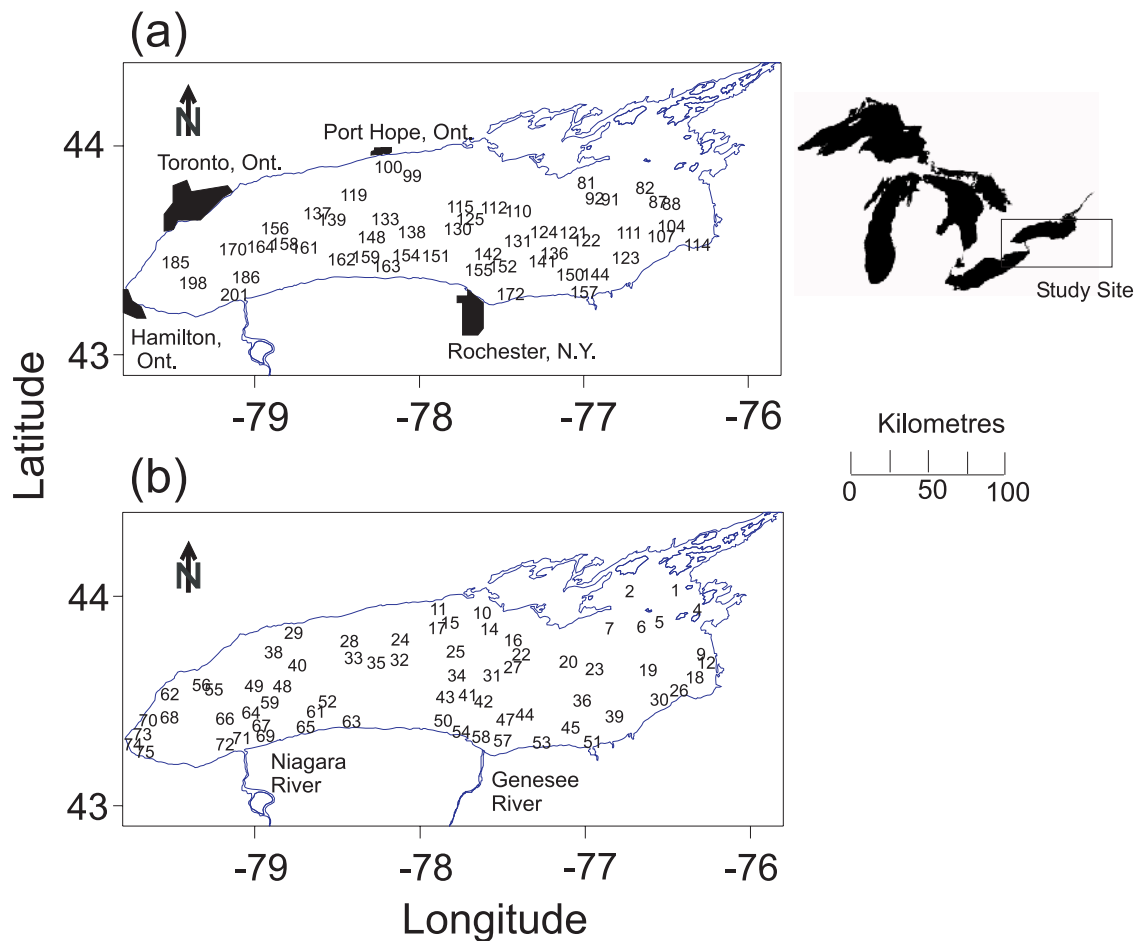
the assimilated energy as lipid. Lipid levels of *Diporeia* are high compared with those of other Great Lakes benthic macro-invertebrates and can account for up to 50% of the amphipods' dry weight after the spring diatom bloom (Gardner et al. 1985). It has been estimated that within deeper water habitats of the Great Lakes, 23% of the total annual carbon production from phytoplankton is consumed by this organism (Flint 1986). Fitzgerald and Gardner (1993) reported that *Diporeia* ingested 61% of the spring diatom bloom in Lake Michigan. A large portion of *Diporeia* biomass is transferred up the food chain to forage fish. *Diporeia* is the dominant food organism of the slimy sculpin in Lake Ontario (Owens and Weber 1995) and most other fish species feed on *Diporeia* at some stage in their life cycle (Mozley and Howmiller 1977). Because of the importance of benthic macroinvertebrates and particularly *Diporeia* in fish diets, changes in the status of *Diporeia* or the other two major taxa could have dramatic effects on fish production in the Great Lakes.

Colonization by the dreissenid mussels *Dreissena polymorpha* and *Dreissena bugensis* is probably one of the more ecologically important events to occur in the Great Lakes during the last decade (MacIsaac 1996). Since their discovery in 1988, dreissenids have colonized both soft and hard substrates to depths of 130 m (Mills et al. 1993) and reached

densities of 340 000·m^{-2} in some areas (Leach 1993). Because of high densities, widespread distribution, and high filtering rates, *Dreissena* populations can filter large volumes of water and have the capacity to decrease algal biomass (Holland 1993; Fahnenstiel et al. 1995). Therefore, this diversion of algal production into dreissenid tissue and biodeposits may deprive *Diporeia* and other deepwater macroinvertebrates of food settling from the water column.

In this study, we examined changes in densities of *Diporeia*, Oligochaeta, and Sphaeriidae in Lake Ontario between 1994 and 1997 and relate these changes to those observed over the past three decades. We present evidence that all three taxonomic groups have declined in density in waters between 12 and 88 m at a time when *Dreissena* densities were increasing.

Methods

Macroinvertebrate sampling design and processing

Benthic samples were collected from Lake Ontario in late August 1994 and early September 1997 at 55 and 75 stations, respectively (Fig. 1). Sampling depths ranged from 12 to 213 m. Station locations in 1994 and 1997 were based on a randomized design using a systematic grid (Stevens 1997). Locations in 1994 were then classified into habitat zones based on principal components analysis (PCA) of physical and chemical data (see below). Because only a subset of physical and chemical measurements were taken in 1997,

Table 1. Physical and chemical characteristics of Lake Ontario sediments from the 1994 survey by three sediment classifications; percentage variation and loadings for the first two axes of the principal components analysis (PCA) for physical and chemical characteristics.

		Physical parameters					Chemical parameters		Survival (%)	
Sediment zones	No.	Depth (m)	Sand (%)	Silt (%)	Clay (%)	Carbon (%)	NH_3 (µg·L^{-1})	Sulfide (µg·L^{-1})	Chironomus	Hyallela
Low-depositional	10	45	74.7 (5.32)	23.8 (4.94)	0.21 (0.04)	1.65 (0.43)	4.28 (1.88)	1.12 (1.10)	93.5 (2.84)	97.6 (0.69)
Transitional	7	81	29.9 (4.41)	67.4 (4.30)	0.43 (.12)	3.23 (0.38)	1.78 (0.30)	14.3 (11.4)	97.5 (0.77)	96.8 (1.41)
High-depositional	34	147	13.2 (2.12)	82.4 (2.11)	1.03 (0.07)	3.24 (0.17)	1.09 (0.21)	2.13 (1.48)	93.1 (1.33)	93.2 (1.07)
Principal component loadings									Survival (%)	
PCA		Depth (m)	Sand (%)	Silt (%)	Clay (%)	Carbon (%)	NH_3 (µg·L^{-1})	Sulfide (µg·L^{-1})	Chironomus	Hyallela
1st Axis (40)[a]		0.83	–0.96	0.96	0.78	0.65	–0.51	0.04	–0.45	–0.06
2nd Axis (14)[a]		–0.96	–0.15	0.15	–0.08	0.43	0.41	0.57	0.36	0.72

Note: No. = number of stations located in each sediment zone. Depth and physical and chemical values are means (±SE).

[a]Values in parentheses represent percentage of variation explained.

classification of these locations was based on grain size and depth, two of the most important discriminating measurements as determined by PCA. Position for sampling was determined by a Loran C navigation.

At each station, three samples were taken with a Ponar grab (area = 0.048 m^2); the samples were pooled into a single sample, placed into an elutriation device, and washed through a nylon sleeve with a 500-µm opening (Mozley and Howmiller 1977). The residue retained was preserved in 5% formalin containing rose bengal stain. In the laboratory, organisms were initially removed from samples under a dissecting microscope and identified into major taxonomic groups. Later, organisms were identified to the lowest possible taxonomic level. *Dreissena* were counted and identified to species in 1997 but not in 1994.

Sediment collection and analysis

In 1994, an additional Ponar grab sample was collected from each station and sediment from the top 2 cm, assumed to represent the biologically active zone, was placed into clean glass containers and kept at 5°C. These sediments were analyzed for grain size, organic carbon, ammonia, sulfide, and relative toxicity. Standard methods for grain size analysis and total organic carbon were followed (ASTM 1991). Results for grain size were reported as percentage clay (<4 µm), silt (4–60 µm), and sand (>60 µm). Ten-day toxicity tests for *Hyalella azteca* and *Chironomus tentans* were conducted according to standard methods (Ingersoll and Nelson 1990). Results were reported as percentage survival of organisms. Measurements of pore-water ammonia and sulfide concentrations followed methods of Ankley et al. (1993).

Statistical analysis

A principal components analysis (PCA, Wilkinson 1996) was performed using physical and chemical characteristics of sediments collected in 1994 to identify different macroinvertebrate habitat zones. Variables included in the analysis were percentage survival of *Hyalella azteca* and *Chironomus tentans* in toxicity tests, percentage sand, silt, clay, and carbon, depth, ammonia, and sulfide. Mean population densities in each zone (numbers of individuals· m^{-2}) and between year(s) were compared with analysis of variance (ANOVA) and Tukey's test ($p \leq 0.05$) using densities at each station as replicates (Wilkinson 1996). Water depth was included as a covariate term. Variance stabilizing transformations were used prior to data analysis. An arcsine – square root transformation was used for percentage data and a log transformation was used for macroinvertebrate density data.

Results

Sediment analysis

Results from PCA indicate that the first principal component accounted for 40% of total variability with depth, % sand, and % silt being the variables that correlated most highly with the first axis (Table 1). In general, sand and silt accounted for the majority of dry sediment mass at all stations, with clay comprising <2% of the remaining sediment mass at each site. Thus deepwater stations with high amounts of silt and clay are located to the right of where the PC1 and PC2 axes intersect (Fig. 2). As a result, a strong negative correlation exists between sand and silt such that areas with high % sand have low % silt, and vice versa. The second principal component accounted for 14% of the variability with percentage survival of *H. azteca*, ammonia, and sulfide levels being most highly correlated with the second axis.

The results of PCA for habitat characteristics with the 1994 data revealed three groupings of stations (Table 1, Fig. 2).

Fig. 2. Classification of Lake Ontario sediments by principal components analysis (PCA) for physical and chemical parameters, 1994. Variables used in PCA included depth, NH_3, and sulfide ($\mu g \cdot L^{-1}$), survival of *Hyalella azteca* and *Chironomus tentans* (percentage survival), and percentage sand, silt, clay, and carbon.
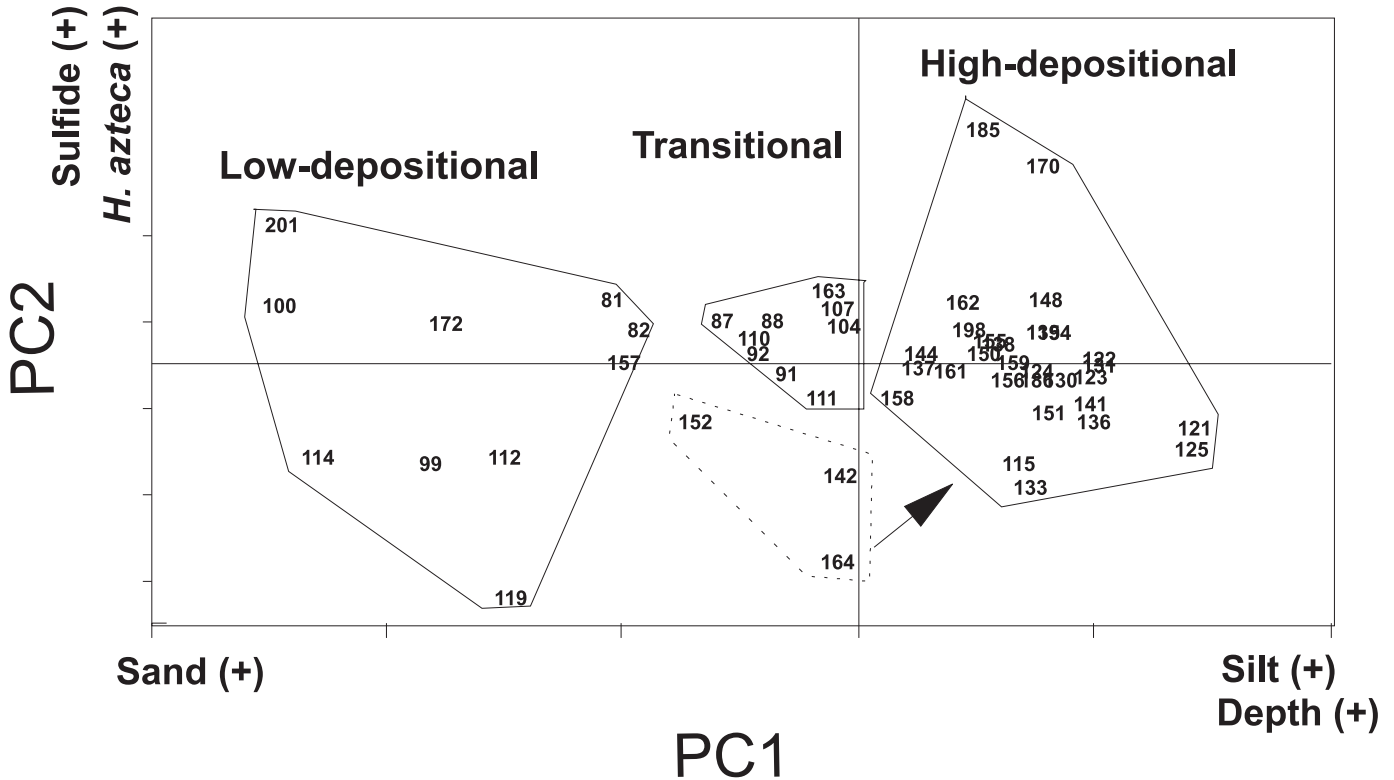
The three groupings were identified as low-depositional, transitional, and high-depositional areas (Table 1, Figs. 1, 2). The low-depositional zone included stations with a high ratio of sand to silt and low % carbon; these stations were generally located in shallower, nearshore regions (12–88 m). The high-depositional zone was characterized by stations with sediments of a higher ratio of silt to sand and high % clay relative to sediments from other stations. High-depositional stations were deeper (90–213 m) and located centrally in the lake. The transitional zone included stations with sediments having a mixture of sand and silt and % clay that was intermediate between low- and high-depositional stations. Depths in this zone were intermediate (63–91 m) and stations were located between the low-depositional and high-depositional zone (Fig. 1, 2). Three stations (stations 142, 152, and 164) were intermediate in sand and silt but located in deeper water, i.e., greater than 134 m (Fig. 1). These stations were located on the Whitby–Olcott and Scotch Bonnet sills (Thomas et al. 1972) that separate the Lake Ontario basin into three deepwater high-depositional zones. For macroinvertebrate analysis, stations located on the sills were placed in the high-depositional group.

Macroinvertebrate densities

Three taxa, *Diporeia* spp., Oligochaeta, and Sphaeriidae, comprised 91–99% of all macroinvertebrates collected in 1994 and 1997. There were significant differences for major taxa within sediment zones. In the low-depositional zone, densities of *Diporeia* were most abundant at depths greater than 42 m in 1994 but no pattern was discernable along the

depth gradient sampled in 1997 (Table 2). At stations where *Diporeia* were abundant, densities averaged $6363 \cdot m^2$ in 1994 compared with $954 \cdot m^2$ in 1997. Further, the percentage of stations where no or very few *Diporeia* ($<5 \ m^2$) were found increased from 40% in 1994 to 84% in 1997. In the transitional and high-depositional zones, there was little association between depth and *Diporeia* densities in 1994 or 1997, and at stations where *Diporeia* were abundant, densities were comparable. There were no apparent patterns between densities of Oligochaeta or Sphaeriidae and depth within any of the three sediment zones.

Results from ANOVA of mean densities with main effects of differences between years and sediment zones were statistically significant for all three taxa and total macroinvertebrate density with *p*-values of 0.001–0.008. The covariate term water depth was never a significant factor in the ANOVA with *p*-values of 0.146–0.504. Densities of *Diporeia*, Oligochaeta, and Sphaeriidae and total macroinvertebrates were significantly (Tukey's test) lower in 1997 compared with 1994 in the low-depositional zone (Table 3), with percentage declines of 95, 61, 45, and 76%, respectively. Densities of Oligochaeta, but not *Diporeia* and Sphaeriidae, were significantly lower in 1997 compared with 1994 in the high-depositional zone, with a percentage decline of 58%. Another general trend, although not always statistically significant, was for densities to be lower in the high-depositional zone compared with the other two sediment zones for all three taxa and total macroinvertebrates (Table 3). In the transitional zone, there were no significant differences in densities of the three taxa and total abundance

Table 2. Densities (no.·m^{-2}) of four major taxa in Lake Ontario are ordered by depth and grouped by sediment zones.

		1994					1997			
Depth (m)	Station	Diporeia	Oligochaeta	Sphaeriidae	Depth (m)	Station	Diporeia	Oligochaeta	Sphaeriidae	Dreissena
Low-depositional zone										
12	114	0	530	155	14	1	0	0	0	1511
12	201	185	5671	237	15	15	276	800	516	920
20	172	0	5662	103	18	75	0	4129	467	93
23	157	0	525	22	19	51	0	342	0	2587
42	81	4	3907	947	20	74	0	2071	280	173
48	100	7528	1277	1477	23	63	0	2218	4	2133
59	82	2054	1369	588	25	30	0	187	0	5640
59	99	6473	1036	327	26	2	4	116	0	49
83	112	6983	1036	207	26	29	4	111	316	22
88	119	5952	1603	172	27	4	0	111	0	9
					27	26	0	53	0	258
					27	62	0	369	440	4
					29	58	0	3280	0	3480
					31	10	0	0	0	2022
					31	54	0	2062	4	1987
					33	12	0	173	18	13
					37	11	0	284	58	3964
					38	9	0	133	9	147
					40	53	4	236	378	1089
					40	73	0	893	462	0
					43	6	0	378	84	0
					45	70	1138	2191	2431	18
					46	7	0	409	40	0
					49	5	0	409	0	9
					51	14	453	649	649	111
					56	16	1564	711	449	187
					57	57	0	542	204	36
					58	18	0	796	169	53
					62	17	1058	449	307	311
					64	65	0	849	0	53
					69	69	0	2053	142	756
Transitional zone										
70	163	1322	960	831	63	22	0	520	98	0
75	88	5267	960	771	74	71	3640	2009	200	13
76	87	6202	1069	952	75	72	1729	764	231	0
82	91	7778	501	646	76	28	3751	809	142	9
82	92	7890	681	573	80	38	6280	1307	4	0
89	185	4556	319	134	81	24	5364	849	111	4
96	110	4763	184	138	83	68	3453	227	98	0
					87	56	8813	1324	316	0
					90	50	0	320	93	0
					91	20	436	209	164	0
High-depositional zone										
93	198	2976	440	108	100	67	1760	280	178	0
100	186	5110	511	174	112	25	2636	107	4	4
103	144	4	430	297	112	33	773	129	22	0
114	107	0	1783	332	122	66	1729	196	36	0
115	104	0	610	263	125	64	996	364	40	0
117	159	1848	166	39	130	48	1107	53	40	0
119	137	2407	199	17	134	19	533	178	138	0
122	155	3062	922	168	134	31	2369	142	31	0
125	115	3618	407	34	136	49	778	18	4	0
133	154	2692	345	82	138	23	1062	111	22	0
134	139	426	270	4	138	59	1831	360	27	0

Table 2 (*concluded*).

		1994					1997			
Depth (m)	Station	*Diporeia*	Oligochaeta	Sphaeriidae	Depth (m)	Station	*Diporeia*	Oligochaeta	Sphaeriidae	*Dreissena*
134	164	2192	199	43	139	35	1387	173	18	0
134	170	2588	851	65	140	32	1582	49	0	0
136	156	1507	175	34	143	45	0	218	111	0
139	158	1658	199	56	147	61	1853	671	89	4
140	151	1848	445	30	155	42	409	204	4	0
141	162	1141	558	56	158	39	0	249	89	0
143	150	1447	1339	146	159	34	1591	204	0	0
145	125	1537	95	9	160	52	693	133	4	0
145	152	1809	899	26	163	43	1569	236	18	0
148	124	2519	142	90	170	41	1436	178	4	0
152	133	1451	180	22	175	47	2036	267	0	0
152	161	1757	317	13	200	44	689	71	9	0
156	142	1537	563	34	209	36	458	89	0	0
160	130	1960	572	13	175	47	2164	283	0	0
165	148	2347	662	22	200	44	732	76	9	0
171	131	1891	468	52	209	36	487	94	0	0
175	121	1826	307	9						
180	138	1899	866	22						
195	122	1624	525	26						
196	141	1856	416	0						
203	111	1662	464	4						
210	136	1873	255	0						
213	123	4	951	185						

Table 3. Comparison between densities (no.·m^{-2}) of three major taxa and total invertebrate densities in Lake Ontario by year and three sediment zones.

	Low-depositional zone		Transitional zone		High-depositional zone	
Taxa	1994	1997	1994	1997	1994	1997
No. of stations	10	31	7	10	34	27
Diporeia	3011 (1098) a	145 (69) b	5570 (876) a	3347 (920) a	1884 (184) a	1419 (190) a
Oligochaeta	2125 (603) a	830 (185) bc	631 (121) abc	874 (182) ab	484 (58) b	203 (27) c
Sphaeriidae	437 (150) a	240 (81) bc	596 (127) a	146 (27) ab	75 (15) bc	35 (8.8) c
Total macroinvertebrate	5831 (1013) a	1376 (282) b	6898 (902) a	4358 (1055) ac	2514 (181) ac	1689 (197) c

Note: Values are means (±SE). Values followed by a different letter are significantly different (ANOVA followed by Tukey's test, $p \leq 0.05$ on log-transformed data). Total macroinvertebrate density does not include densities of *Dreissena* spp.

between years and other sediment zones. The lack of significant differences may be partially due to the small number of stations located in this zone.

The spatial distribution pattern of *Diporeia* was different between 1994 and 1997, especially in the low-depositional zone. In 1994, highest population densities were found at stations located along the northern shoreline and at the far eastern end of the lake (Fig. 3a). A contiguous zone of stations with population densities of <4 individuals·m^{-2} occurred along the southeastern shore between the Genessee River outlet and Mexico Bay. In 1997, the number of stations with population densities of <4 individuals·m^{-2} increased and these stations extended all around the lake. The exception was Station 62 near Toronto where densities were 1311·m^{-2}. In some areas, this depauperate zone extended as far as 26 km offshore and to a depth of 160 m and encompassed over 40% of the total area of the lake. The most severe effect was along the southern and eastern shoreline from the outlet of the Niagara River to Point Petre, where *Diporeia* were absent from samples collected in waters 140 m deep or less.

In 1994, there were large numbers (>5000·m^{-2}) of oligochaetes near the mouths of the Niagara (Station 201) and Genessee (Station 172) rivers and along Point Petre (Station 81, Fig. 3b). *Stylodrilus heringianus* was the most abundant oligochaete at these stations, accounting for over 30% of the total number. In 1997, the spatial pattern of Oligochaeta was similar to 1994 but with lower numbers in the low-depositional and high-depositional zones. Relatively high population densities of Sphaeriidae were present at stations located near the Kingston basin (Fig. 3c) in 1994. In 1997, the spatial pattern of Sphaeriidae was different from 1994 with fewer organisms near the eastern end of the lake.

Ponar grab samplers were used to estimate densities of dreissenids in 1997. Although dreissenids were present in 1994, the mussels were not collected or counted. The efficiency of this sampler for collecting attached mussels has

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Fig. 3. Distribution and density (no.·m^{-2}) of (*a*) *Diporeia*, (*b*) Oligochaeta, and (*c*) Sphaeriidae in 1994 and 1997. Kingston basin was not sampled in 1994 (hatched area on map).
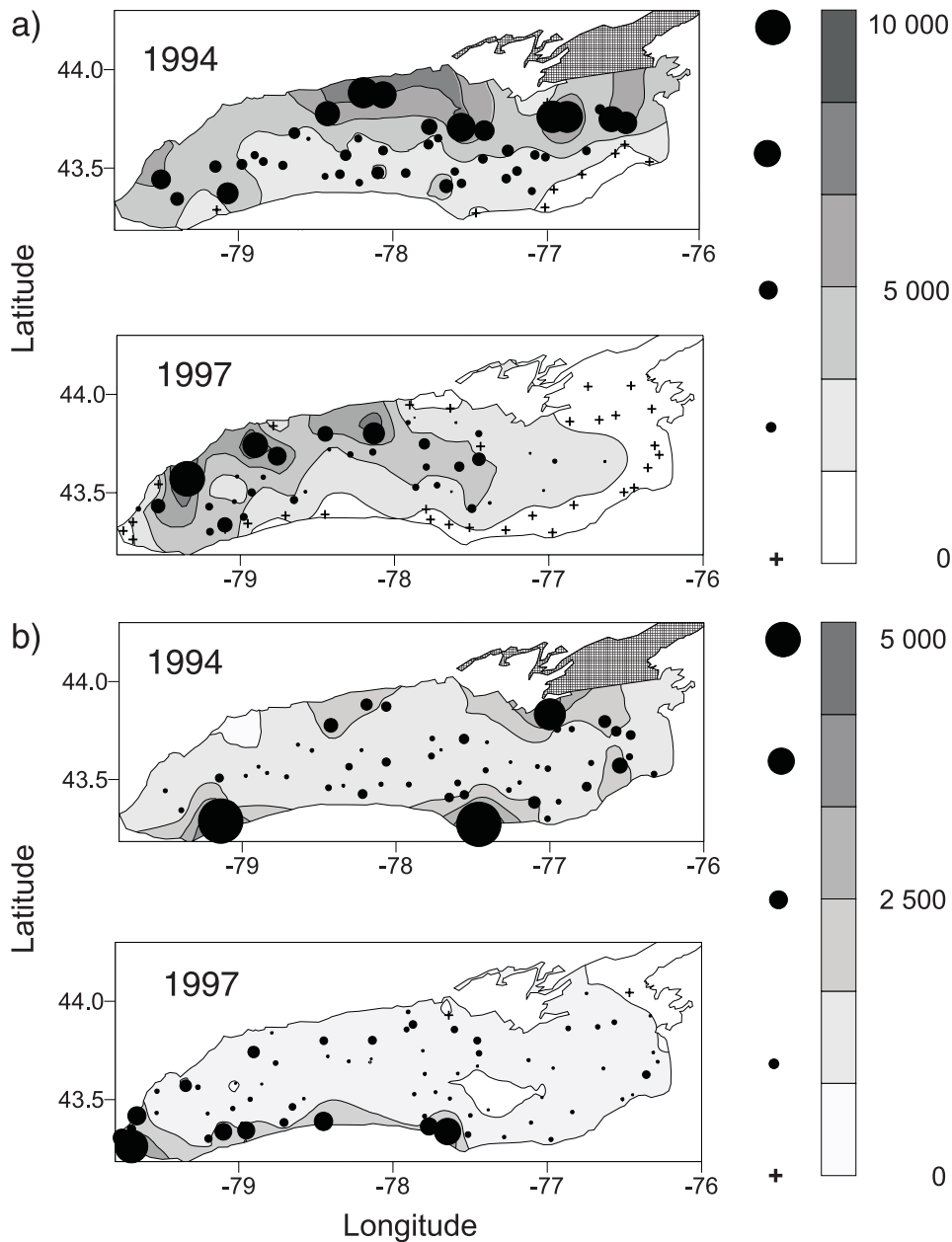
not been quantified so our results are a relative measure of population density and distribution. Mean densities of *Dreissena polymorpha* and *D. bugensis* in 1997 were highest in the low-depositional zone, intermediate in the transitional zone, and lowest in the high-depositional zone (Table 4). Neither species of *Dreissena* was abundant in waters deeper than 70 m. Stations along the south shore from the outlet of the Niagara River to Mexico Bay had the largest numbers of *Dreissena* in waters less than 40 m deep (Fig. 4). There were also large numbers of *Dreissena* near Port Hope, Ontario, and in the Kingston basin. Species richness (mean number of species·site^{-1}) in waters <40 m was greater at stations where *Dreissena* were present (10.1 ± 0.4 (mean ± SE), *t* test, *p* < 0.05) compared with stations where *Dreissena* were absent (6.4 ± 0.3). Several species of Naididae (*Chaetogaster*

diaphanus, *Ophidonais serpentina*, *Stylaria lacustris*, *Vejdovskyella intermedia*), Tubificidae (*Potamothrix moldaviensis*, *P. vejdovskyi*, *Rhyacodrilus coccineus*, *Spirosperma ferox*), and Chironomidae (*Heterotrissocladius* sp., *Chironomus* sp., *Cryptochironomus* sp., *Paracladopelma* sp., *Paralauterborniella* sp., *Tribelos* sp., *Micropsectra* sp., *Tanytarsus* sp.) were more abundant or only found in stations where dreissenids were present.

Discussion

Our data suggest a large change in total and relative density of the macroinvertebrate community in Lake Ontario for areas of the lake deeper than 12 m. If *Dreissena* spp. are excluded from population estimates, our data indicate a major
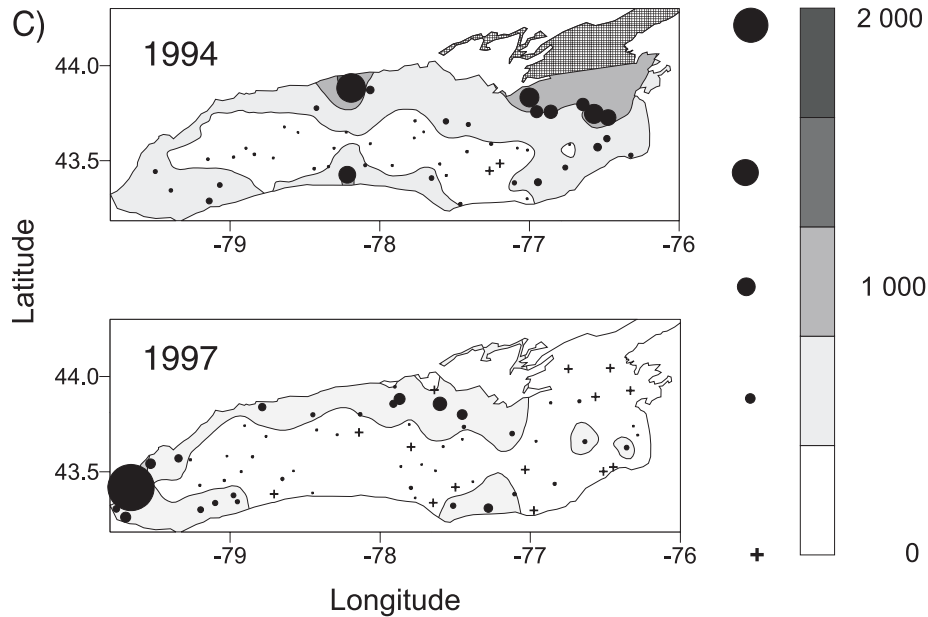
Fig. 3 (*concluded*).

Table 4. Comparison between densities (no.·m^{-2}) of two species of *Dreissena* at three sediment zones.

	Low-depositional zone	Transitional zone	High-depositional zone
No. of stations	31	10	27
Dreissena polymorpha	357 (195) a	0.4 (0.4) bc	0 (0) bc
Dreissena bugensis	535 (174) a	2.2 (1.2) bd	0.3 (0.2) bd

Note: Values are means (±SE). Values followed by a different letter are significantly different (ANOVA followed by Tukey's test, $p \leq 0.05$ on log-transformed data).

decline in total macroinvertebrate densities between 1994 and 1997 in the low-depositional zone (12–88 m). Our results contrast those summarized by Nalepa (1991), who found no change in macroinvertebrate densities in shallow waters (10–35 m) between 1964 and 1988 and an increase in numbers of *Diporeia* in the Kingston basin. To allow comparisons to these earlier studies, we grouped our densities of *Diporeia*, Oligochaeta, and Sphaeriidae by the three depth intervals (Table 5) used by Nalepa (1991) for the two Lake Ontario surveys and tested for differences between years (analysis of variance, ANOVA, Tukey's test, $p < 0.05$) in each depth interval. These comparisons are important because the surveys of Hiltunen (1969) and Nalepa and Thomas (1976) were completed before the invasion of *Dreissena*.

In the shallow depth interval, *Diporeia*, Oligochaeta, and Sphaeriidae were significantly lower in 1997 compared with densities found in 1964 and 1972 (Table 5). Mean densities of *Diporeia* were at least 130 times greater in 1964 and 1972 than in 1997, while mean densities of Sphaeriidae and Oligochaeta were at least nine times greater in 1964 and 1972 than in 1997. The mean density of *Diporeia* in 1994 was 40·m^{-2} but the lack of statistically significant differences compared with earlier surveys is partially due to the small number of stations ($n = 4$) sampled in the shallow depth interval (10–35 m). In the intermediate depth interval, densities of *Diporeia* were significantly greater in 1972 and 1994 (2131–4537·m^{-2}) than in 1997 (1282·m^{-2}). Mean densities of *Diporeia* were much greater in 1964 (9077·m^{-2}) than in

1997 but the lack of statistical significance is also partially due to the small number of stations ($n = 2$) sampled in the intermediate depth interval (36–90 m) in 1964. In the deepest depth interval, results were mixed. Densities of *Diporeia* were variable but never significantly different between years. Densities of Oligochaeta and Sphaeriidae were significantly greater in 1964 than in 1972, 1994, and 1997 but there were no consistent trends after 1972. The spatial distribution of stations where *Diporeia* were absent in Lake Ontario sediments was similar in 1964 and 1972, i.e., the area extended along the south shore from the Niagara River eastward to Rochester, N.Y. (Hiltunen 1969; Nalepa and Thomas 1976). In 1997, we found the area where *Diporeia* was absent to have expanded to all areas around the lake in waters between 10–40 m and down to a depth of 140 m in the zone from the Niagara River eastward and northward to Point Petre, Ont. In addition to whole-lake surveys, Nalepa (1991) also provided a compilation of Lake Ontario benthic studies showing trends from a nearshore area (Kingston basin) of Lake Ontario before the invasion of *Dreissena*.

Between 1964 and 1988, *Diporeia* densities in the Kingston basin (28–35 m) of Lake Ontario were variable. Populations fluctuated between 3000·m^{-2} and 10 000·m^{-2} during the period of 1964 to 1984 and then rose to 13 900·m^{-2} by 1988. We found a mean population of *Diporeia* of less than 1·m^{-2} at six stations (stations 1–7) in the Kingston basin in 1997. Overall, the greatest change from 1964 to the present is a lake-wide decline in density of

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Fig. 4. Distribution and densities (no.·m^{-2}) of the mussel *Dreissena* spp. in 1997.
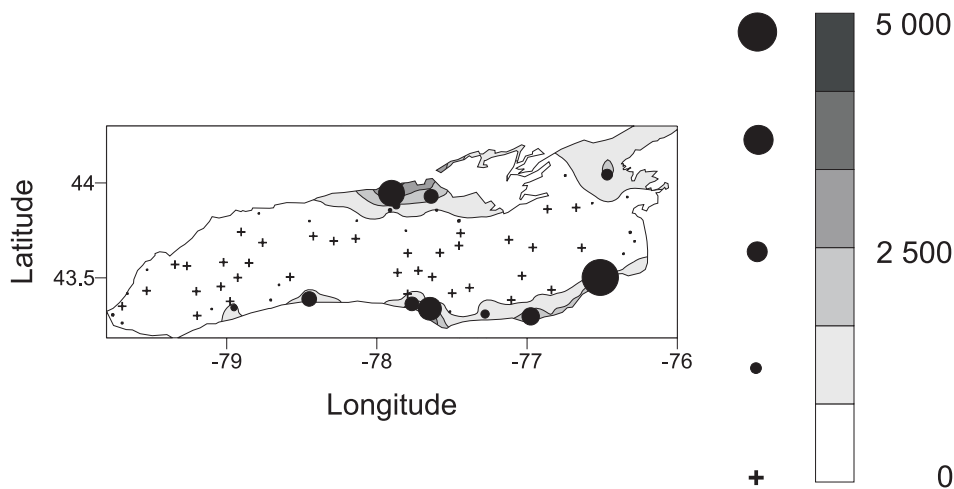
Table 5. Comparison between densities of three major benthic taxa found in 1964 (Hiltunen 1969), 1972 (Nalepa and Thomas 1976), 1994 and 1997 (present study) within three depth intervals.

	1964	1972	1994	1997
Depth 10–35 m				
No. of stations	14	22	4	16
Diporeia	2122 (815) a	2058 (598) a	40 (40) ab	15 (15) b
Oligochaeta	8536 (3203) a	9648 (3197) a	2476 (1186) ab	856 (280) b
Sphaeriidae	3223 (641) a	973 (275) b	113 (40) bc	109 (42) c
Depth 36–91 m				
No. of stations	2	13	12	25
Diporeia	9077 (891) ab	2131 (467) a	4537 (675) a	1281 (405) b
Oligochaeta	2607 (685)	2382 (816)	983 (210)	658 (100)
Sphaeriidae	3697 (262) a	107 (48) b	558 (100) a	233 (81) b
Depth >91 m				
No. of stations	8	20	35	27
Diporeia	1250 (356)	793 (141)	1677 (169)	1207 (162)
Oligochaeta	767 (128) a	353 (56) bc	405 (49) ab	174 (23) c
Sphaeriidae	244 (76) a	17 (12) b	65 (13) c	29 (7) c

Note: Values are means (±SE). Values followed by the same letter identify a significant grouping; values in bold are significantly different (ANOVA, Tukey's test, $p \leq 0.05$ on log-transformed data).

Diporeia down to depths of 140 m and lower densities of all three taxa in the shallow depth interval (10–35 m) and the low-depositional zone.

After the invasion of *Dreissena* spp. into the Great Lakes, ecosystem changes included loss of edible particles (e.g., phytoplankton) and subsequent decline of phytoplankton consumers, diversion of material from the open water to surface sediments as bivalve tissue and biodeposits, and subsequent increase of benthic resources in and around mussel beds (Strayer et al. 1999; Haynes et al. 1999). The negative impact of *Dreissena* spp. on *Diporeia* and other benthic macroinvertebrate species is attributed to its high filtering capacity and large population densities. Since their introduction to Lake Ontario in 1988 or 1989, *Dreissena* populations have expanded, reaching densities of 82 000·m^{-2} in Lake Ontario by 1998 (Schaner 1998). Increased water clarity and declines in phytoplankton density are directly correlated with increased densities of *Dreissena* in Lake Erie and Lake Huron (Fahnenstiel et al. 1995). Mean densities of planktonic diatoms were reduced by 80–92% compared with pre-

mussel periods in Hatchery Bay, western Lake Erie (Holland 1993). Although the reduction of diatom biomass could be the result of other system changes (e.g., reduced phosphorus loadings), concentrations of phosphorus in the open waters of Lake Ontario have remained approximately 10 µg·L^{-1} since 1985 (Neilson et al. 1995).

Some of our results contrast those of Haynes et al. (1999), who found greater densities of Gammarid amphipods but no long-term changes in densities of oligochaetes and other species of macroinvertebrates at 7 m in cobble and artificial substrates after colonization by *Dreissena* in Lake Ontario. We found densities of three taxa to be lower in the low-depositional zone and shallow water interval (10–35 m) of Lake Ontario but species richness to be greater at stations where *Dreissena* were present. The diversion of algae, especially diatoms, from open waters to mussel beds and hard substrates and incorporated into bivalve tissue and biodeposits would benefit species that can use the shells for habitat and (or) biodeposits for food.

Changes in benthic populations in deep lakes have been

Fig. 5. Comparison of the dreissenid densities calculated from regression analysis (dashed line) of 1997 data (open circles) and Bailey et al.'s (1999) estimates (solid line).
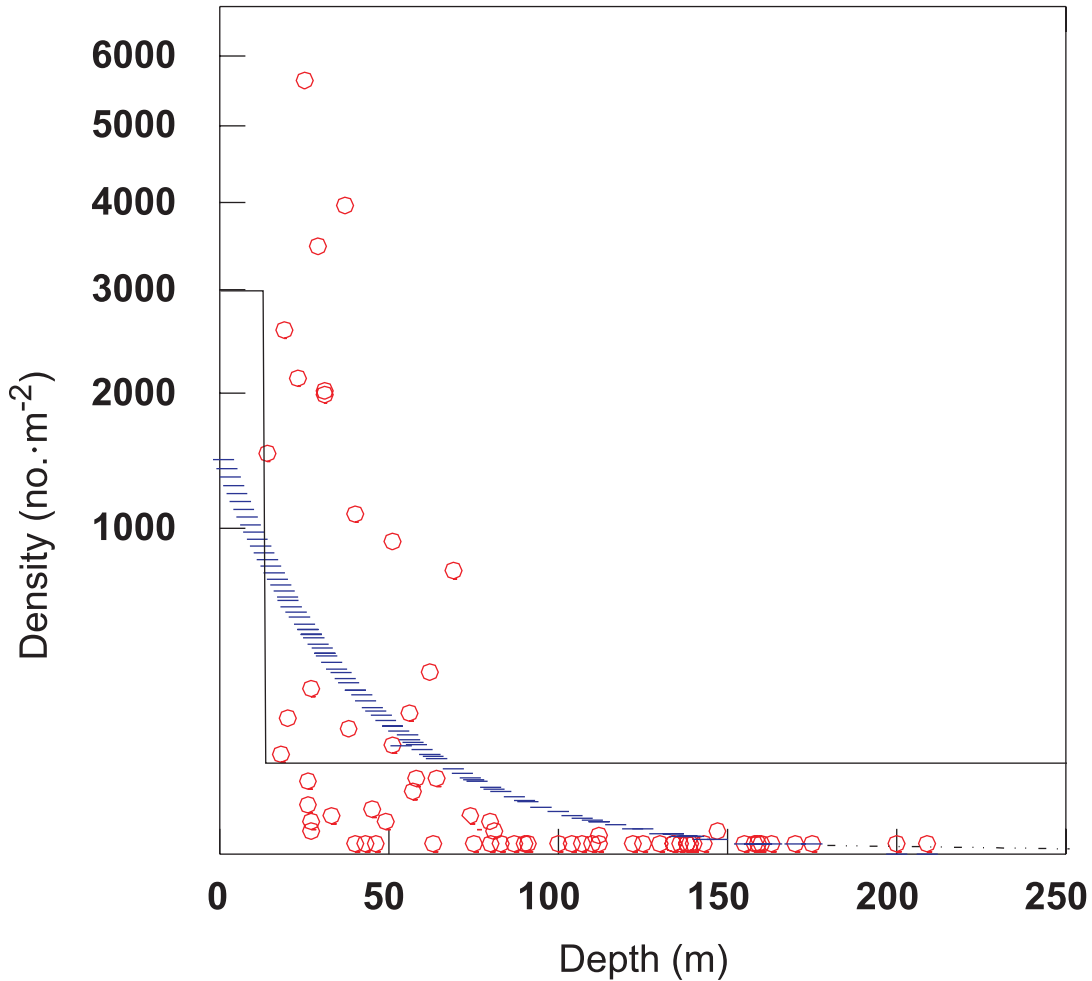

Table 6. Comparison of total turnover (days) at five depth intervals calculated with two dreissenid density estimates.

	Depth intervals (m)				
Density estimates from	0–15	0–30	0–45	0–60	0–75
Bailey et al. (1999)	0.1[a]	10.4	24.1	40.6	62.6
1997 Ponar grabs	0.4	2.4	7.4	19.3	51.4

[a]Total turnover is a summation of area-weighted average of the depth intervals (Bailey et al. 1999).

attributed to trends in water column productivity (Saether 1980) because the density of the benthos is directly related to the amount of food material settling from the water column. Earlier studies have shown that the amphipod *Gammarus fasciatus*, a shallow water species (<10 m), increased after invasion of mussels in southwestern Lake Ontario (Stewart and Haynes 1994; Haynes et al. 1999). The authors suggested that *Gammarus fasciatus* growth is facilitated by the additional food source from pseudofeces/feces deposited by *Dreissena* and additional habitat provided by mussel shells. Unlike *Gammarus*, *Diporeia* does not actively feed on *Dreissena* fecal pellets (Lydy and Landrum 1993). It has been shown that *Diporeia* is a discriminating feeder re-

quiring a high quality food in the spring (diatoms) to complete its life cycle (Dermott and Corning 1988; Gardner et al. 1985). The inability of *Diporeia* to use *Dreissena* biodeposits as a food source and the reduction in its original food source may have contributed to its decline. The large decline in densities of *Diporeia* and other benthic macroinvertebrates in Lake Ontario was most pronounced near areas where dreissenids were most abundant and we postulate that these declines could have resulted from a redirection of energy from open waters to *Dreissena* beds.

Recent changes in densities of benthic macroinvertebrates after invasion of *Dreissena* are not restricted to Lake Ontario. Dramatic declines of *Diporeia* in deeper waters of eastern Lake Erie also coincided with colonization by dreissenids (Dermott and Kerec 1997). Mean densities of *Diporeia* declined from 1844·m^{-2} in 1979 to 218·m^{-2} in 1993; *Diporeia* was found at all 13 deepwater stations in 1979 but only five stations in 1993. Dermott and Kerec (1997) suggest that competition for diatoms between *Dreissena* and *Diporeia* led to the exclusion of amphipods from areas where *Dreissena* was abundant. In southern Lake Michigan, Nalepa et al. (1998) reported declines of *Diporeia*, Oligochaeta, and Sphaeriidae. Declines in oligochaetes and sphaeriids occurred uniformly throughout the

nearshore region (<50 m), whereas declines of *Diporeia* were greatest in the southeastern region of the lake. The region where *Diporeia* declined more than 60% between 1980 and 1993 corresponded to areas where *Dreissena* was found in largest numbers. Nalepa et al. (1998) also hypothesized that the filtering activities of *D. polymorpha* were having a negative impact on *Diporeia*.

In Lake Ontario, *Diporeia* populations are declining even in areas with low dreissenid densities. *Dreissena* are not present in large numbers at depths greater than 40 m; greatest densities occur in waters less than 30 m. We hypothesize that filtering capacity of dreissenids may be enhanced and the reduction of *Diporeia* densities may be partially explained by the seasonal occurrence of isolated water masses in nearshore areas of the lake. The formation of a thermal bar in spring and early summer isolates nearshore waters from offshore waters. The progression of the thermal bar from areas near the shoreline to deeper waters (>100 m) usually begins in March and ends with the formation of the summer thermocline (Thomas et al. 1972). During the spring diatom bloom, diatoms shoreward of the thermal bar are exposed to warmer, nutrient-rich water and, because the waters are well mixed, are also exposed to the filtering activity of *Dreissena*, thus allowing *Dreissena* to intercept diatoms before they settle on deeper sediments. Scavia and Bennett (1980) used field observations and simulation models to demonstrate the relative importance of vertical mixing and in situ production to observed nutrient and algal biomass in Lake Ontario. During the spring, increased algal production occurs on the shoreward side of the 4°C isotherm (Stadelmann et al. 1974). The impact of dreissenids in the spring is directly related to their filtering capacity.

The seasonal impact of dreissenids was assessed by estimating their filtering capacity in comparison to volumes of water isolated by the thermal bar. Bailey et al.'s (1999) filtration model was used to calculate total turnover times (in days) at different depth intervals as

$$T = \sum_{i=1}^{S} [p_i \cdot v_i]/[f \cdot a_i \cdot x_i]$$

where p_i is the proportion of total bottom area in stratum i, v_i is the volume of stratum i, f is the filtering rate of an average-sized mussel (100 mL·h^{-1}·mussel^{-1}), a_i is the area of bottom in stratum i, and x_i is the density of mussels in stratum i. Total turnover times were estimated from dreissenid densities used by Bailey et al. (1999) and from Ponar data collected in 1997 (Fig. 5). To obtain total turnover times, we needed dreissenid densities at 1-m intervals; therefore, we used regression analysis of dreissenid densities on depth to find these values, i.e.,

$$\log (x_i) = 7.335 - 0.045 \cdot d_i$$

where d_i represents depth at stratum i. We found that total turnover times were similar for depth intervals less than 30 m but much smaller based on our dreissenid estimates at depth intervals between 30 and 75 m (Table 6). At depth intervals greater than 80 m, Bailey et al.'s (1999) total turnover times were substantially lower that those calculated from our estimates of dreissenid densities. It is clear that better estimates of dreissenid densities must be made before we can

determine the true potential effect of dreissenid filtering on algal biomass in the spring. However, if our model and density estimates are fairly accurate, isolated water masses in Lake Ontario could be turned over in less than 10 days when the thermal bar is located at depth contours of 60 m or less.

The loss of *Diporeia* from large areas of Lake Ontario may be affecting fish production. Prey fish species such as slimy sculpin use *Diporeia* as a key food source in Lake Ontario (Owens and Weber 1995). Recently, there has been a decline in populations of this fish species in U.S. waters; estimates of densities of slimy sculpins have declined by 95% between the late 1980s and 1996 (New York Department of Environmental Conservation Annual Report 1998). Hoyle et al. (1999) found a sharp decline in both densities and body condition of lake trout and lake whitefish from the eastern region of the lake (Kingston basin) after 1990, which corresponds to the time that *Diporeia* were disappearing. In the past, the Kingston basin had produced the largest fish yields and supported a number of important commercial and sport fisheries. In 1997, a single specimen of *Diporeia* was collected from a total of 18 Ponar grab samples in the Kingston basin, where mean densities of *Diporeia* reached levels of 14 000·m^{-2} before the invasion of *Dreissena*.

In summary, the status of the benthic macroinvertebrate community of Lake Ontario has changed during the last 10 years. Densities of *Diporeia*, Oligochaeta, and Sphaeriidae have declined in soft substrate habitats of deep water, whereas dreissenid populations have increased in both hard and soft sediments. A zone of very low *Diporeia* density (<4 individuals·m^{-2}) extends as far as 26 km offshore and as deep as 200 m, encompassing over 40% of the total surface area of Lake Ontario soft sediments sampled in 1997. The reduction of benthos, especially populations of *Diporeia*, in the nearshore of Lake Ontario is expected to have a major impact on the upper trophic levels of the lake.

Acknowledgments

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