Status and Trends of the Lake Ontario Macrobenthos[1]

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The benthic macroinvertebrate community of Lake Ontario was examined relative to communities found in the other Great Lakes and also relative to trends over time. In the nearshore, populations are heavily influenced by municipal and industrial inputs. For example, oligochaete abundances in the nearshore are higher than in any of the other Great Lakes (excluding shallow Lake Erie), communities have been altered even to relatively deep depths near the major river mouths, and the pollution-sensitive *Pontoporeia hoyi* is scarce along the southern shoreline east of the Niagara River mouth. In the profundal, benthic composition is similar to that found in the other Great Lakes, but biomass is less than might be expected given the amount of organic material settling to the bottom. Benthic standing stocks in this region have apparently declined almost threefold since the 1960s. Reasons for this decline do not appear to be related to trends in water column productivity or to predation pressure, but may be related to the accumulation of contaminants. Research needs include studies to assess benthic trends over a much broader area of the lake and studies to examine the impact of sublethal levels of contaminants.

La communauté des macroinvertébrés benthiques du lac Ontario a été comparée à d'autres communautés des Grands Lacs et son évolution a été examinée. Près des rives, les populations animales sont gravement affectées par les déchets municipaux et industriels. Par exemple, les oligochètes sont plus abondants dans le lac Ontario que dans tous les autres Grands Lacs (sauf le lac Érié, lequel est peu profond) près des rives; les communautés ont subi des changements même dans les eaux relativement profondes près de l'embouchure des principales rivières et; *Pontoporeia hoyi*, organisme sensible à la pollution, est rare le long de la rive sud à l'est le l'embouchure de la rivière Niagara. Dans les profondeurs, la composition du benthos est semblable à celle des autres Grands Lacs, mais la biomasse est inférieure à ce qu'on pourrait s'attendre vu la quantité importante de matière organique déposant au fond. Les stocks d'organismes benthiques de cette région sont apparemment presque trois fois moins importants que dans les années 1960. Il ne semble pas que ce déclin soit attribuable à une chute de la productivité biologique du lac ou à une prédation accrue : il serait plutôt relié à l'accumulation des contaminants. Les recherches futures devront tenter d'évaluer l'évolution du benthos en couvrant une portion du lac beaucoup plus importante et, par ailleurs, examiner l'impact de doses subléthales de contaminants.

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As a result of numerous field investigations over the past few decades, our knowledge of the benthic community in Lake Ontario is perhaps the most extensive of any of the Great Lakes. Surveys over the entire lake (Hiltunen 1969; Kinney 1972; Nalepa and Thomas 1976; Golini 1979) and more limited surveys in the open waters and in selected bays, harbors, and nearshore areas (Judd and Bocsor 1972; Brinkhurst 1970; Johnson and Matheson 1968; Johnson and Brinkhurst 1971; Barton and Hynes 1978; Johannsson et al. 1985a; Johnson and McNeil 1986; Barton 1986) have not only provided information on abundance and composition, but have also provided insights into some of the more important factors which influence distributions. In addition, the major findings of these surveys have been summarized in two excellent review articles. One review gave a historical perspective of benthic research throughout the Great Lakes, examined the taxonomic status of Great Lakes fauna, and provided a zoogeographical perspective of distributional patterns (Cook and Johnson 1974). More specifically, benthic communities in Lake Ontario were described and compared with communities found in the other Great Lakes. A more detailed, systematic review of the Lake Ontario benthos was presented in a summary of findings up until about 1976 (Mozley 1990). Distributions and relative abundances were given for each common species, along with pertinent information on life cycle, habitat, and feeding modes. Also, spatial distribution patterns were described and related to such factors as water depth, water quality, and physicochemical features of the sediments.

This review is not intended to be an exhaustive account of the Lake Ontario benthos, since, as noted above, detailed summaries have already been presented. Rather, its purpose is to focus on features of the benthos that are unique to this lake when compared with the other Great Lakes and to examine long-term trends in populations. Since most benthic studies in Lake Ontario have examined only the macrobenthos, or those invertebrates retained on a screen with 0.5- to 0.6-mm mesh openings, this review will be limited to this group of organisms.

Distinctive and Comparative Features of the Lake Ontario Benthos

Nearshore

Because species composition and distributions in relation to depth and substrate are generally similar to those found in the other Great Lakes (Cook and Johnson 1974), most distinctive

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TABLE 1. Total mean abundance of macroinvertebrates (thousands per square metre) at different depth intervals in each of the Great Lakes except Lake Erie. The data are taken from surveys conducted in the 1960s and early 1970s. Each survey employed similar sampling and sorting techniques.

Lake	Year sampled	Depth interval (m)			
		14–30	31–50	51–90	>90
Superior	1970[a]	0.2	1.0	0.9	0.3
Huron	1970[a]	2.9	3.4	3.0	
Michigan	1964–67[b]	6.2	10.5	5.9	2.9
Ontario	1964[c]	14.7	15.2		2.3
	1972[d]	8.8	7.2	8.1	1.2

[a]Schelske and Roth (1973).
[b]Alley and Mozley (1975).
[c]Hiltunen (1969).
[d]Nalepa and Thomas (1976).

features of nearshore benthic populations in Lake Ontario can be attributed to the great impact of polluting substances. Of the Great Lakes, Lake Ontario receives the largest burden of municipal and industrial effluents, mainly via the Niagara River (Allan et al. 1983). Excluding atypically shallow Lake Erie, total mean abundance of the benthos in Lake Ontario's nearshore region (<30 m), at least in the 1960s and early 1970s, was higher than abundances in nearshore regions of the other three Great Lakes (Table 1). These relatively high abundances, along with dominance of the community by oligochaetes (72% of the total; Nalepa and Thomas 1976), are a general reflection of the enriched nature of the nearshore zone. Nutrients enter this zone from the major rivers and concentrations tend to remain high because of the prominent thermal bar in the spring, which traps nutrients along the shoreline and stimulates phytoplankton productivity (Shiomi and Chawla 1970), and also because of the frequency of upwelling episodes later in the year, which replenishes depleted nutrient supplies (Stadelmann and Fraser 1974).

In most of the other Great Lakes, the impact of pollution on the benthic community is mainly restricted to nearshore areas, harbors, river mouths, and the shallow bays and basins. However, because of Lake Ontario's relatively small surface area and steep contours, an impacted fauna is evident even at relatively great depths off the major river mouths. For example, the amphipod *Pontoporeia hoyi* and the oligochaete *Stylodrilus herigianus*, both oligotrophic indicator species, were found in reduced numbers at depths as great as 70 m directly off the mouth of the Niagara River (Kinney 1972). Also, reduced numbers of the same two species, along with high densities ($46\,000 \cdot m^{-2}$) of the pollution-tolerant oligochaete *Tubifex tubifex*, were found at a depth of 54 m off Toronto Harbour (Nalepa and Thomas 1976). These distributions demonstrate the widespread and profound impact of riverborne pollutants on the Lake Ontario benthos. Not coincidently, some of the highest oligochaete densities ever reported from the Great Lakes have been from Lake Ontario or surrounding harbors. For example, densities of $61\,700 \cdot m^{-2}$ have been found near the mouth of the Niagara River (Nalepa and Thomas 1976) and up to $200\,000 \cdot m^{-2}$ have been reported from Toronto Harbour (Brinkhurst 1970).

Considering its habitat preferences and distribution patterns in the other Great Lakes, in no other open water area of the Great Lakes is there such a widespread scarcity of *Pontoporeia hoyi* as along the southern shoreline of Lake Ontario. Low densities in the area east of the Niagara mouth to Rochester at depths up to 30 m have been attributed to the deposition of riverborne pollutants (Hiltunen 1969; Nalepa and Thomas 1976). An alternative explanation for the scarcity of *Pontoporeia* in this area, however, is completely unrelated to loadings from the Niagara River. The prevailing westerly winds tend to pile up water along the southern shoreline, causing the downwelling of warm, epilimnetic waters (to 19°C) (Lee 1972). *Pontoporeia*, a glaciomarine relict, does best when temperatures are consistently less than 10°C (Smith 1972), and populations may be adversely affected by these frequent intrusions of warmer water. Another possible theory for the lack of *Pontoporeia* along the southern shoreline may be derived from examining the distribution of *Stylodrilus*. Like *Pontoporeia, Stylodrilus* is a pollution-sensitive form and also a coldwater stenotherm (Mozley and Howmiller 1977). Yet, although not found directly off the Niagara River mouth, it was found in great numbers in the same areas where *Pontoporeia* was absent (Nalepa and Thomas 1976). In laboratory bioassays, *Stylodrilus* was found to be relatively sensitive (compared with other oligochaete species) to high temperatures and conditions associated with organic pollution (i.e. sewage sludge, anoxia) (Chapman et al. 1982a, 1982b). This finding was not unexpected considering its distribution in the field. However, it was also found to be relatively more tolerant of certain chemical compounds that might otherwise be considered toxic. Because *Stylodrilus* occurs in great numbers along the southern shoreline, the low densities of *Pontoporeia* in this area may not be from the relatively higher water temperatures or from organic loadings from the Niagara River, but from chemical contaminants that may be affecting this organism specifically. The Niagara River is the source of many persistent contaminants, and high levels of mirex, PCBs, and mercury among other chemicals have been noted along the southern shoreline (Thomas 1983). Unfortunately, despite its importance in Lake Ontario and the rest of the Great Lakes, the relative tolerance of *Pontoporeia* to various types of chemical pollutants has not been thoroughly investigated. In laboratory experiments, this species avoided sediments from polluted harbors (Gannon and Beeton 1969), but its response to specific contaminants remains largely unknown.

Another noteworthy aspect of benthic distributions in nearshore Lake Ontario is the scarcity of insect fauna along the northern shoreline; the number and diversity of both mayflies and trichopterans in the wave zone (0–2 m) were impoverished compared with the fauna in similar areas in Lakes Superior, Huron, and Erie (Barton and Hynes 1978). It was hypothesized that the frequent upwelling of cold, hypolimnetic water in the summer may limit populations either by killing them directly or by preventing the number of degree-days needed for complete life-cycle development. Another factor mentioned as being potentially harmful was the poor water quality of the nearshore zone. In comparing nearshore (5–20 m) benthic communities of Lakes Ontario and Huron, Barton (1986) noted fewer species but greater abundances in Lake Ontaro in all types of substratum; this suggests more enriched conditions in Lake Ontario.

Offshore

While the benthic community of nearshore Lake Ontario is variable and dependent upon proximity to waste inputs, the community found in offshore areas is more uniform and con-

TABLE 2. Comparison of water column productivity, organic sedimentation rates, and benthic biomass in the profundal (>90 m) in Lakes Superior (Whitefish Bay), Michigan, and Ontario. Dry-weight biomass was converted to organic carbon by assuming an organic carbon content of 50%. The sedimentation rate for Lake Superior was for the July–September period, while the sedimentation rate for the other two lakes was for the April–November period.

Variable	Lake		
	Superior	Michigan	Ontario
Chlorophyll *a* ($mg \cdot m^{-2}$)		20–80[a]	60–120[b]
Primary production ($g\ C \cdot m^{-2} \cdot y^{-1}$)		100–140[c]	170–220[d]
Sedimentation rate ($mg\ C \cdot m^{-2} \cdot d^{-1}$)	46[e]	104[f]	176[g]
Sediment carbon content (%)	1–3[h]	3–5[i]	3–4[j]
Benthic biomass ($g\ C \cdot m^{-2}$)	1.1[k]	0.9[l]	0.4[m]
Biomass composition (%)			
Pontoporeia hoyi	91	69	85
Oligochaeta	8	26	14

[a]Parker et al. (1977) and Bartone and Schelske (1982).
[b]Charlton (1983).
[b]Parker et al. (1977) and Fee (1973).
[d]Stadelmann et al. (1974).
[e]Eadie (Great Lakes Environmental Research Laboratory, Ann Arbor, MI, unpublished data).
[f]Eadie et al. (1984).
[g]Rosa (1985).
[h]Thomas and Dell (1978).
[i]Cahill (1981).
[j]Thomas et al. (1972) and Nalepa and Thomas (1976).
[k]Nalepa et al. (1988).
[l]Nalepa (1989).
[m]Johannsson et al. (1985a).

sistent. Like offshore communities in the other Great Lakes, the dominant form is *Pontoporeia* followed by oligochaetes, of which most are *Stylodrilus* (Cook and Johnson 1974). Yet, although similar in composition, standing stocks of the macrobenthos in the profundal (>100 m) are lower than might be expected given the productivity of the system. In Table 2, benthic biomass and composition, organic inputs, and water column productivity in the profundal of Lake Ontario are shown relative to most of the same variables in two other profundal regions of the Great Lakes. Inputs were determined from amounts of organic carbon collected in sedimentation traps placed just below the thermocline. In most lake systems, standing stocks of the macrobenthos are generally related to variables indicative of water column productivity, i.e. chlorophyll *a*, total phosphorus, and Secchi disc transparency (Hanson and Peters 1984; Rasmussen and Kalff 1987). Organic material produced in the water column eventually settles to the bottom and serves as food for the benthos. While the amount of organic carbon settling from the epilimnion in Lake Ontario was far greater than in Lake Michigan or in Lake Superior (Whitefish Bay), benthic biomass was less than one half the biomass found in these other two lakes (Table 2). In all three profundal areas, *Pontoporeia* was the dominant form, accounting for 69–91% of the biomass total.

Persistent Contaminants

Because of the high contaminant loads into Lake Ontario, benthic organisms in both nearshore and offshore areas are exposed to elevated levels of many persistent chemicals. Yet, the impacts of acute and chronic exposures are not readily discernible from the many other environmental factors that can influence benthic abundances and distributions (Nalepa and Landrum 1988). Only one study in Lake Ontario has clearly shown a negative relationship between a specific chemical compound and benthic abundances. In Hamilton Bay, oligochaetes (and all other organisms) were absent from an area having an iron content greater than 25% (Johnson and Matheson 1968). Even at these high concentrations, however, the conclusion was that the iron content per se was not necessarily detrimental, but conditions associated with the high iron levels, such as high oxygen demand and continuous inorganic siltation, were likely responsible for the observed effect. While several studies in nearshore areas have implicated heavy metals in having a negative impact on the nearshore benthic community (Hart et al. 1986; Poulton et al. 1988), other factors including organic pollution were also recognized as an influencing factor.

TABLE 3. Mean concentration of various contaminants in the sediments of depositional zones in four of the Great Lakes.

Lake	Contaminant (ppb)			Source
	PCB	HEOD	DDT	
Superior	4.8	0.25		Frank et al. 1980
Huron	15.0	<0.20	18.4	Frank et al. 1979b
Michigan	17.3	0.41	24.4	Frank et al. 1981
Ontario	85.0	0.50	62.2	Frank et al. 1979a

On a lakewide basis, benthic populations are probably most influenced by low, sublethal levels of contaminants because low concentrations of contaminants are more widespread and occur throughout the offshore depositional basins of the lake. Contaminant levels in the depositional basins of Lake Ontario are higher than levels in the depositional basins of the other Great Lakes (Table 3). Although no studies of Lake Ontario sediments or benthos have been specifically designed to assess the effects of low-level, long-term exposures, some evidence suggests that such effects may exist. In laboratory experiments, sublethal effects were apparent at lower concentrations than those reported from Lake Ontario sediments. For instance, *Stylodrilus* ceased feeding after 58 d at PCB concentrations over 50 $ng \cdot g^{-1}$ (D. S. White, Murray State University, Murray, KY, unpublished data). Concentrations this high are found over broad areas in Lake Ontario, with concentrations greater than 200 $ng \cdot g^{-1}$ quite common (Thomas 1983). Similarly, while zinc concentrations of between 58.5 and 123.5 $\mu g \cdot g^{-1}$ lowered the swimming activity of *Pontoporeia* (Magnuson et al. 1976), concentrations of 100–500 $\mu g \cdot g^{-1}$ have been reported from the surficial sediments of Lake Ontario (Mudroch 1983). In a study on the effects of long-term exposures to the chlorinated pesticide endrin, reworking rates of *Stylodrilus* were affected by concentrations as low as 3.1 $ng \cdot g^{-1}$ (Keilty et al. 1988b); endrin concentrations in sediments from some nearshore sites in Lake Ontario were as high as 29 $ng \cdot g^{-1}$ (Stevens 1987). While results of laboratory experiments may not be applicable to the field situation, these studies do demonstrate the potential for long-term chronic impacts on populations.

Consistent with higher contaminant levels in the sediments, levels in the benthos also appear to be higher in Lake Ontario when compared with other parts of the Great Lakes system (Table 4). In addition, bioaccumulation factors (BAF, i.e. concentration in organism/concentration in sediments) indicate a significant increase in organism levels over sediment levels. For instance, oligochaetes had a BAF of 2–8, while *Pontopor-*

TABLE 4. Levels of various contaminants found in benthic macroinvertebrates in the Great Lakes. The number in parentheses is the bioaccumulation factor (concentration in organism/concentration in sediment) (modified from Nalepa and Landrum 1988).

	Organic contaminant (ng·g·dry wt^{-1})						
Organism	PCB	DDE	DDD	HEOD	HCB	Location	Source
Pontoporeia	4215–11 000 (9.0–19.0)				230–895 (1.6–6.0)	4 sites, western Lake Ontario	Fox et al. 1983
Pontoporeia	1378	292		226		3 sites, western Lake Ontario	Whittle and Fitzsimons 1983
Pontoporeia	1849	730		376		1 site, eastern Lake Ontario	Whittle and Fitzsimons 1983
Pontoporeia	560	58	62	35		1 site, eastern Lake Erie	Whittle and Fitzsimons 1983
Pontoporeia	1305	154	96	141		1 site, eastern Lake Michigan	Evans et al. 1982
Oligochaeta	930–3650 (2.4–7.8)				105–735 (0.7–2.3)	4 sites, western Lake Ontario	Fox et al. 1983
Oligochaeta	440 (0.7)	5.9 (4.9)	1.5 (0.7)		3.6 (1.2)	1 site, Detroit River	Smith et al. 1985

TABLE 5. Benthic surveys conducted in the open waters of Lake Ontario.

Study	Year	Stations	Sampler	Mesh
Adamstone 1924	1922	7	Ekman	"Factory cotton"
Hiltunen 1969	1964	24	Smith–McIntyre	595 μm
Kinney 1972	1967–69	38	Ponar	595 μm
Nalepa and Thomas 1976	1972	55	Ponar	595 μm
Golini 1979	1977	153	Shipek	153 μm
Johannsson et al. 1985a	1981–83	4	Ponar	250 μm

eia had a BAF of 9–19 for PCBs in western Lake Ontario (Fox et al. 1983). These bioaccumulation factors are, of course, important when considering the transfer of contaminants to higher trophic levels. Of particular importance is the body burden and BAF of *Pontoporeia*, since it is an effective bioaccumulator of organic contaminants (Landrum 1988) and also a preferred food item of many Great Lakes fish (Mozley and Howmiller 1977). When PCB concentrations in various sized organisms in Lake Ontario were compared, *Pontoporeia*, slimy sculpin (*Cottus cognatus*), and lake trout (*Salvelinus namaycush*) had higher PCB concentrations than might be expected from a strict size-dependent relationship (Borgmann and Whittle 1983). Lake trout feed on slimy sculpin, which, in turn, feed on *Pontoporeia*.

Long-Term Trends

The open waters of Lake Ontario were first sampled quantitatively in 1922 when Adamstone (1924) gave abundances of the major benthic groups in seven samples taken on a transect from Toronto to the mouth of the Niagara River. Unfortunately, further openwater surveys were not conducted until four decades later. Then, within a 14-yr period (1964–77), five lakewide surveys were conducted (Table 5) along with numerous localized surveys in bays, harbors, and adjacent waters. This period of intense sampling in the late 1960s and early 1970s was prompted by the demonstrated usefulness of benthic communities as indicators of trends in environmental quality. The Great Lakes were becoming increasingly eutrophic, and trends in benthic populations provided a basis for assessing the severity of the problem. Studies to assess changes in the benthic community in many portions of the Great Lakes indicated a degradation of environmental quality in the 1960s compared with a period some 10–30 yr earlier (Carr and Hiltunen 1965; Robertson and Alley 1966; Schneider et al. 1969; Howmiller and Beeton 1971). Unfortunately, in Lake Ontario, long-term trends in benthic populations during this period could not be established simply because good quantitative data were not available prior to the 1960s. As noted, the only quantitative, open-lake data available for Lake Ontario prior to the 1960s were from the survey of Adamstone (1924), and his sampling techniques probably underestimated the benthos when compared with the more quantitative techniques used in later surveys.

Since most surveys in the 1960s and thereafter employed similar techniques, comparisons at selected sites should provide an indication of any recent changes in benthic populations. The first comparison involves abundances reported in 1964 (Hiltunen 1969) and in 1972 (Nalepa and Thomas 1976). Stations of these two surveys that were of similar depth and location were paired and then compared (total of 13 pairs). Abundances of all groups were lower in 1972 than in 1964, particularly at the deeper stations (>100 m), and the difference was significant (sign test; $P<0.05$) over all 13 locations for sphaeriids and chironomids (Table 6). Total mean abundance of the benthos was 10 200·m^{-2} in 1964 compared with only 5400·m^{-2} in 1972. In terms of species composition, the oligotrophic indicator *Stylodrilus* accounted for a greater percentage of the oligochaete community in 1972 when compared with 1964, but this increase was not significant (sign test; $P<0.05$). On the other hand, the chironomid *Heterotrissocladius*, also an oligotrophic indicator, accounted for a significantly (sign test; $P<0.05$) lower percentage of the chironomid community in 1972. Although different grabs were used in the two surveys (Table 5), potential differences resulting from the sampling device appear to be irrelevant. Hiltunen used a Smith–McIntyre for collection, while Nalepa and Thomas used a Ponar; the latter grab is at least as efficient as the former and, in fact, consistently collected more sphaeriids in comparative trials (Powers and Robertson 1967). Seasonal influences would be minimal, since both surveys were conducted in the fall. To further examine the apparent decline in numbers between 1964 and 1972,

TABLE 6. Comparison between abundances (thousands per square metre) of major benthic taxa found in 1964 (Hiltunen 1969) and 1972 (Nalepa and Thomas 1976) at each of 13 different locations.

Station number		Depth (m)		Major benthic taxa							
				Pontoporeia		Oligochaeta		Sphaeriidae		Chironomidae	
1964	1972	1964	1972	1964	1972	1964	1972	1964	1972	1964	1972
4	12	14	14	0	0.1	20.4	12.3	4.8	3.2	<0.1	<0.1
11	1	19	22	2.0	4.8	7.2	11.3	2.6	1.1	0.3	0.1
50	66	19	21	4.2	0.3	5.4	8.2	7.6	0.6	0.2	0.1
59	60	19	20	0	<0.1	13.5	4.6	9.9	1.7	0.1	0.9
78	103	18	22	1.1	0.8	6.7	1.5	3.1	0.1	0.7	0.3
45	50	39	35	8.2	5.0	1.9	0.2	3.5	0.5	<0.1	<0.1
99	78	48	54	10.0	2.4	3.3	1.5	4.0	<0.1	<0.1	0
5	15	92	106	0.4	1.0	0.3	1.0	0.2	<0.1	0.3	<0.1
8	5	92	90	1.0	1.0	0.4	0.5	0.2	0	0.1	<0.1
57	62	92	87	1.7	0.4	0.9	0.1	0.6	0	0.3	0
38	38	92	99	1.8	0.6	1.0	0.2	0.2	0	0.2	0
71	85	183	167	0.4	0	0.8	0.1	0.1	0	0.2	0
65	75	225	223	0.5	0.2	0.4	0.1	<0.1	0	<0.1	0
Mean				2.4	1.5	4.8	3.2	2.8	0.6[a]	0.2	0.1[a]

[a]Abundances are significantly different (sign test; $P < 0.05$).

abundances reported by Kinney (1972) from a survey conducted during 1967–69 are shown with the 1964 and 1972 data (Table 7). Kinney did not give abundances at each of his 38 stations, but gave only mean abundances at each of three depth intervals. If the stations sampled in 1964 and 1972 are also grouped into the same depth intervals and abundances then compared, the Kinney data confirm the trend toward lower abundances of chironomids and sphaeriids after 1964.

In the early 1970s, both Canada and the United States enacted legislation to limit phosphorus in detergents and signed the Great Lakes Water Quality Agreement limiting phosphorus in the effluent of municipal waste treatment plants. Phosphorus is the most important limiting nutrient for summer phytoplankton production in the lake (Dobson et al. 1974; Sridharan and Lee 1977). As a result of these control measures, phosphorus loadings into Lake Ontario in the early 1980s were reduced by 39% and midlake spring concentrations of soluble reactive phosphorus were reduced by 33% (Stevens and Neilson 1987). While chlorophyll *a* concentrations did not decline, mean phytoplankton biomass in the early 1980s was reduced 43–58% compared with the early 1970s (Gray 1987). To determine whether corresponding changes occurred in benthic populations, the second comparison involved comparing data collected in 1964 (Hiltunen 1969) and in 1972 (Nalepa and Thomas 1976) with data collected during 1981–83 (Johannsson et al. 1985a) and 1985–87 (R. Dermott, Department of Fisheries and Oceans, Burlington, Ont., unpublished data). The latter two data sets are from the inclusive Bioindex Monitoring Program, Department of Fisheries and Oceans, Canada. As part of this program, benthic samples were regularly collected at three sites during 1981–83 and at two sites during 1985–87. Each of these sites (one or two profundal and one nearshore) was located near sites sampled in both 1964 and 1972. At the two profundal sites (>90 m), abundances of oligochaetes, sphaeriids, and chironomids in the 1980s were similar to abundances found in 1972, having remained lower than abundances found in 1964 (Table 8). Trends in abundances of *Pontoporeia* were not apparent; year-to-year fluctuations were high and trends at the two sites were inconsistent (Table 8).

Although benthic biomass estimates in the profundal are limited, data comparisons seem to suggest that a large decline in biomass occurred between the 1960s and the 1980s that is consistent with declines in abundances of many groups. In 1967–68, dry-weight biomass in the central profundal region was reported to be 2.12 $g \cdot m^{-2}$ (Johnson and Brinkhurst 1971); however, in the 1980s, mean dry-weight biomass was only 0.83 $g \cdot m^{-2}$ (Table 9). Declines in biomass were evident for all the major groups.

In addition to biomass, annual production of *Pontoporeia* in the profundal was determined in both 1967–68 (Johnson and Brinkhurst 1971) and in 1981–82 (Johannsson et al. 1985b). Production in 1967–68 was 1.59 $g \cdot m^{-2} \cdot yr^{-1}$ (this value is based on a given production rate of 0.025 $kcal \cdot m^{-2} \cdot d^{-1}$, a mean caloric content of 6.6 $cal \cdot mg^{-1}$, and an ash content of 15%), while production in 1981–82 was 1.86 $g \cdot m^{-2} \cdot yr^{-1}$. Thus, although biomass declined, production actually increased, resulting in an increase in the turnover rate (*P/B*) from about 0.9 in 1967–68 to about 2.2 in 1981–82. The turnover rate in 1967–68 might be considered more "typical" of profundal *Pontoporeia* populations; the value of 0.9 was generally similar to values reported from the profundal (65–115 m) of Lake Michigan in the late 1970s (Lubner 1979).

Trends in abundances of benthic populations at the nearshore site, located at a depth of about 28–35 m in the Kingston Basin, are given in Table 10. Included in this table are data from a recent study of benthic changes in the Bay of Quinte and adjacent waters of Lake Ontario between 1966 and 1984 (Johnson and McNeil 1986). This study documented changes in the benthos in response to phosphorus control measures in the 1970s. After point-source control of phosphorus became fully implemented in 1977, water quality, at least in the bay, improved almost immediately (Robinson 1986). In the Kingston basin, abundances of *Pontoporeia*, oligochaetes, and sphaeriids generally declined in the early 1980s when compared with abundances before 1977. Although in some years (1972 and 1982), differences between data sets were apparent, this trend was noted in the data of both Johnson and McNeil (1986) and in the comparative data of the other surveys (Hiltunen 1969; Nalepa

TABLE 7. Comparison between abundances (thousands per square metre) of major benthic taxa found in 1964 (Hiltunen 1969), 1967–69 (Kinney 1972), and 1972 (Nalepa and Thomas 1976) at each of three depth intervals.

	Shallow (<36 m)			Intermediate (36–90 m)			Deep (>91 m)		
Taxa	1964	1967–69	1972	1964	1967–69	1972	1964	1967–69	1972
Pontoporeia	2.1		2.1	9.1		2.1	1.3		0.8
Oligochaeta	8.6	5.5	8.4	2.6	1.7	4.7	0.8	0.4	0.4
Sphaeriidae	3.3	1.1	1.0	3.7	0.7	0.1	0.3	0.1	<0.1
Chironomidae	0.5	0.1	0.1	<0.1	<0.1	<0.1	0.2	0.1	<0.1
Gastropoda	0.3	0.2	0.2	<0.1	<0.1	<0.1	0	0	0

TABLE 8. Abundances (thousands per square metre) of major benthic taxa found in 1964, 1972, 1981–83, and 1985–87 at each of two profundal sites in Lake Ontario. 1964 = Station 18 (western profundal) and Station 38 (central profundal) (Hiltunen 1969); 1972 = Stations 5 and 10 (western profundal) and Stations 34, 38, and 46 (central profundal) (Nalepa and Thomas 1976); 1981, 1982, 1983 = Stations 12 (western profundal) and Station 41 (central profundal) (Johannsson et al. 1985a); 1985, 1986, 1987 = Station 41 (central profundal) (R. Dermott, unpublished data).

	Year							
	1964	1972	1981	1982	1983	1985	1986	1987
Western profundal (91–114 m)								
Pontoporeia	3.4	0.6			1.4			
Oligochaeta	1.0	0.3			0.4			
Sphaeriidae	0.6	0.0			<0.1			
Chironomidae	0.3	<0.1			<0.1			
Central profundal (91–126 m)								
Pontoporeia	1.8	1.4	2.1	2.3	1.3	2.4	2.1	2.1
Oligochaeta	1.0	0.3	0.4	0.4	0.3	0.3	0.5	0.4
Sphaeriidae	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Chironomidae	0.2	<0.1	<0.1	0.0	0.0	<0.1	<0.1	<0.1

TABLE 9. Comparisons between dry-weight biomass (milligrams per square metre) of the major benthic taxa found in 1967–68 (Johnson and Brinkhurst 1971), 1981–83 (Johannsson et al. 1985a), and 1985–87 (R. Dermott, unpublished data). Sampling site was in the main basin of the lake (>100 m). In the Johnson and Brinkhurst study, ash-free dry weight was converted to dry weight by assuming an ash content of 15%.

	Year						
Taxa	1967–68	1981	1982	1983	1985	1986	1987
Pontoporeia	1.73	0.80	0.80	0.50	1.14	0.43	0.58
Oligochaeta	0.36	0.11	0.10	0.06	0.17	0.15	0.13
Sphaeriidae	0.02	<0.01	<0.01	<0.01	0.01	<0.01	<0.01
Chironomidae	0.01	<0.01	0.0	0.0	<0.01	<0.01	<0.01
Total	2.12	0.90	0.90	0.56	1.32	0.58	0.71

and Thomas 1976; Johannsson et al. 1985a). Continued sampling since 1985, however, seems to indicate a reversal of earlier trends (Table 10). Abundances of all three groups have increased to levels not found since 1964. Trends in biomass were generally similar to those of abundances except for *Pontoporeia* (Table 11). While abundances of this species after 1985 were generally similar to abundances prior to 1977, biomass values were only one half as great. For the two time periods when annual production of *Pontoporeia* was estimated, 1967–68 and 1981–82, mean production was 9.3 and 5.2 $g \cdot m^{-2} \cdot yr^{-1}$ respectively, and turnover rates were 2.0 and 1.8.

Discussion

Although trends in the benthic fauna of Lake Ontario prior to the mid-1960s cannot be established, there is strong evidence suggesting that populations have changed since the 1960s. As noted by Nalepa (1987), one should be cautious when assessing trends in populations based on data from distinctly different surveys separated in time, but comparisons of several surveys have indicated a decline in both abundances and biomass of benthic populations, particularly at profundal depths. Reasons for this decline are not clearly defined. Typically, changes in benthic populations in deep lakes have been attributed to trends in water column productivity (Saether 1980); standing stocks of the benthos are directly related to the amount of food material settling from the water column. Yet, benthic populations in Lake Ontario declined in the late 1960s/early 1970s at a time when nutrients levels (and likely productivity) continued to increase (Stevens and Neilson 1987). Also, abundances in the 1980s have remained similar to abundances found in the early 1970s although phytoplankton biomass has declined (Gray 1987). Fish predation can certainly affect populations of preferred prey items (Johnson and McNeil 1986; Nalepa 1987), but it is unlikely that fish predation played a major role in the decline of the profundal benthos in the early 1970s. In a 1972 survey, fish biomass at depths below 55 m in Lake Ontario was

TABLE 10. Comparison of abundances (thousands per square metre) of the major benthic taxa found by various surveys[a] in the Kingston Basin of Lake Ontario at a depth of 28–35 m.

	Year												
Taxa	1964	1967	1968	1972	1977	1981	1982	1983	1984	1985	1986	1987	1988
Pontoporeia		6.7	9.0	2.7	9.6		6.5	3.2	2.6				
Oligochaeta		0.5	1.0	0.8	3.3		0.6	0.6	0.4				
Sphaeriidae		1.8	2.4	1.0	3.6		3.6	0.4	0.2				
Chironomidae		0.4	0.4	0.2	0.4		0.3	<0.1	<0.1				
Pontoporeia	5.9			6.8		6.9	8.8	3.9		6.9	6.6	9.6	13.9
Oligochaeta	2.8			1.2		0.6	0.8	0.5		2.0	3.2	3.0	
Sphaeriidae	2.2			0.3		0.6	0.4	0.2		<0.1	1.4	2.5	
Chironomidae	0.4			<0.1		<0.1	0.0	<0.1		<0.1	<0.1	<0.1	

[a]Upper half: 1967–84 = Lake Ontario Index Station of Johnson and McNeil (1986). Lower half: 1964 = Station 85 and 89 of Hiltunen (1969); 1972 = Station 96 and 97 of Nalepa and Thomas (1976); 1981–1983 Station 81 of Johannsson et al. (1985a); 1985–88 = Station 81 of R. Dermott (unpublished data).

TABLE 11. Comparison of dry-weight biomass (grams per square metre) of the major benthic taxa found by various surveys[a] in the Kingston Basin of Lake Ontario at a depth of 28–35 m. In the Johnson and McNeil (1986) study, ash-free dry weight was converted to dry weight by assuming an ash content of 15%.

	Year									
Taxa	1967	1968	1977	1981	1982	1983	1984	1985	1986	1987
Pontoporeia	5.09	5.53	6.90		2.99	2.19	1.59			
Oligochaeta	0.16	0.18	0.83		0.52	0.32	0.20			
Sphaeriidae	0.17	0.28	0.18		0.37	0.16	0.05			
Chironomidae	0.15	0.05	0.01		0.05	0.01	0.01			
Total	5.57	6.04	7.92		3.93	2.68	1.85			
Pontoporeia				3.02	2.45	1.56		2.38	1.60	2.78
Oligochaeta				0.17	0.28	0.17		0.90	0.60	0.79
Sphaeriidae				0.14	0.03	0.02		0.12	0.10	0.10
Chironomidae				<0.01	0.0	<0.01		0.01	<0.01	<0.01
Total				3.33	2.76	1.75		3.41	2.30	3.67

[a]Upper half: 1967–84 = Lake Ontario Index Station of Johnson and McNeil (1986). Lower half: 1981–83 = Station 81 of Johannsson et al. (1985a); 1985–87 = Station 81 of R. Dermott (unpublished data).

relatively small and consisted mainly of alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) (Christie and Thomas 1981). While these species feed on *Pontoporeia*, there were no significant trends in abundances of either species between the 1960s and early 1970s (Christie 1973, 1974).

Benthic trends in the shallower Kingston Basin are also difficult to explain. The decline in the abundance and biomass of oligochaetes and sphaeriids in the Kingston Basin between 1977 and 1984 was attributed to a decline in productivity as a result of phosphorus input reductions in adjacent Bay of Quinte (Johnson and McNeil 1986). Yet, after 1984, despite continued low phosphorus loadings, numbers of oligochaetes and sphaeriids have increased to levels found prior to phosphorus reductions and recent numbers of *Pontoporeia* are the highest ever recorded (Table 10). Trophic interactions in nearshore areas are complex and controlling influences on a particular component are not always apparent. For instance, although phosphorus loadings in the upper Bay of Quinte have remained low, phytoplankton biomass has recently increased; it was hypothesized that phytoplankton biomass was partly controlled by changes in fish predation on the benthos (Nicholls and Hurley 1989). Since the Kingston Basin is currently being monitored for trends in both water column productivity and fish standing stocks, future works will hopefully provide insights into reasons for recent changes in the benthic populations.

At both the profundal (midlake) and nearshore (Kingston Basin) sites, numbers of *Pontoporeia* have remained the same or increased since the 1960s, while biomass has declined. Thus, either the size structure of the population has shifted toward smaller individuals, or the weight per unit length has decreased. Information on the size structure of the population is not available, but such a shift would most likely be caused by an increase in fish predation (McDonald et al. 1990). In the profundal, as noted earlier, fish predation was minimal when the biomass decline occurred (late 1960s/early 1970s), while major changes in fish populations in the Kingston Basin during this period were not apparent (Christie et al. 1987). On the other hand, a comparison between length–weight relationships for *Pontoporeia* in 1967–68 and 1981–82 shows a major decline in the weight per unit length, along with a corresponding increase in the metabolic rate (Fig. 1).

Given the relatively high contaminant exposures and body burdens of the Lake Ontario benthos, it remains a question whether contaminants have induced any of the changes noted in the populations. While organisms may tolerate sublethal concentrations of toxicants over the short term, long-term exposures may invoke physiological, histological, and biochemical

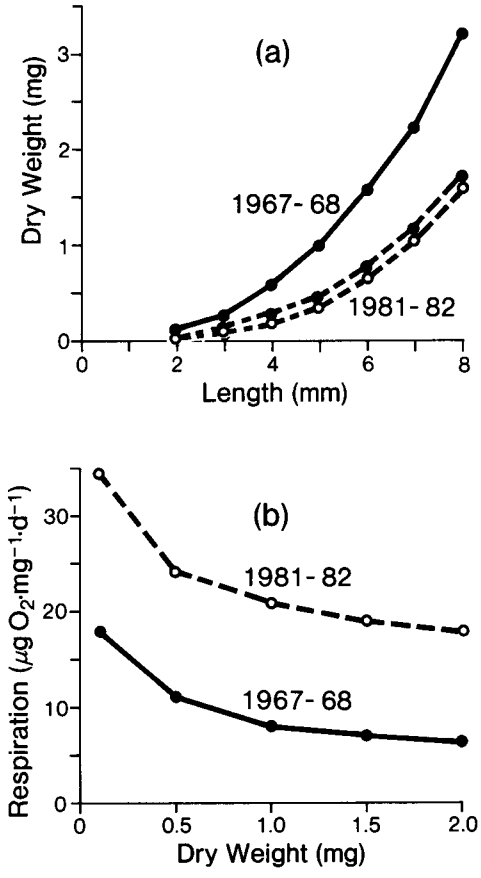

FIG. 1. (a) Length–weight relationship and (b) respiration rate of *Pontoporeia hoyi* in Lake Ontario in 1967–68 (Johnson and Brinkhurst 1971) and 1981–82 (Dermott and Corning 1988; Johannsson et al. 1985b). In the 1967–68 study, ash-free dry weight was converted to dry weight by assuming an ash content of 15%. Respiration rate calculated at 4°C. ●—●, 1967–68 (Kingston Basin); ○---○, 1981–82 (midlake). ●---●, 1981–82 (Kingston Basin). There was no difference in the respiration rate of *Pontoporeia* at the two 1981–82 sites (Johannsson et al. 1985b).

changes in the individual that may ultimately lead to changes at the population level. The organism requires energy to metabolize the toxicant and to replace or repair materials that have been damaged. Increased energy requirements for such nonproductive functions decrease the energy available for growth, given the same amount of energy intake. The decline in biomass of all the major macrobenthic groups in the profundal region in the 1960s corresponded to the time period when contaminant levels in the sediments were at an all-time peak in the 1960s and early 1970s (Durham and Oliver 1983) and may be a stress response manifested at the population level. In some groups, the decline in biomass coincided with a decline in numbers, but for *Pontoporeia*, lower biomass values can apparently be attributed to a decline in the weight per unit length of the individual. Weight loss has been observed in organisms exposed to sublethal levels of contaminants over a prolonged period (Keilty et al. 1988a). Inconsistent with the hypothesis that contaminants may have been a factor in the biomass decline, however, is the fact that contaminant levels have declined by the early 1980s (Durham and Oliver 1983), but standing stocks have remained lower than in the 1960s.

Summary of Research Needs

In addition to the research recommendations of previous reviews (Cook and Johnson 1974; Mozley 1990), and in view of the current status of the Lake Ontario macrobenthos, several immediate research needs have become apparent. The recent data sets available to examine long-term trends represent perhaps the longest record of benthic abundance and biomass in the Great Lakes. Nevertheless, these data have been collected from just a few sites. A lakewide survey is needed to document changes over a much broader area of the lake, and sampling sites should correspond as closely as possible to the sampling sites of previous surveys. Of particular interest are areas near major river mouths and along the southern shoreline east of the Niagara River.

Considering the relatively high concentrations of contaminants in the sediments and in the macrobenthos, studies to examine biochemical and physiological indicators of stress (Giesy et al. 1988) in Lake Ontario populations should be initiated. Comparative studies with organisms from the other Great Lakes would be useful in assessing relative impacts.

The effects of contaminants on the benthic community are difficult to assess from field measurements alone because of the complexity of the environment and the influences of natural events. In addition to examining community structure, assessments should include measures of contaminant concentrations and bioassays for acute and chronic impacts ("Sediment Quality Triad") (Chapman et al. 1987). Probably the most informative site to use this approach in Lake Ontario would be near the Niagara River mouth using *Pontoporeia* as the test organism.

Finally, the apparent discrepancy between pelagic inputs and benthic standing stocks in the profundal of Lake Ontario needs further attention. While the mass flux of organic material settling to the bottom has been quantified (Charlton 1983; Rosa 1985), information is needed on the nutritional value and source of these materials on a seasonal basis. The lipid composition of settling material can be useful in determining its food potential (Currie and Johns 1988; Gardner et al. 1989). Such information should further define the relationship between food inputs and benthic production and provide more realistic estimates of energy flow through the benthic system (i.e. Flint 1986). Conceivably, although the evidence seems to suggest otherwise, low benthic standing stocks in the profundal may be a result of high predation pressure by fish populations. Comparative studies using refined techniques such as manned submersibles (Eisenreich and Long 1989) or hydroacoustics (Burczynski and Johnson 1986) to estimate fish standing stocks are needed to put predation pressure in Lake Ontario in perspective.

NOTE ADDED IN PROOF: Since this article was written, the name *Pontoporeia hoyi* has been changed to *Diporeia* spp.

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