RESULTS FROM GLNPO’S BIOLOGICAL OPEN WATER SURVEILLANCE PROGRAM OF THE LAURENTIAN GREAT LAKES

1999

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Introduction

The Great Lakes National Program Office (GLNPO) of the United States Environmental Protection Agency (USEPA) has been conducting regular surveillance monitoring of the Great Lakes since 1983. This monitoring is intended to fulfill the provisions of the Great Lakes Water Quality Agreement (International Joint Commission, 1978) calling for periodic monitoring of the lakes to:

1) assess compliance with jurisdictional control requirements;
2) provide information on non-achievement of agreed upon water quality objectives;
3) evaluate water quality trends over time; and
4) identify emerging problems in the Great Lakes Basin Ecosystem.

The monitoring effort is focused on whole lake responses to changes in loadings of anthropogenic substances, so sampling is largely restricted to the relatively homogeneous offshore waters of each lake. Because of the daunting logistical exigencies of sampling such a large area, temporal resolution is currently limited to two well-defined periods during the year: the spring isothermal period and the stable, stratified summer period.

GLNPO's monitoring of the Great Lakes was initially limited to Lakes Michigan, Huron and Erie. In 1986 sampling was extended to include Lake Ontario, and in 1992 sampling of Lake Superior was added. In addition to a wide range of physical and chemical parameters, the lakes have been sampled for phytoplankton and zooplankton, including crustaceans and rotifers, since the inception of the program. In 1997, a benthic invertebrate biomonitoring program was added to complement the existing open water surveillance sampling.

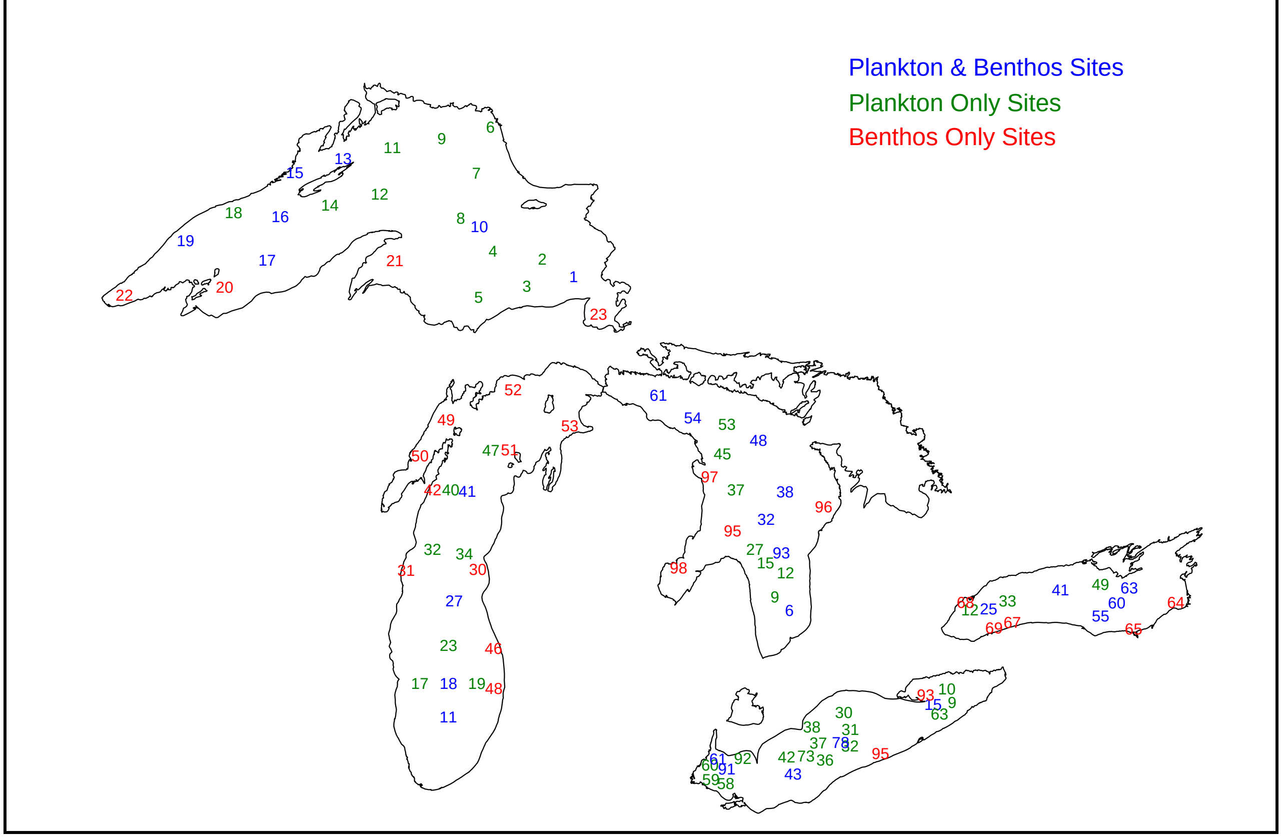
In this report we will present results of GLNPO's biological surveillance sampling program from all five Laurentian Great Lakes. Our goal here is to provide a general description of the offshore planktonic and the benthic communities of all five Great Lakes from GLNPO's 1999 surveys. In addition, we will present information detailing the use of benthos data for the assessment of the ecological health of the Great Lakes.

Methods

Field Methods

In the spring of 1999, samples were taken from Lake Erie aboard the Canadian vessel Risley between 10 and 13 March. The remaining four lakes were sampled from the R/V Lake Guardian between 17 April and 6 May. All five lakes were sampled from the R/V Lake Guardian during the summer survey, which ran from 3 August to 1 September. Between 13 and 23 stations were sampled on each lake for plankton, benthos, or both (Figure 1). In each lake, two or three stations were designated master stations. These were located at the deepest point in sub-regions of each lake determined to be homogeneous from previous studies.

Figure 1. Stations sampled during GLNPO's 1999 survey.



At each station integrated samples for phytoplankton enumeration were created from a composite of water samples taken at discrete depths (spring: surface, 5M, 10M, and 20M; summer: surface, 5M, 10M, and upper metalimnion) with Niskin bottles mounted on a SeaBird Carousel Water Sampler. Samples were preserved in the field with Lugol's solution, and with formalin upon return to the laboratory.

Two net tows were performed at each site for zooplankton sample collection, using a 0.5 m diameter conical net (D:L = 1:3). The first tow was taken from 20 meters below the water surface or 1 meter above the bottom, whichever was less, using a 64 µm mesh net, and the second tow from 2 meters above the bottom or 100 m, whichever was less, using a 153 µm mesh net. If the station depth was less than 20 m, both tows were taken from one meter above the bottom. Triplicate tows of each depth were taken at the master stations. After collection, zooplankton were immediately narcotized with soda water, and were preserved with sucrose formalin solution (Haney and Hall, 1973) approximately twenty minutes later.

During the summer survey, quantitative samples for benthic invertebrate analysis were collected from selected sites using a Ponar grab sampler. Samples were taken in triplicate, and material sieved through a 500 µm mesh net. Samples were preserved with buffered formaldehyde with Rose Bengal to a final concentration of 5-10 % formaldehyde.

Laboratory Methods

Phytoplankton were identified and abundances were estimated using the Utermöhl technique (Lund et al. 1958) at a magnification of 500x, with diatoms other than *Urosolenia* (=*Rhizosolenia*) identified as either centrics or pennates. Diatoms were identified, and relative abundances determined, from permanent slide mounts at 1250x. Relative proportions of each taxon of centrics and pennates were then multiplied by the appropriate Utermöhl counts. At least 10 individuals of each taxon were measured per sample, and cell volumes computed using appropriate geometrical formulae. Primary taxonomic keys used were Prescott (1962), Kramer and Lange-Bertalot (1986, 1991, 1997), Patrick and Reimer (1966, 1975) and Germain (1981).

Samples for zooplankton analysis were split in the lab using a Folsom plankton splitter, and four stratified aliquots examined per sample for crustaceans using a stereoscopic microscope. In addition, duplicate 1 ml aliquots were drawn from an appropriate split of samples collected with the 64 µm mesh net, and were examined for rotifers and nauplii under a compound microscope. Immature calanoids and cyclopoids were identified to the lowest taxonomic level possible, usually suborder or genus. The primary key used to identify crustaceans was Balcer et al. (1984), with Hudson et al. (1998), Brooks (1957), Edmundson (1959) and Rivier (1998) also consulted. Rotifers were identified according to Edmonson (1959) and Stemberger (1976). Length measurements were made on the first twenty individuals of each species encountered per sample (crustaceans) or per lake (rotifers). Crustacean biovolumes were computed using length-weight relationships found in the literature, while rotifer biomass was calculated according to A. Ruttner-Kolisko (in Bottrell et al., 1976).

Organisms were picked out of benthos samples under low magnification using a dissecting microscope. Oligochaetes and chironomids were mounted on slides and identified under a compound scope at 63x; other organisms were identified under a dissecting scope. Taxonomy followed Kathman and Brinkhurst, 1998 (oligochaetes); Holsinger, 1972 (amphipods); Wiederholm, 1983 (chironomids) and Merritt and Cummins, 1996 (all else).

Results

Phytoplankton

Spring

During spring, a total of 289 phytoplankton taxa were found in the 72 samples examined. All lakes supported well over one hundred taxa, with slightly over 200 taxa found in Lake Erie (Figure 2a). Our definition of phytoplankton taxa here is somewhat more broad than that reported in 1998, in that strictly benthic taxa, excluded in 1998, are included here. This no doubt would increase taxa numbers in Lake Erie to a greater extent than in the other lakes due to its shallowness. In spite of greater overall taxa richness, the average number of taxa per site was lowest in Lake Erie (55), while for the other lakes this figure ranged from 65 to 74. Diatoms, overwhelmingly the most diverse group across all lakes, contributed between 40 and 55% of the species found in each lake (Figure 2b). Chlorophytes and chrysophytes each contributed between 16 and 36 species per lake, or about 15% to 23% of species, while between 11 and 14 species of cryptophyte were found in each lake. Other groups, while occasionally responsible for high numbers of individuals, were considerably less diverse. The contributions of these major taxonomic groups to taxa richness were very similar to what was found in 1998.

Total phytoplankton biovolumes across the lakes ranged from $4.6 \cdot 10^4\ \mu m^3\ ml^{-1}$ at a site in Lake Superior to $3.8 \cdot 10^6\ \mu m^3\ ml^{-1}$ at a site in the western basin of Lake Erie (Figure 3). Biovolumes were relatively uniform within each lake, with the dramatic exception of Lake Erie, where biovolumes spanned over 1.5 orders of magnitude. This spatial heterogeneity was apparent within as well as between basins.

Whole-lake median biovolumes were fairly similar from lake to lake, ranging from $4.4 \cdot 10^5\ \mu m^3\ ml^{-1}$ in Lake Huron to $8.7 \cdot 10^5\ \mu m^3\ ml^{-1}$ in Lake Erie, with the exception of Lake Superior where the median biovolume was only $6.5 \cdot 10^4\ \mu m^3\ ml^{-1}$.

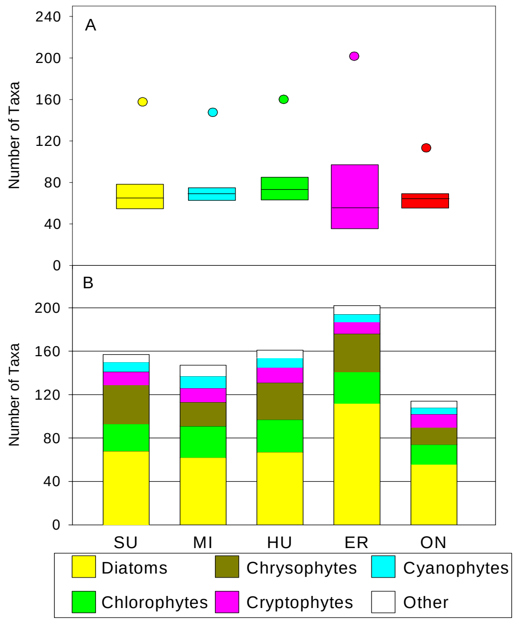
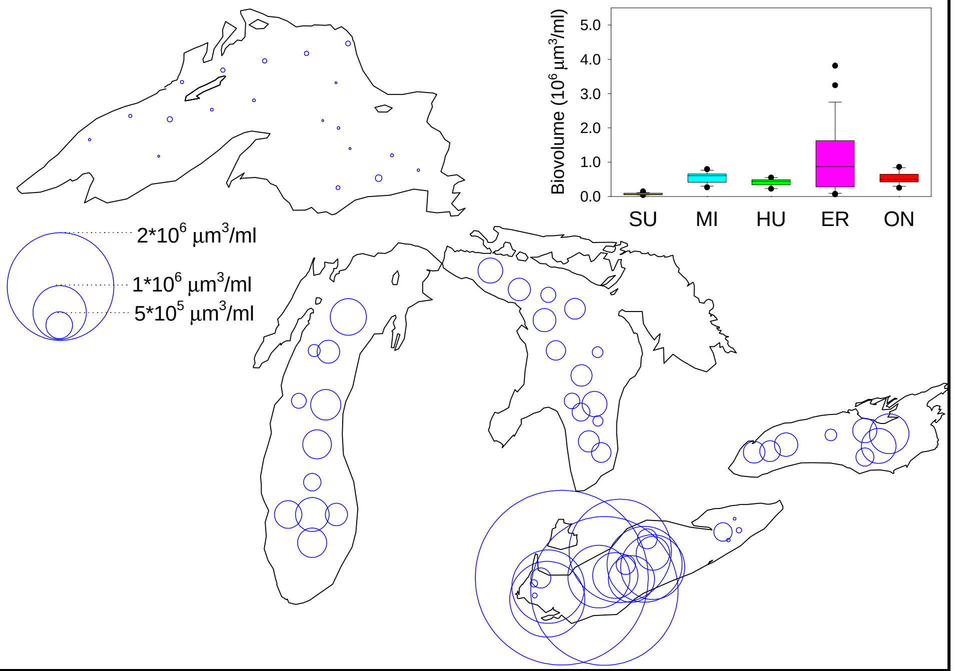


Figure 2. A.) Phytoplankton species richness, spring cruise, 1999. Boxes represent minimum, mean, and maximum numbers of taxa per station at each lake; circles represent total numbers of taxa found in each lake; B.) Contribution of major taxonomic groups to species richness.

Diatoms were the dominant phytoplankters at most sites, making up between 76 and 92% of phytoplankton biovolume, on a lake-wide basis, in all lakes except Superior, where on average diatoms made up just under half of the biovolume (Figure 4; Table 1). Either chrysophytes or cryptophytes were second in importance, although neither division contributed more than 11% of the phytoplankton biovolume in any lake except Lake Superior. Cyanophytes contributed about 10% to Lake Superior phytoplankton biovolume, but only made up minor amounts of biovolume to the other lakes. Biovolumes of chlorophytes were uniformly low throughout the lakes in spring.

Figure 3. Biovolume of the total phytoplankton community in the Great Lakes, spring 1999. Inset shows box plots of phytoplankton biovolumes for each lake.



The dominant species in all five lakes was the typical spring centric diatom *Aulacoseira islandica* (Table 1). This species contributed between 22% (Superior) and 78% (Erie) of total phytoplankton biomass, on a lake wide basis. The congener *Aulacoseira subarctica* achieved relatively high abundances in Lake Michigan, as has been seen before, but not in any other lakes. Dominance in Lake Huron was shared by the pennate diatom *Tabellaria flocculosa*, a species which also showed up in notable numbers, along with the pennate *Asterionella formosa*, in Lake Superior. In Lake Erie, *Stephanodiscus alpinus* and *Stephanodiscus hantzschii* f. *tenuis* accounted for much of the biovolume not contributed by *A. islandica*.

Summer

A total of 305 phytoplankton taxa were identified from epilimnetic samples taken during the summer survey. Overall patterns of taxa richness from lake to lake was similar to that in spring (Lake Erie highest, Lake Ontario lowest, upper lakes intermediate), as were average numbers of taxa found at sites within lakes, although Lake Erie had slightly greater species richness in summer compared to spring (Figure 5a). The diversity of the diatom communities was reduced in summer, compared to spring, while the numbers of chrysophyte, and in the lower lakes chlorophyte, taxa increased (Figure 5b). The contribution of cryptophytes and cyanophytes to species richness was 12% or less.

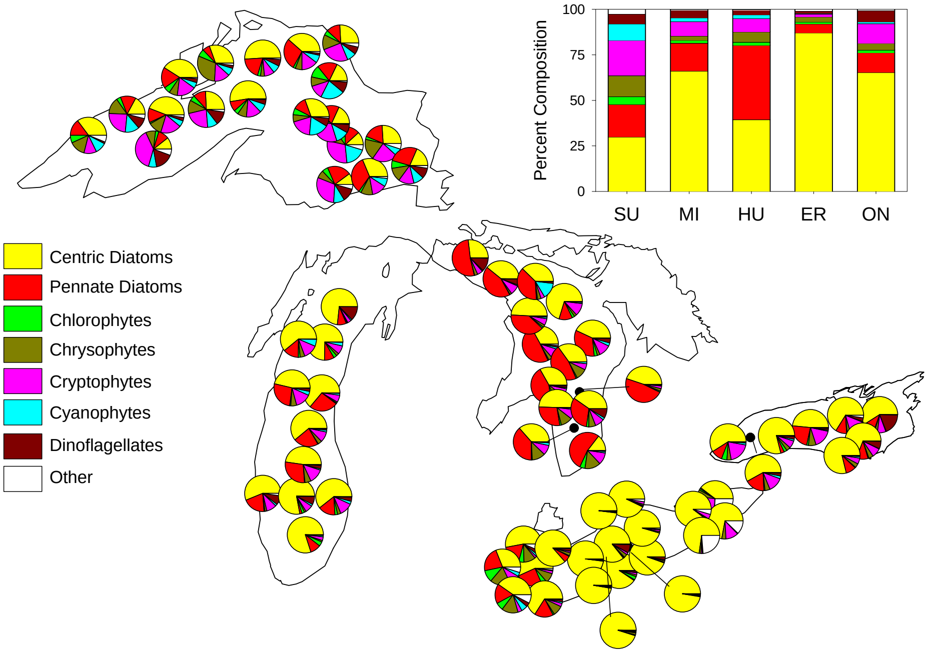


Figure 4. Relative biovolumes of major phytoplankton groups in the Great Lakes, spring cruise, 1999. Inset shows whole-lake averages.

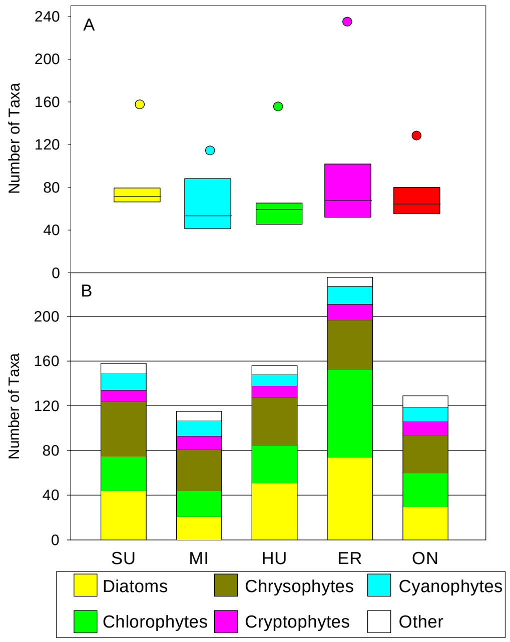
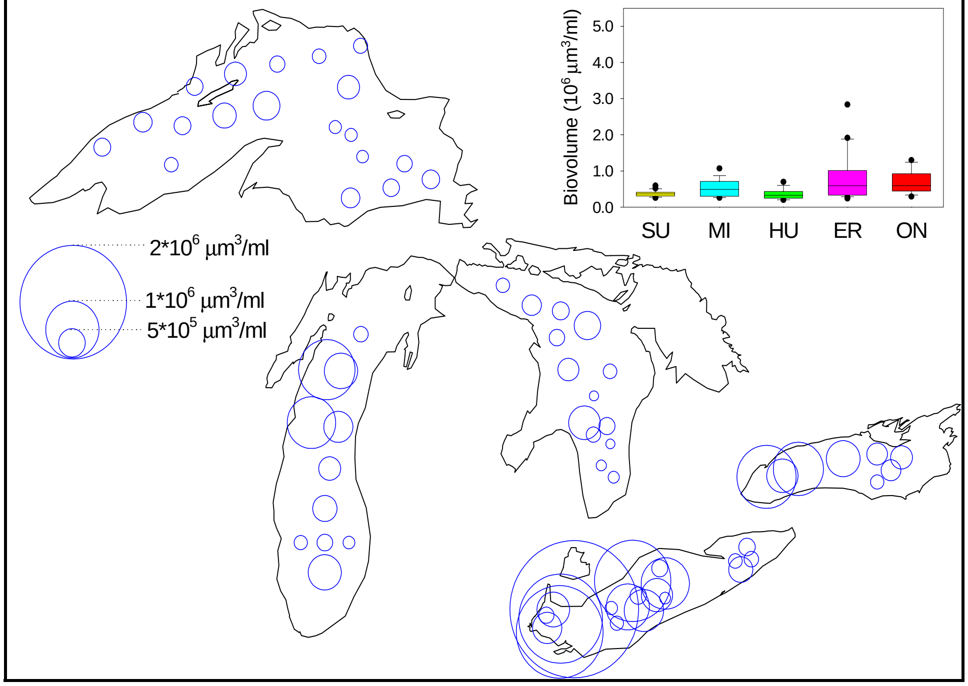


Figure 5. A.) Phytoplankton species richness, summer cruise, 1999. Boxes represent minimum, mean, and maximum numbers of taxa per station at each lake; circles represent total numbers of taxa found in each lake; B.) Contribution of major taxonomic groups to species richness.

Phytoplankton biovolumes were considerably more similar across the lakes in summer, compared to spring, due in large part to increases in biovolume in Lake Superior and the eastern basin of Lake Erie (Figure 6). Consequently, median biovolumes were confined to a smaller range than in spring, varying only from 3.3 10^5 μm^3 ml^{-1} in Lake Huron to 5.9 10^5 μm^3 ml^{-1} in Lakes Erie and Ontario.

All lakes with the exception of Lake Superior experienced substantial reductions in the proportion of diatoms in the summer (Figure 7; Table 2). The average proportion of diatoms in Lake Superior, in contrast, increased from 48% to 62%. The importance of dinoflagellates increased in all lakes but Superior, with the largest populations found in Lake Michigan,

Figure 6. Biovolume of the total phytoplankton community in the Great Lakes, summer 1999. Inset shows box plots of phytoplankton biovolumes for each lake.



where a majority of phytoplankton biovolume at many sites was contributed by dinoflagellates. While estimation of dinoflagellate biovolume is problematic, in that individuals can be extremely large and therefore the chance occurrence of a single individual in a counting chamber can constitute the majority of biovolume in that sample, the high proportion of dinoflagellate biovolume across many sites in Lake Michigan suggests that this group did in fact maintain large populations in the summer. Proportions of chrysophytes increased in Lake Huron, while chlorophytes increased substantially in Lakes Erie and Ontario. There was some indication of north/south differentiation in Lake Huron, with communities in the north supporting a higher percentage of diatoms. The difference in community composition between Lakes Michigan and Huron, and in particular the great proportion of diatoms in the latter lake, contrasts with what was found in 1998 (Barbiero and Tuchman, 2001), and suggests that year may have been anomalous.

Dominance during the summer cruise was for the most part distributed amongst a larger number of species (Table 2). *Ceratium hirundinella* figured prominently in all lakes but Superior; both *Fragilaria crotonensis* and various species of the summer centric diatom *Cyclotella* appeared in substantial numbers across all lakes, although each lake, and in the case of Erie each basin, supported fairly species assemblages of this latter genus (Figure 8).

Figure 7. Relative biovolumes of major phytoplankton groups in the Great Lakes, summer cruise, 1999. Inset shows whole-lake averages.

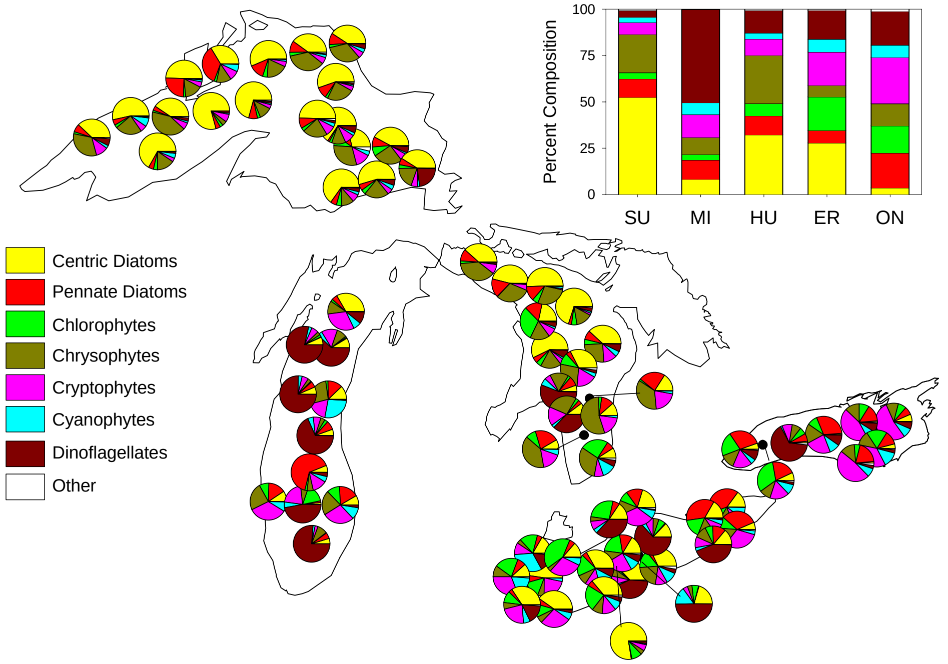
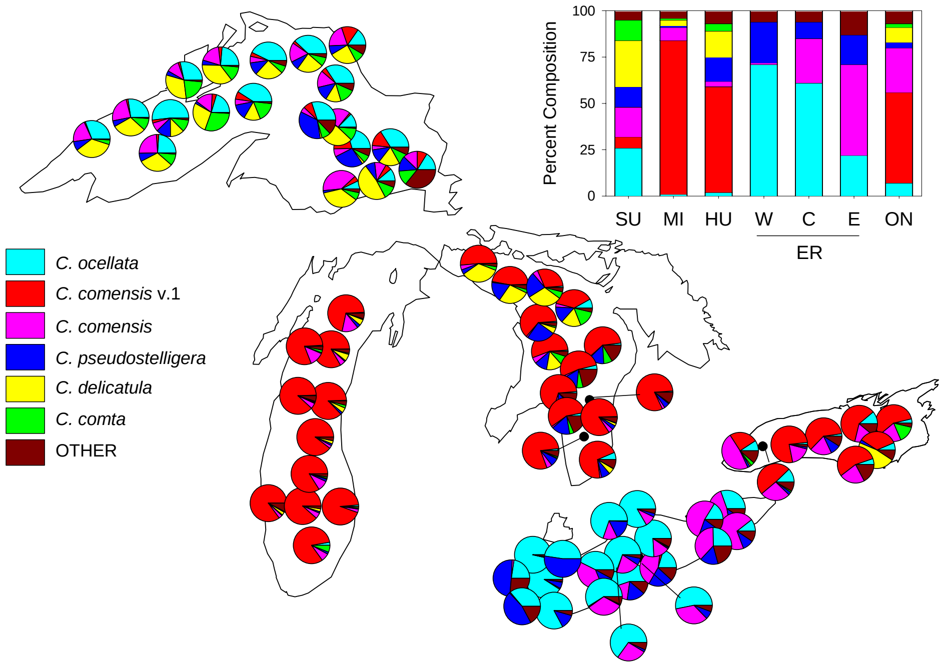


Figure 8. Relative abundance of *Cyclotella* species, summer cruise, 1999. Inset shows whole-lake averages.



Zooplankton

Spring

Crustacean community diversity was low across the lakes, with almost all sites supporting less than 10 taxa (Figure 9a). Species richness was lowest in Lake Superior, where no more than 5 taxa were found at any site, while average numbers of taxa per site ranged only between 6 and 8 for the other four lakes. Total numbers of taxa found in each lake ranged from 9 (Superior) to 21 (Erie), which is very similar to what was found in 1998.

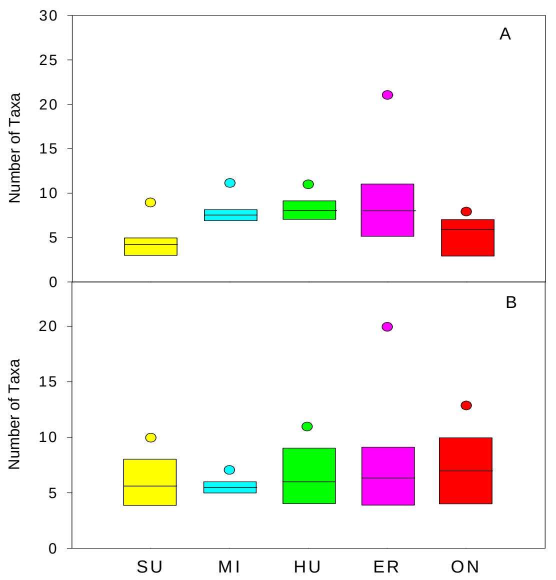
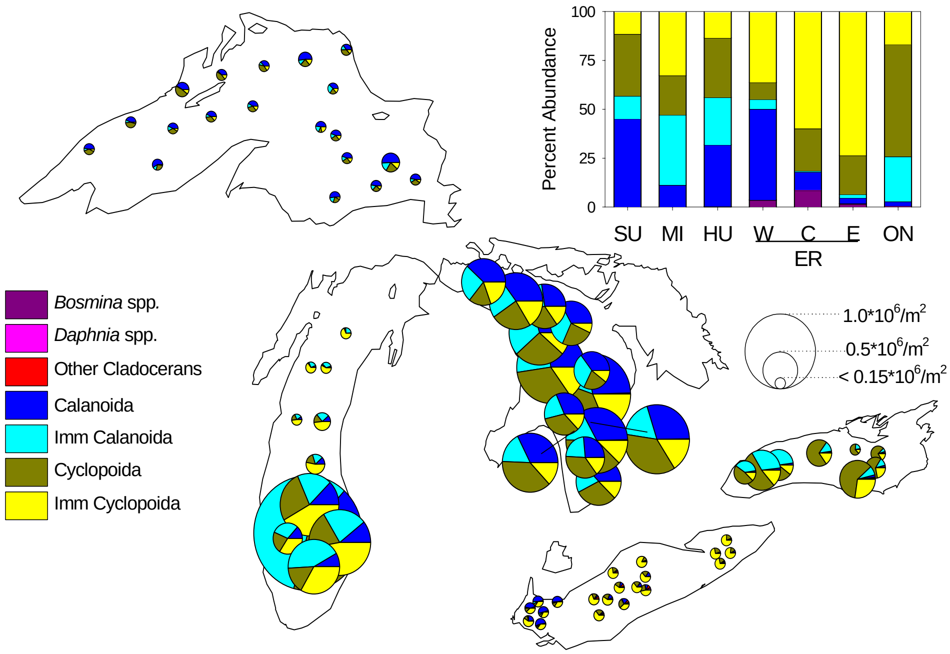


Figure 9. Minimum, maximum and mean number of taxa per site (boxes), and total number of taxa per lake (circles), for A.) crustaceans; and B.) rotifers, spring 1999.

Areal abundances of crustaceans (excluding nauplii) varied from 1,727 animals m^{-2} at a site in eastern Lake Erie to over 1.5·10^{6} m^{-2} at a site in southern Lake Michigan (Figure 10). Abundances overall were lowest in Lake Erie and highest in Lake Huron. It should be borne in mind that, given the shallowness of most sites in Lake Erie, abundances would be relatively higher in that lake if considered volumetrically, although they would still be low compared to the other lakes (see Table 4). Within each lake abundances were fairly uniform, with the exceptions of Lake Michigan, where there appeared to be strong north-south differentiation in abundances, and Lake Erie, where abundances varied substantially between basins. Spatial heterogeneity is not apparent in the case of the latter lake in Figure 10 due to scaling of the figure.

During spring, crustacean communities across all five lakes were dominated by copepods, although the relative importance of calanoids and cyclopoids varied from lake to lake. Immature copepods made up a substantial portion of the individuals found at all sites. In the upper lakes and the western basin of Lake Erie, calanoid and cyclopoid copepods were present in approximately equal numbers. In Lakes Michigan and Huron, *Leptodiaptomus ashlandi* and *Leptodiaptomus minutus*, along with the large, deep-water species *Limnocalanus macrurus*, accounted for most of the calanoids (Table 3). There was a slight tendency towards an increase in the relative importance of cyclopoid copepods at the northern stations in Lake Michigan, though differences were slight. In the shallow western basin of Lake Erie *L. ashlandi* and *L. minutus* were also the dominant calanoids, with *L. marcrurus* largely absent, while in Lake Superior *L. macrurus*, along with its immatures, and another large, deep-water form *Leptodiaptomus sicilis*, were the dominant calanoids. In the central and eastern basins of Lake Erie, as well as Lake Ontario, cyclopoid copepods accounted for the great majority of individuals; in all lakes *Diacyclops thomasi* was the dominant cyclopoid. Only the central basin of Lake Erie supported significant numbers of cladocerans, mostly *Bosmina* and *Eubosmina*, in

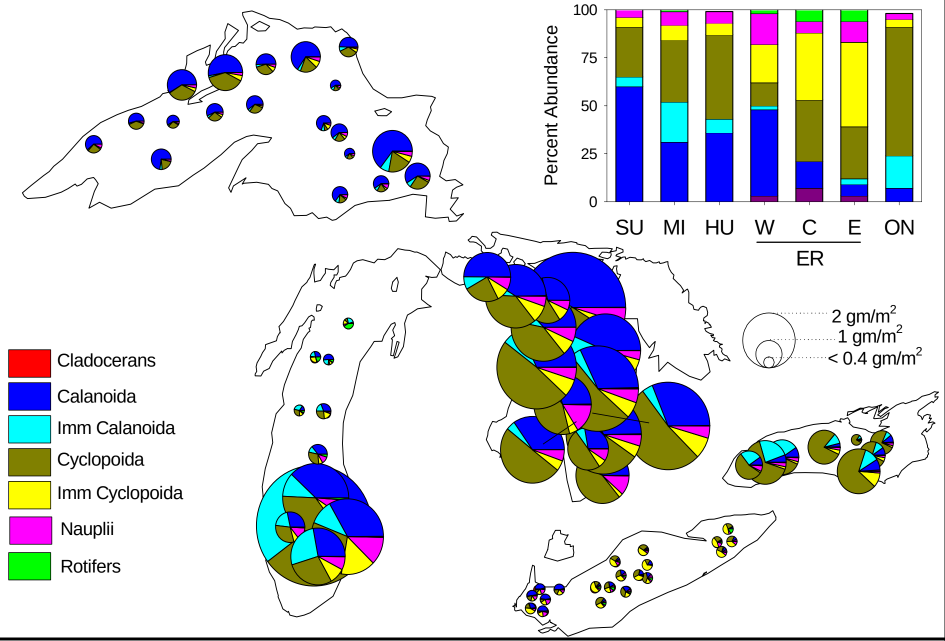
Figure 10. Areal abundances of major crustacean groups in the Great Lakes, spring 1999. Inset shows whole lake averages.



the spring. In all lakes (or in the case of Lake Erie, basins), 95% of the crustacean community was made up of 4 species or less.

Comparing the relative contribution of rotifers and nauplii to zooplankton community biomass is problematic, since the former are enumerated only from shallow tows, which have been shown to provide highly misleading estimates of adult crustacean biomass, particularly if taken during the day. Crustacean abundances are here given on the basis of areal units, which assumes that the entire community is captured at the depth to which tows are taken. Judging from the results of previous studies examining the depth distribution of crustaceans in the Great Lakes, this is probably a reasonably safe assumption for all species except the deep-living *Leptodiaptomus sicilis* and *Limnocalanus macrurus*. To compare rotifer and nauplii biomass on an areal basis to crustacean biomass would similarly assume that tows to a depth of 20 m capture the majority of populations of the former, an assumption which is difficult to assess due to a lack of information. In lieu of more comparable data, however, combining areal abundances for the two groups (i.e. rotifers and nauplii and crustaceans) based on estimates from the two different tows probably provides the best estimate of the relative contribution of nauplii and rotifer biomass to the total zooplankton community. It should be borne in mind, however, that distribution of a substantial portion of rotifer or nauplii biomass below 20 m would result in underestimation of their relative importance.

Figure 11. Areal biomass of major zooplankton groups in the Great Lakes, spring 1999. Inset shows whole lake averages.



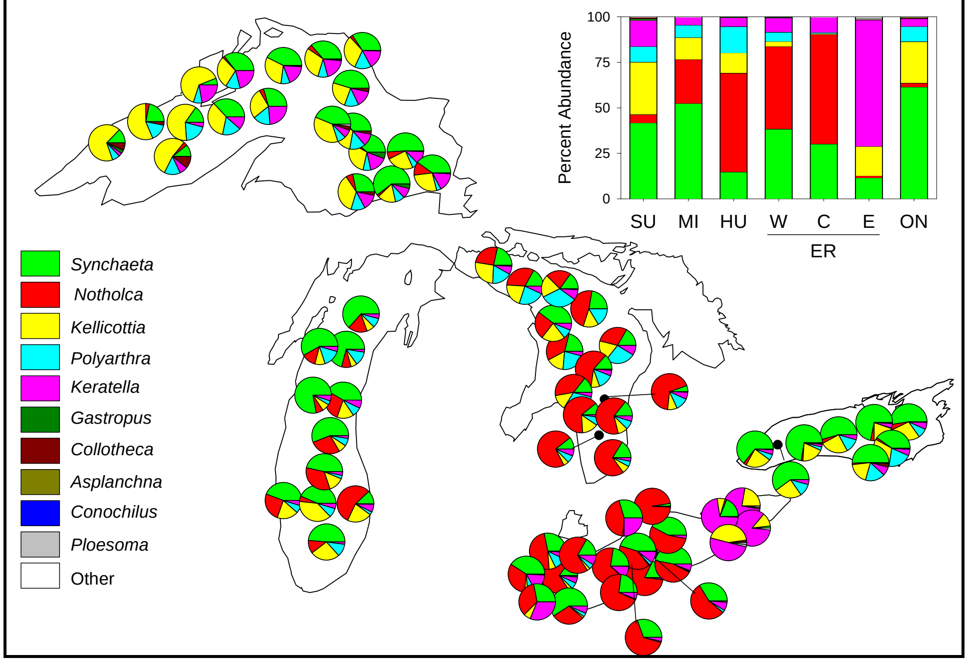
Nauplii contributed between 3% and 16% of zooplankton biomass across the lakes, with the highest contribution in western and eastern Lake Erie, and the lowest in Lake Ontario (Figure 11). Rotifers made up a small portion of zooplankton biomass, contributing at most only 6% in central and eastern Lake Erie. Species richness of rotifers, however, was roughly similar to that of crustaceans, averaging between 4 and 10 taxa per site for the five lakes. In all between 17 and 20 taxa were found in each lake (Figure 9b). *Synchaeta* was the most widely distributed genus, while *Notholca* was particularly abundant in the central and western basins of Lake Erie and in Lake Huron. *Kellicottia* was most abundant in Lake Superior, but was also present at most sites except the western and central basins of Lake Erie, while the eastern basin of Lake Erie was unusual in its large population of *Keratella* (Figure 12).

Summer

Species richness of the crustacean community was substantially higher during the summer, compared to spring, with sites supporting between 4-15 taxa (Figure 13a). Total numbers of taxa found in each lake varied from 13 to 24. Again, Lake Erie had the greatest number of species overall, and Lake Superior the lowest.

Total crustacean abundances (excluding nauplii) were substantially higher during the summer than in spring across all lakes (Figure 14). The greatest increase was seen in the eastern basin of Lake Erie, where areal abundances increased by several orders of magnitude. The upper lakes

Figure 12. Relative abundance of rotifer genera, spring cruise, 1999. Inset shows whole-lake averages.



exhibited more modest increases of 2-4 x spring numbers. The prominent north/south differences in abundances seen in Lake Michigan in the spring were not apparent in the summer, though substantial intersite differences were still found in Lake Erie.

As in spring, copepods, particularly immatures, contributed significant numbers to all sites. Immature cyclopoids were abundant in all lakes, while large numbers of immature calanoids were found in all lakes except Lake Ontario and the western basin of Lake Erie. As in spring, calanoid copepods in Lakes Michigan and Huron were primarily the diaptomids *L. ashlandi* and *L. minutus*; *Skistodiaptomus oregonensis* was the most common calanoid in Lake Erie, while *L. macrurus* and *L. sicilis* were again the

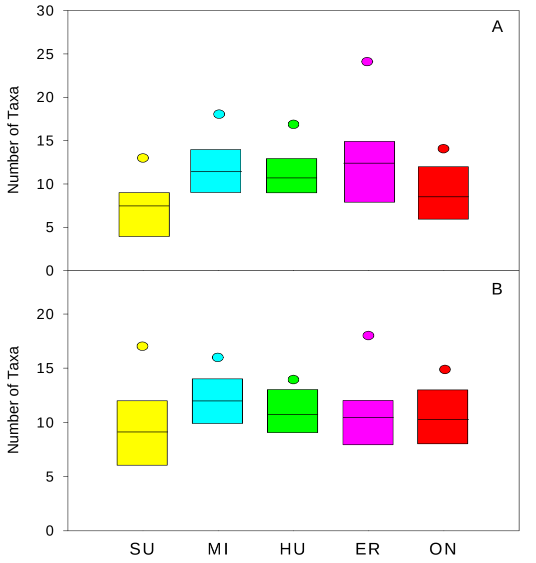
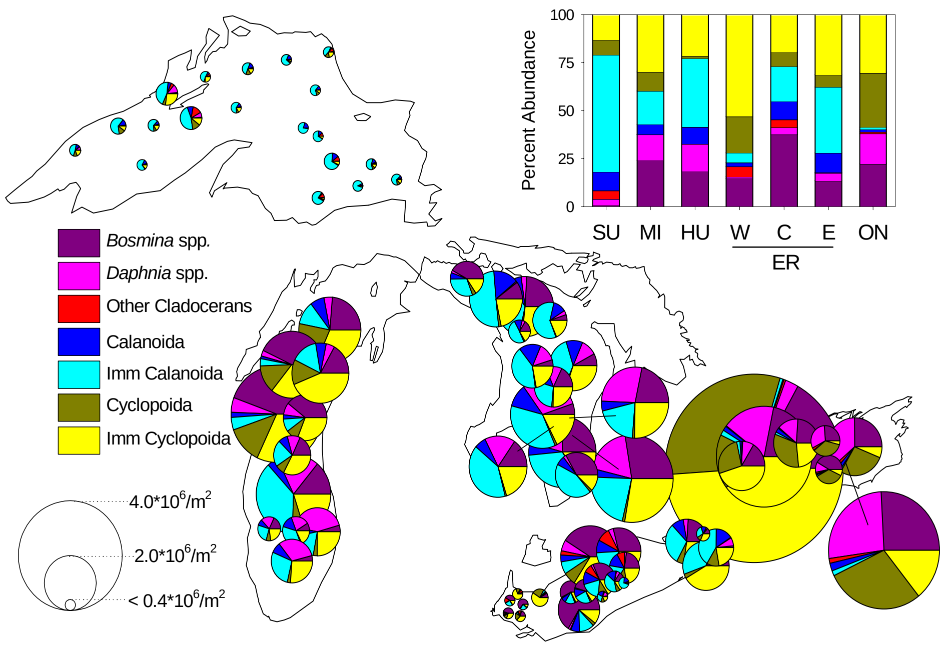


Figure 13. Minimum, maximum and mean number of taxa per site, and total number of taxa per lake, for A.) crustaceans; and B.) rotifers, summer 1999.

Figure 14. Areal abundances of major crustacean groups in the Great Lakes, summer 1999. Inset shows whole lake averages.



predominant calanoids in Lake Superior. *Diacyclops thomasi* was the dominant cyclopoid species in all lakes except Erie, where *Mesocyclops edax* was most numerous. There was some indication of spatial heterogeneity in Lake Michigan; calanoid copepods were relatively more important in the south and cyclopoids more important in the north, as was seen in the spring. Cladocerans, largely absent in the spring, made up a substantial portion of the crustacean communities in the summer in all lakes except Lake Superior. Species of *Bosmina*/ *Eubosmina* were the most prominent cladoceran in all lakes except Lake Superior; *Daphnia galeata mendotae* was the other dominant cladoceran in Lakes Huron and Michigan, as was *Daphnia retrocurva* in Lake Ontario. In Lake Michigan, *D. galeata endotae* populations were notably higher in the southern area of the lake, and *Bosmina longirostris* populations higher in the northern region. The abundance of the smaller bodied *Bosmina* in both Lakes Michigan and Huron contrasts with the *Daphnia* dominated community seen in 1998 (Barbiero et al., 2001), and suggests greater predation pressure on the zooplankton community in 1999. As was seen in 1998, *Holopedium gibberum* and *Daphnia galeata mendotae* were present in approximately equal numbers in Lake Superior, though neither organism was particularly abundant in that lake. *Daphnia* species weren't as numerous in Lake Erie, compared to the other lakes. This genus typically experiences its seasonal maximum in late June or July in that lake, and it is likely that our sampling occurred after populations had already declined.

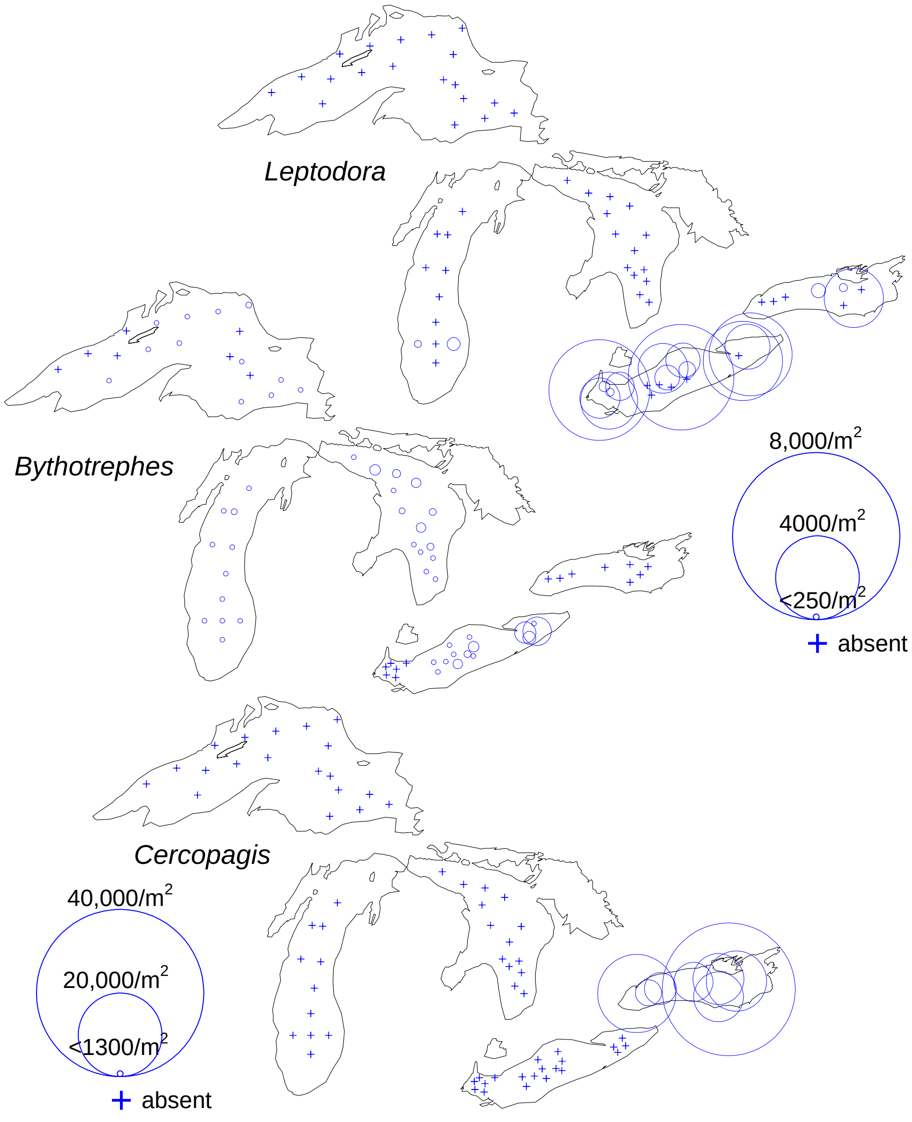
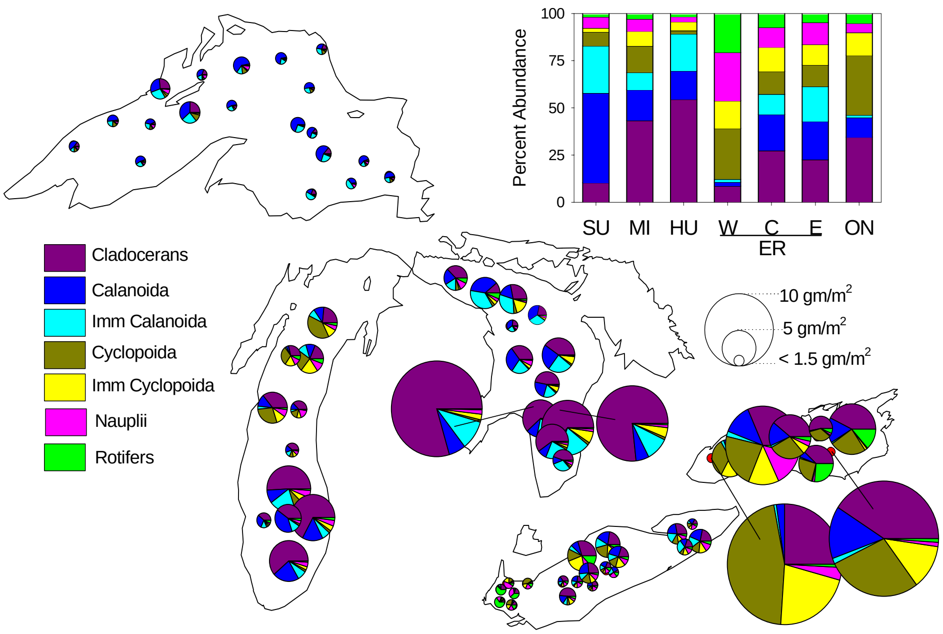


Figure 15. Areal abundances of predatory cladocerans in the Great Lakes, summer, 1999, as estimated from 100 m tows. Note differences in scale.

The three major predatory cladocerans found in the lakes are the native *Leptodora kindtii*, and the two exotic cladocerans *Bythotrephes cederstroemi* and *Cercopagis pengoi* (Figure 15). Of the three, *Bythotrephes* was the most widely distributed, showing up, albeit in small numbers, in all parts of the lakes with the notable exceptions of western Lake Erie and Lake Ontario. *Leptodora* was almost entirely restricted to the lower lakes, although small numbers were found at two sites in southern Lake Michigan. While less widely distributed than *Bythotrephes*, densities of *Leptodora* were substantially larger. Offshore

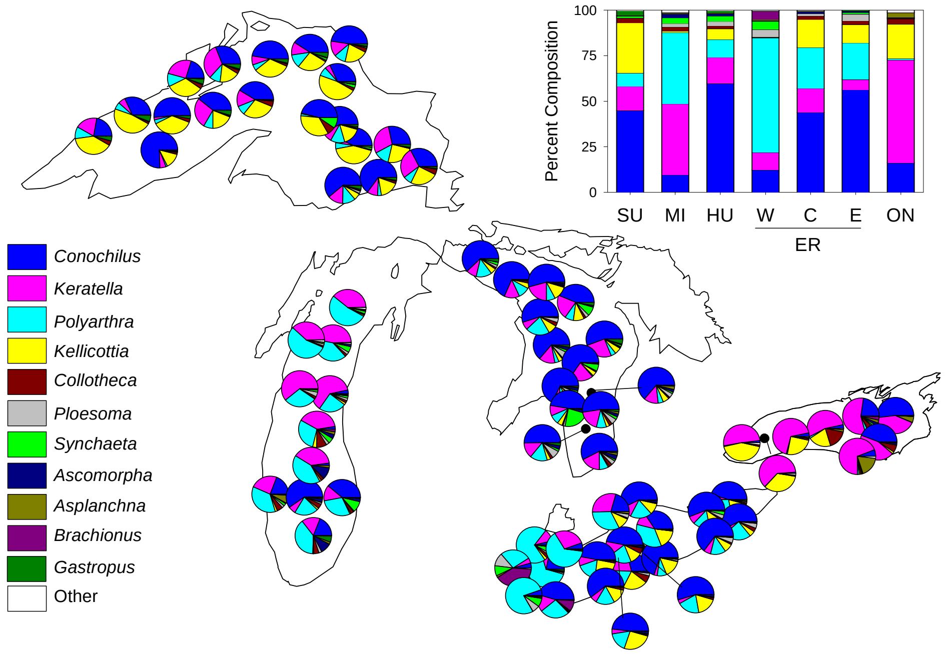
Figure 16. Areal biomass of major zooplankton groups in the Great Lakes, summer 1999. Inset shows whole lake averages.



populations of *Cercopagis* in the Great Lakes were still restricted to Lake Ontario, where this recent invader was first recorded in 1998, although in 1999 it had spread throughout the lake (Ojaveer et al., 2001). Individuals had also been found in nearshore waters of southern Lake Michigan in August of 1999 (Charlebois et al., 2001), but populations had apparently not extended to offshore sites. Abundances of this organism were markedly higher than for both *Bythotrephes* and *Leptodora*; a maximum density of 37,000 m^{-2} was recorded for *Cercopagis* at a site in the eastern portion of Lake Ontario, compared to maximum densities of 6,000 for *Leptodora* in central Lake Erie, and 1,600 for *Bythotrephes* in eastern Lake Erie.

Rotifer diversity, like that of crustaceans, was higher in the summer compared to the spring (Figure 13b). Numbers of taxa per site ranged between 6 and 14, with each lake supporting between 14 and 18 taxa overall. Rotifers made up slightly larger percentage of total biomass across the lakes in summer, compared to spring, although in all but the western and central basins of Lake Erie their contribution to biomass was still 5% or less (Figure 16). The contribution of nauplii to biomass increased in the western and central basins of Lake Erie, but remained unchanged elsewhere, ranging between 3% and 5% in the other lakes. The relative importance of rotifers and nauplii in Lake Erie was related, no doubt, to the overall low crustacean biomass seen in that lake, which,

Figure 17. Relative abundance of rotifer genera, summer cruise, 1999. Inset shows whole-lake averages.



as noted, was probably due in part to seasonality of the cladoceran community.

Dominant rotifer genera in the summer included *Conochilus*, abundant in Lakes Huron, Superior, and the central and eastern basin of Lake Erie, *Keratella*, achieving notable populations in Lake Ontario and Lake Michigan, and *Polyarthra*, which was most prominent in the western basin of Lake Erie and in Lake Michigan (Figure 17). Populations of *Keratella* were also found, notably in Lake Superior, Lake Ontario, and parts of Lake Erie. A shift in the rotifer community away from *Notholca*, *Synchaeta* and *Kellicottia* to *Polyarthra* and *Conochilus* from spring to summer was also seen in 1998.

Benthos

Most sites supported a very limited number of benthic taxa, with numbers of taxa found per site ranging from 1 to 22 for the five lakes, and all lakes but Erie averaging less than 10 taxa per site (Figure 18). Lake Erie supported the greatest number of taxa overall (40), while benthic invertebrate communities in Lake Superior relatively taxa poor, with a total of 12 taxa found in the lake.

Depth appeared to be an important factor in determining the number of taxa found at a site. Regression analysis found a highly significant ($p < 0.001$) inverse relationship between depth and taxa number for sites shallower than 70 m (Figure 19); beyond this depth sites supported uniformly low numbers of taxa with little apparent relationship to depth.

Areal abundances of benthic organisms varied greatly within each lake, although lake-wide averages were fairly similar amongst all lakes but Superior (Figure 20). Abundances varied from site to site within each lake by about an order of magnitude, two orders of magnitude in the case of Lake Superior. At least part of this variability was due to depth, which set a clear upper limit to benthic abundances, although low abundances were also seen at some shallow sites (Figure 21).

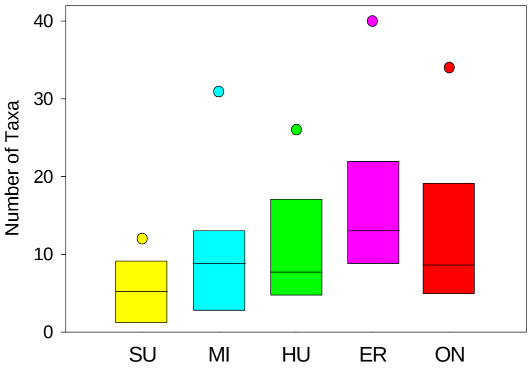


Figure 18. Minimum, maximum and mean number of benthic taxa per site, and total number of taxa per lake, summer 1999.

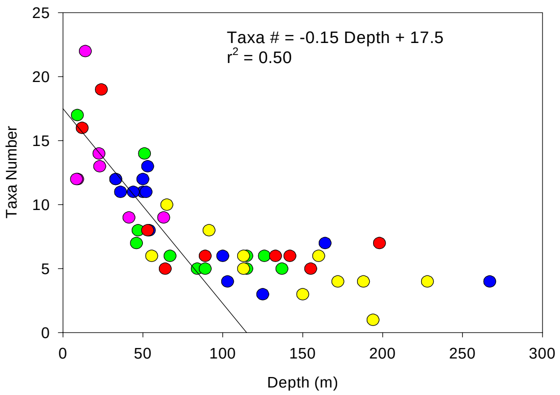


Figure 19. Relationship between depth and benthic taxa richness, summer 1999.

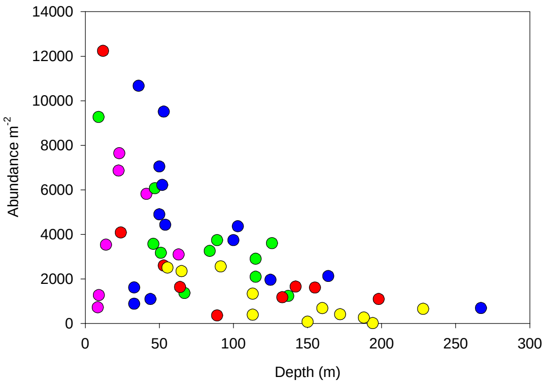


Figure 21. Relationship between depth and benthic abundance, summer 1999.

The amphipod *Diporeia* is a glacial relict that has historically been one of the most abundant and widespread organisms in the Great Lakes, and indeed in most large lakes in previously glaciated regions of the Holarctic (Dermott and Corning, 1988). In 1999 it was by far the dominant benthic invertebrate in the upper three lakes, although it was absent from Lake Erie, nearshore sites in Lake Ontario, Saginaw Bay in Lake

Figure 20. Areal abundance of benthos in the Great Lakes, summer 1999.

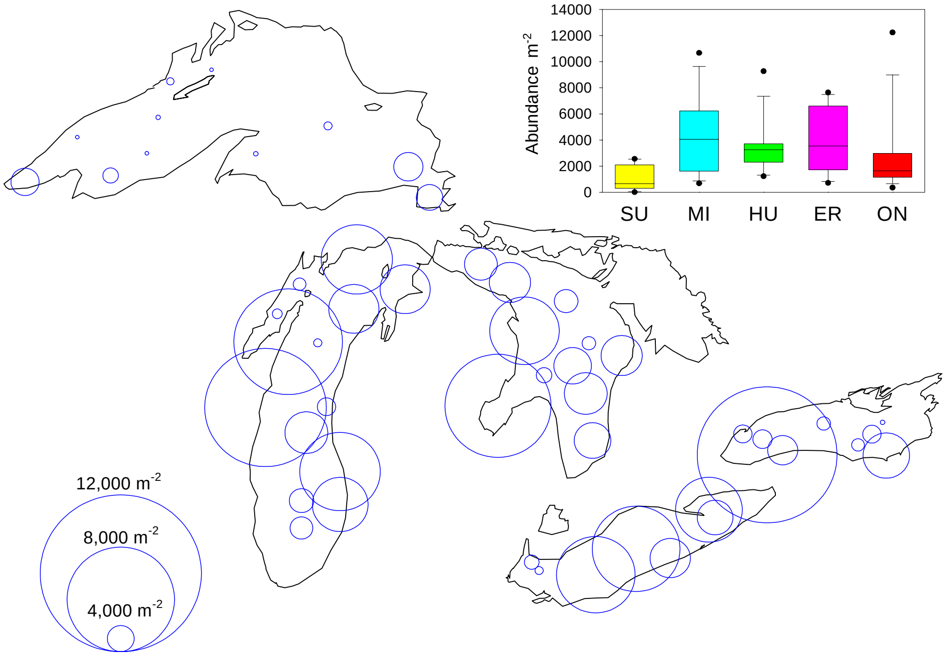
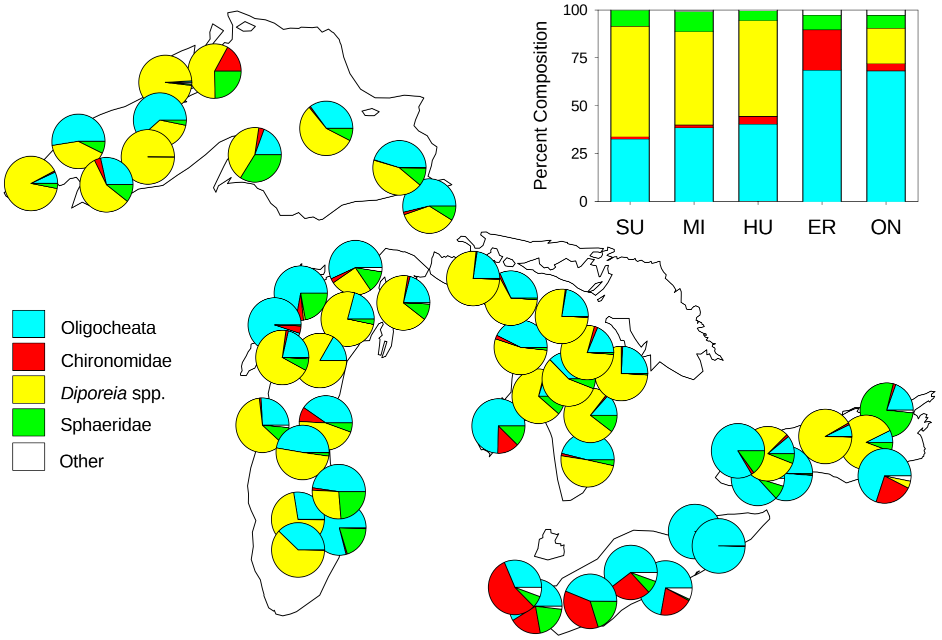


Figure 22. Relative abundances of major benthic groups in the Great Lakes, summer 1999. Inset shows whole lake averages.



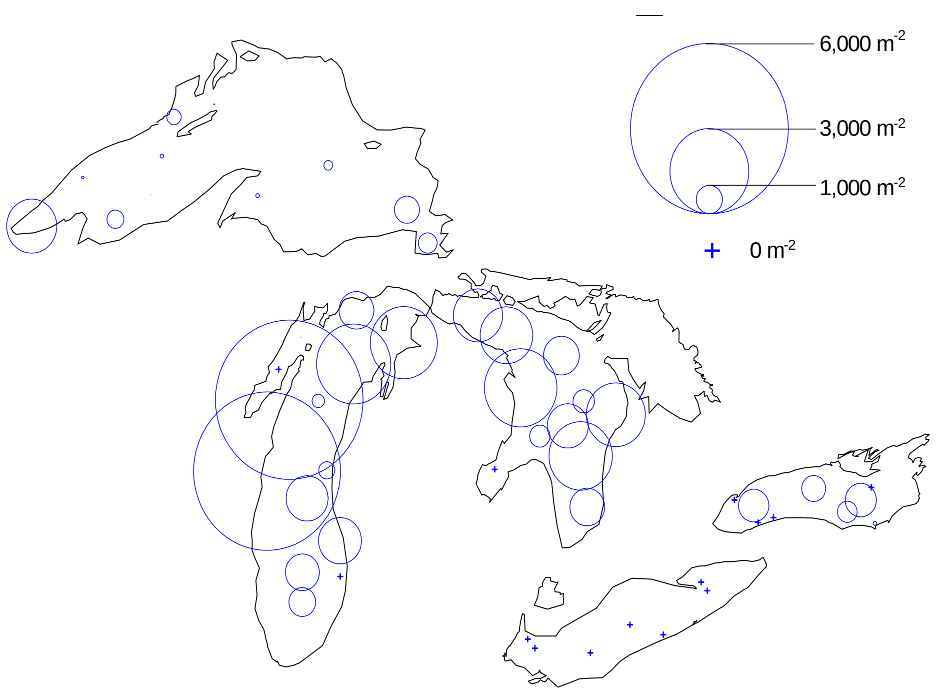


Figure 23. Abundance of *Diporeia* spp. in the Great Lakes, summer 1999

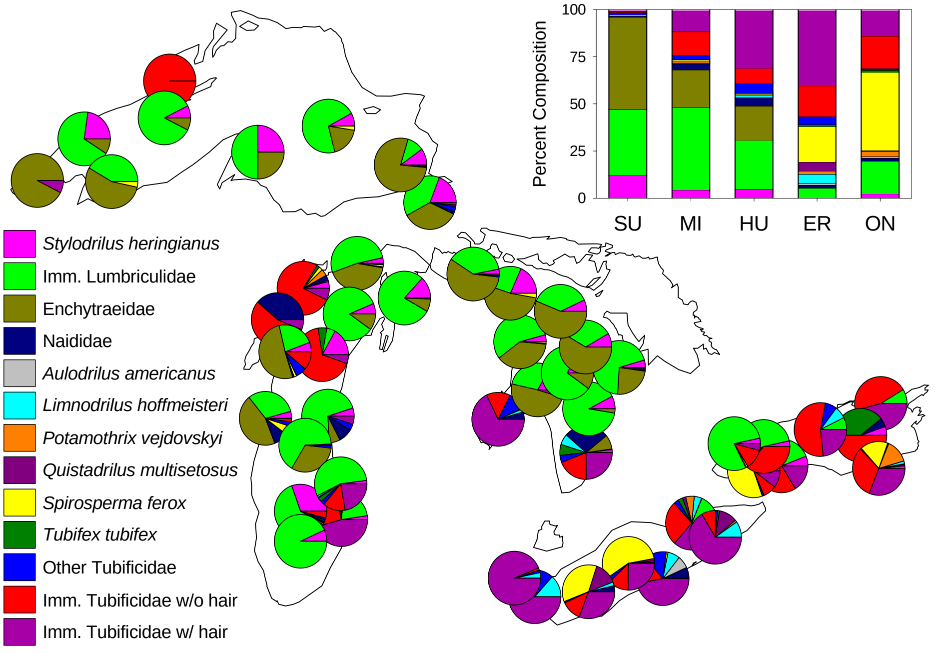
Huron and Green Bay in Lake Michigan (Figures 22, 23).

Recently it appears that this organism has been in decline in significant portions of its range in the Great Lakes. Dramatic declines have been reported at shallow stations in both southeastern Lake Michigan (Nalepa et al. 1998) and eastern Lake Ontario (Dermott, 2001), and it is no longer found in Lake Erie (GLNPO data).

In general, *Diporeia* populations have declined between 1997 and 1999 at most of our Lake Michigan stations. Significantly, these declines have not been restricted to shallow southeastern stations, but have occurred at both northern and deep station where populations have dropped from thousands of individuals/m^2 to hundreds during the past three years. Similar declines have been seen at most stations in Lake Huron between 1997 and 1999. While overall abundances in Lake Huron were lower in 1999 than in 1998, and in 1998 than in 1997, these abundances have still tended to be substantially higher than those reported historically (e.g. Teter 1960, Henson 1970, Shrivastava 1974).

In Lake Ontario, *Diporeia* was absent from stations < 100 m in depth in our study, while in 1972 (Nalepa and Thomas 1976) this organism accounted for 22% and 61% of the benthic community at sites between 7 - 35 m and 40 - 90 m, respectively. No consistent trends have been noted at our deeper stations in the years 1997-1999, and abundances at these stations, generally between 1,000 and 2,000/m^2, have tended to be substantially higher than most historical reports (e.g. Kinney 1972, Nalepa and Thomas 1976,

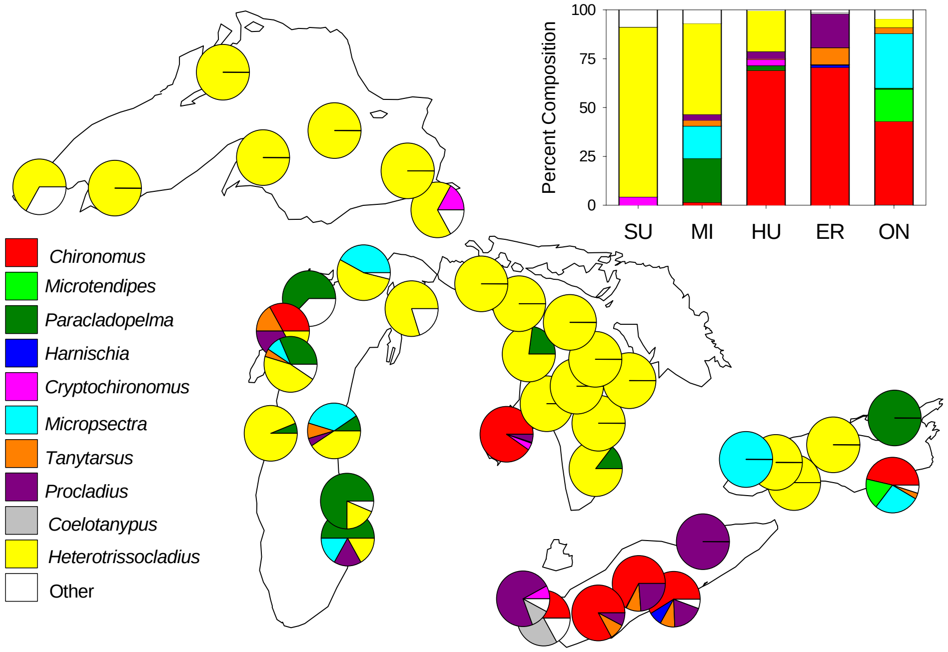
Figure 24. Relative abundances of oligochaete taxa in the Great Lakes, summer 1999. Inset shows whole lake averages.



Golini, 1979). Our study does not include substantial coverage in the eastern and southeastern areas of the lake where the most dramatic declines have been seen (Dermott, 2000). Similarly, we have seen no consistent trends in Lake Superior between 1997 and 1999. While declines had been seen at most stations in the lake between 1997 and 1998, these were largely reversed in 1999. Abundances recorded during those three years are generally in line with, or slightly higher than, historical reports (e.g. Hiltunen 1969b, Schelske and Roth 1973, Cook 1975).

Oligochaetes were the second most dominant group, and made up the greatest percentage of individuals at those sites where *Diporeia* did not. They were the most diverse group, with over 30 different species identified in 1999. Members of the oligochaete family Lumbridulidae increased in importance along the sequence Erie->Ontario->Huron/Michigan->Superior, which is in keeping with their preference for lower productivity environments, while members of the Tubificidae were more common in the lower lakes and at shallower sites in Lakes Michigan and Huron (Figure 24).

Figure 25. Relative abundances of chironomid taxa in the Great Lakes, summer 1999. Inset shows whole lake averages.



Over 20 genera of Chironomidae were also found in the lakes (Figure 25). The oligotrophic genus *Heterotrssocladius* was the only chironomid found in Lake Superior, and also dominated the off-shore sites of Lakes Michigan and Huron. Communities in the lower lakes were more diverse, supporting notable populations of *Chironomus*, *Procladius* and *Micropsectra*, among other genera.

Benthic Indices

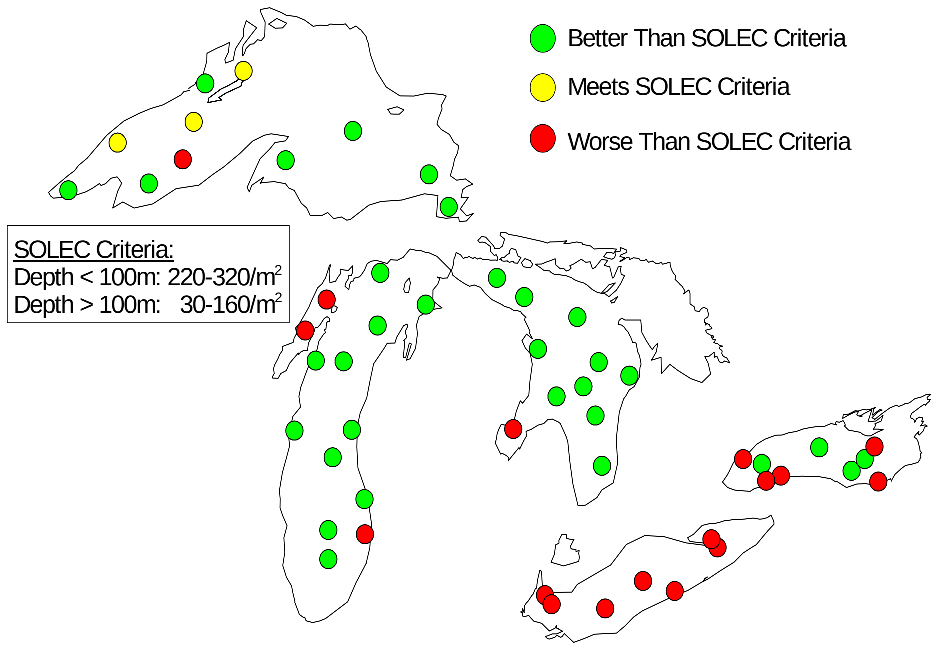
Direct assessment of benthic communities has long been considered an essential element in determining the impacts of anthropogenic stress on aquatic systems (Wilhm and Dorris, 1968). Benthic invertebrates exhibit a number of characteristics that make them particularly well suited for use as biomonitoring tools: they have differing sensitivities to stressors, thus community make-up can be expected to vary in a predictable way with the level of anthropogenic stress; they are longer lived than most planktonic organisms, and thus can integrate the effects of environmental conditions over time; and they are relatively sedentary, and are therefore easier to sample than nektonic organisms, such as fish, and can serve as indicators of specific areas. In addition to serving as indicators of general ecosystem condition, the health of the benthic communities is of inherent interest due to their pivotal ecological role. Many benthic invertebrates are detritivores, feeding on organic material produced in the pelagic zone. Since these organisms are often important components of fish diets, they provide an important link in the food chain.

Two common approaches to using benthic invertebrates as indicators of aquatic systems involve focusing on populations of particularly sensitive indicator species, or examining associations of species with differing, and known, tolerances to environmental perturbations. Here we combine both approaches, assessing the population of the sensitive species *Diporeia*, and using an index of oligochaete community makeup.

Diporeia

As seen, Diporeia is a widely occurring amphipod in the deeper waters of the Great Lakes. This surface-feeding detritivore is an important

Figure 26. Abundance of *Diporeia* abundance across the Great Lakes in summer, 1999, in relation to SOLEC criteria.



fish food item (Scott and Crossman, 1973), and is thought to obtain a large portion of its annual energy directly from the spring diatom bloom (Gardner et al., 1990), thus providing an important direct link between pelagic production and higher trophic levels. This glacial relic is sensitive to low oxygen concentrations and to many toxicants (Nalepa and Landrum, 1988), and due to its high lipid content and absence of biotransformation capability has a high bioaccumulation potential for organic contaminants (Landrum and Nalepa, 1998). These characteristics make it an appropriate organism for biomonitoring, both for its inherent ecological importance, and for its potential usefulness as an indicator of overall system health.

Provisional target abundances of *Diporeia* have been established for different depth ranges in the Great Lakes (SOLEC, 1998). When applied to GLNPO's benthos data from 1997, all stations in the upper lakes either met or exceeded these criteria. While historically present there, *Diporeia* is not currently found in Lake Erie. *Diporeia* was absent from half the sites examined in Lake Ontario in 1997, and met the criteria in four of the remaining, mostly offshore, five sites. In 1998, four sites in Lake Superior that had exceeded abundance criteria in 1997 simply met the criteria, while two sites in Lake Michigan that had exceeded the criteria slipped below criteria. Two sites were added in 1998, one in northern Green Bay and one in Saginaw Bay; both were below criteria. In contrast, abundances of *Diporeia* at one site in Superior increased sufficiently to exceed the criteria when in 1997 it had merely met criteria. Results from Lakes Erie and Ontario were identical to the previous year. Results from 1999 were similar to 1998; classifications of sites changed only in Lake Superior, where one site fell below criteria, while a second site went from exceeding to simply meeting criteria. In general, these results indicate that *Diporeia* populations are at sub-optimal levels, according to SOLEC criteria, in shallower regions of all lakes except Lake Superior. This is most notable in Lake Erie, where this genus appears to have disappeared. On the other hand, offshore populations meet or exceed SOLEC criteria. In Lake Superior, populations have shown a greater tendency to fluctuate, at least in comparison to the SOLEC criteria. While it is possible that these changes might reflect changes in water quality in the lakes, it is also possible that they merely represent natural annual fluctuations in recruitment or mortality. It will be necessary to continue to monitor these populations to establish ranges of natural variation.

Milbrink Oligochaete index

The association of oligochaetes with organic enrichment of water was first noted by Aristotle (Hynes, 1960). A number of classification systems have since been developed to try and quantify that relationship, a great number of these, significantly, developed by investigators working on the Great Lakes. Initially, these systems used total oligochaete numbers to reflect trophic conditions (Wright, 1955; Carr and Hiltunen, 1965; U.S. Department of the Interior, 1968). However, since different species within the class have widely differing sensitivities to organic enrichment, much information is lost with this approach. Further refinements have therefore focused on particular families (e.g. Tubificidae: King and Ball, 1964; Goodnight and Whitley, 1960) or species (e.g. *Limnodrilus hoffmeisteri*: Brinkhurst, 1967). Using data from Green Bay, Howmiller and Scott (1977) introduced an index based on community structure which incorporated information on the ecological attributes of a number of the constituent species. In this index, species were assigned to categories depending on their preference for/ tolerance of oligotrophic, mesotrophic or eutrophic conditions. Milbrink (1983) pointed out that this index did not take into account differences in absolute oligochaete abundance, nor did it accommodate the flexible ecological affinities of *Tubifex tubifex*, which can be extremely abundant both in conditions of gross pollution, and in situations of limited competition where anthropogenic influences are slight, such as in deep oligotrophic waters (Milbrink, 1973). He therefore added a scaling factor based on total oligochaete abundance, and gave *T. tubifex* a dual ranking, depending on both the co-dominant species and the total abundance of oligochaetes. In addition, he added a fourth category to Howmiller and Scott's original three, with this limited to the typical eutrophic indicator species *Limnodrilus hoffmeisteri*, and *T. tubifex* in instances where total numbers are high and *L. hoffmeisteri* is a co-dominant. When *T. tubifex* occurs with *Stylodrilus* as a co-dominant, it is included in Group 0. We have adopted Milbrink's modifications of Howmiller and Scott's original index, while retaining the latter's original classification of species on the basis of these being more appropriate to the Great Lakes. The index is calculated as:

$$c\,\frac{{}^{1}\!/_{2}\sum n_0+\sum n_1+2\sum n_2+3\sum n_3}{\sum n_0+\sum n_1+\sum n_2+\sum n_3}$$

where n_0, n_1, n_2 and n_3 are the total numbers of individuals belonging to each of the three ecological groups. Species characteristic of oligotrophic waters are assigned to Group 0, those of mesotrophic waters Group 1; those of eutrophic waters Group 2; while *L. hoffmeisteri* and *T. tubifex* (under the conditions stated above) comprise Group 3. The coefficient c depends upon total oligochaete number as outlined in the following table:

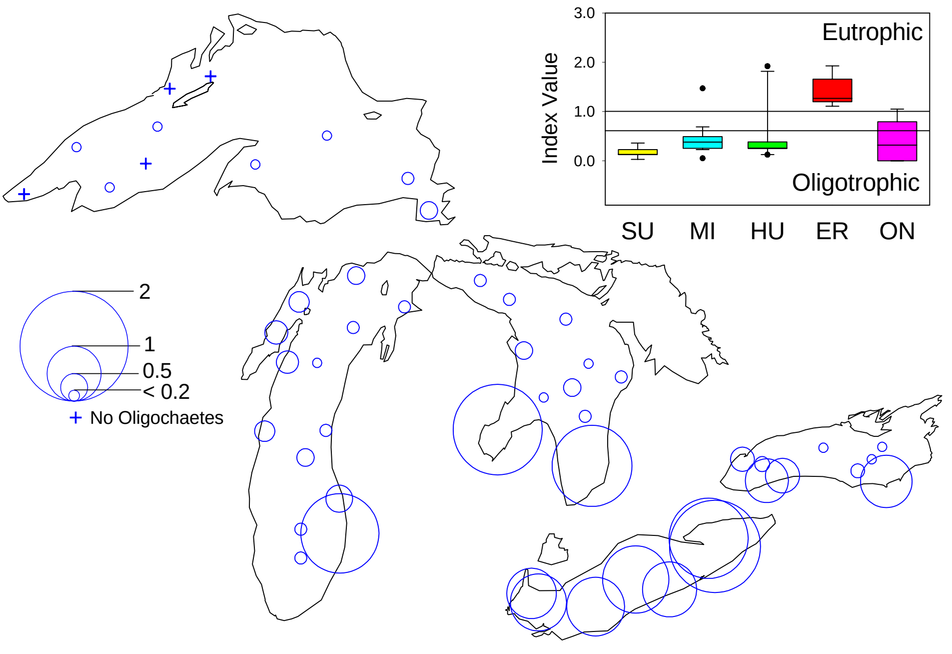
c=1	n > 3 600
c=3/4	1 200 < n < 3 600
c=1/2	400 < n < 1 200
c=1/4	130 < n < 400
c=0	< n < 130

Milbrink considered index values between 0.6 and 1.0 suggestive of mesotrophic conditions, while higher and lower values indicated eutrophic and oligotrophic conditions, respectively.

A number of limitations of this approach should be pointed out. Most importantly, it is only applicable in environments that support oligochaete communities. For instance, it is not possible to classify many of the deeper sites in Lake Superior using this index. The accuracy of the index depends upon correct taxonomical identification of the oligochaete community, a highly specialized activity requiring considerable training and experience. While the relationship between oligochaete abundances and organic enrichment is well established, the response of oligochaete communities to other stressors is still largely unknown. Therefore the utility of this index is limited to assessments of the former. Abundances of some oligochaete species, e.g., *Limnodrilus hoffmeisteri*, an indicator species featured prominently in the index, are subject to seasonal variation, thus compromising studies relying on a single annual sampling effort (Howmiller and Beeton, 1970). Finally, information about ecological tolerances of oligochaetes continues to be refined, therefore it is expected that changes in the classification of constituent species will occur.

In general, however, when the index is applied to data generated from GLNPO's monitoring program, it appears to give a reasonable evaluation of trophic conditions in the lakes (Figure 27). Most sites in the upper lakes fall into the oligotrophic category, with areas of known

Figure 27. Milbrink's (1983) Modified Environmental Index, applied to data from GLNPO's summer 1999 Survey



higher productivity (nearshore southern Lake Michigan; Saginaw Bay, Lake Huron) exhibiting higher index values. Sites in Lake Erie generally fall in the eutrophic range, while in Lake Ontario nearshore sites are classified as mesotrophic, and offshore sites are oligotrophic.

It should be noted that these two approaches complement each other. While the primary strength of Howmiller and Scott's Environmental Index is in assessing organic enrichment, *Diporeia* should provide a more sensitive indicator of other environmental stressors, such as toxics, and can presumably respond to changes in pelagic productivity, particularly in environments that don't support substantial oligochaete communities. It should be noted, however, that no benthic index has been routinely applied to the open waters of all the Great Lakes, and therefore that refinements in interpretation should be expected.

Summary

Spring phytoplankton communities in the Great Lakes were dominated by diatoms in all lakes. Biomass was highest in the western basin of Lake Erie and lowest in Lake Superior. Summer communities shifted away from diatoms, except in Lake Superior, where they remained co-dominant with chrysophytes. Dinoflagellates contributed a substantial amount of biovolume in Lake Michigan, while in communities in Lake Huron contained large populations of chrysophytes in the south and diatoms in the north. Both Lakes Erie and Ontario supported mixed communities with chlorophytes, cryptophytes and dinoflagellates all prominent.

Crustacean zooplankton communities were composed in most cases of less than a dozen species. Communities in the upper lakes contained about equal proportions of cyclopoid and calanoid copepods, in contrast to the clear dominance by calanoids in 1998. Lake Michigan exhibited marked north south differentiation in population sizes. Aside from the western basin of Lake Erie, the lower lakes were dominated by cyclopoid copepods. In summer, both Lakes Michigan and Huron supported populations of *Bosmina* relatively larger than were seen in 1998.

Benthos communities showed strong relationships between depth and both species richness and total abundance. The amphipod *Diporeia* dominated most deeper communities in the upper lakes and in Lake Ontario, while oligochaetes were most important at shallower sites. Comparison of *Diporeia* abundances with SOLEC criteria indicated that populations were less than desired at shallow stations in Lake Ontario and Michigan, Green Bay and Saginaw Bay. This organisms has entirely disappeared from Lake Erie. Use of an oligochaete community index classified most sites in the upper lakes as oligotrophic, all sites in Lake Erie as eutrophic, and deep and shallow sites in Lake Ontario oligotrophic and mesotrophic, respectively.

Acknowledgements

The data presented in this report was largely a result of the efforts of the following individuals: Jennifer Gronefeld, Larissa Granovski and Joseph B. Volerman (phytoplankton), Linda A. Kuhns, Lori L. Schacht and Ruth E. Little (zooplankton), and Ken K. Klubek (benthos) of Grace Analytical Lab. Their hard work and dedication is highly appreciated. Excellent graphical and analytical support was provided by Mark A. DiMartino. We would also like to express our great appreciation to captain Dave Moser and the entire crew of the *R/V Lake Guardian* for their assistance throughout the course of this work, and in particular the captain and crew of the Canadian Coast Guard Ship Samuel Risley for their extraordinary hospitality during the spring Lake Erie survey.

Literature Cited

Balcer, M.D., N.L. Korda and S.I. Dodson. 1984. Zooplankton of the Great Lakes. A Guide To The Identification And Ecology Of The Common Crustacean Species. Madison, WI: University of Wisconsin Press.

R.P. Barbiero, R.E. Little and M.L. Tuchman. 2001. Results from the USEPA's biological open water surveillance program of the Laurentian Great Lakes: III. Zooplankton. J. Great Lakes Res. 27:167-184

R.P. Barbiero and M.L. Tuchman. 2001. Results from the USEPA's biological open water surveillance program of the Laurentian Great Lakes: I. Introduction and phytoplankton results. J. Great Lakes Res. 27:134-154.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P., Weglenska, T. 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24:419-956.

Brinkhurst, R.O. 1967. The distribution of aquatic oligochaetes in Saginaw Bay, Lake Huron. Limnol. Oceanogr. 12:137-143.

Brooks, J.L. 1957. The systematics of North American *Daphnia*. Mem. Connecticut Acad. Arts and Sci. 13:1-180.

Carr, J.F., and J.K. Hiltunen. 1965. Changes in the bottom fauna of western Lake Erie from 1930 to 1961. Limnol. Oceanogr. 10:551-569.

Charlebois, P.M., M.J. Raffenberg, and J.M. Dettmers. 2001. First Occurrence of *Cercopagis pengoi* in Lake Michigan. J. Great Lakes Res. 27:258-261

Cook, D.G. 1975. A preliminary report on the benthic macroinvertebrates of Lake Superior. Canadian Fisheries and Marine Service Tech. Rpt. No. 572.

Dermott, R. 2001. Sudden disappearance of the amphipod *Diporeia* from eastern Lake Ontario. J. Great Lakes Res. 27:423-433.

Dermott, R. and K. Corning. 1988. Seasonal ingestion rates of *Pontoporeia hoyi* (Amphipoda) in Lake Ontario. Can. J. Fish. Aquat. Sci. 45:1886-1895.

Edmondson, W.T. 1959. Fresh-water Biology. (2nd ed.) New York, NY: Wiley.

Gardner, W.S., M.A. Quigley, G.L. Fahnenstiel, D. Scavia and W.A. Frez. 1990. *Pontoporeia hoyi* - a direct trophic link between spring diatoms and fish in Lake Michigan. In: Large Lakes: Ecological Structure and Function, eds. M.M. Tilzer and C. Serruya, pp. 632-644. Springer-Verlag, New York, NY.

Germain, H. 1981. Flore des Diatomées Eaux Douces et Saumâtres. Paris: Société Nouvelle des Éditions Boubée.

Golini, V.I. 1979.Benthic macro and meioinvertebrates of Lake Ontario 1977: Distribution and relative abundance. Canadian Fisheries and Marine Service, Ms. Rpt. No. 1519.

Goodnight, C.I. and T.S Whitley. 1960. Oligochaetes as indicators of pollution. Proc. 15th Industr. Waste Conf. Purdue Univ. Ext. Eng. 106:139-142.

Haney, J.F. & Hall, J.D. 1973. Sugar coated *Daphnia*: a preservation technique for Cladocera. Limnol. Oceanogr. 18:331-333.

Henson, E.B. 1970. *Pontoporeia affinis* (Crustacea, Amphipoda) in the Straits of Mackinac region. In Proc. 13th Conf. Great Lakes Res. pp. 601-610. Internat. Assoc. Great Lakes Res.

Hiltunen, J.K. 1969b. Invertebrate macrobenthos of western Lake Superior. Mich.

Holsinger, JR. 1972. The freshwater amphipod crustaceans (Gammaridae) of North America. U.S.E.P.A. Biota of Freshwater Ecosystems Identification Manual No. 5.

Howmiller, R.P. and A.M. Beeton. 1970. The oligochaete fauna of Green Bay, Lake Michigan. In Proc. 13th Conf. Great Lakes Res., pp. 15-46. Internat. Assoc. Great Lakes Res.

Howmiller, R.P. and M.A. Scott. 1977. An environmental index based on relative abundance of oligochaete species. J. Water Pollut. Control Fed. 49:809-815.

Hudson, P.L., J.W. Reid, L.T. Lesko, & J.H. Selgeby. 1998. Cyclopoid and Harpacticoid Copepods of the Laurentian Great Lakes. Ohio Biological Survey Bulletin NS 12(2).

Hynes, H.B.N. 1960. The Biology of Polluted Waters. Liverpool Univ. Press, Liverpool, 202 pp.

International Joint Commission. 1978. Great Lakes Water Quality Agreement of 1978. Ottawa: International Joint Commission.

Kathman, RD and R.O. Brinkhurst. 1998. Guide to the Freshwater Oligochaetes of North America. College Grove, TN: Aquatic Resources Center.

King, D.Z. and R.C.I. Ball. 1964. A quantitative biological measure of stream pollution. J. Wat. Pollut. Control Fed. 36:650-653.

Kinney, W.L. 1972. The macrobenthos of lake Ontario. Proc. 15th Conf. Great Lakes Res. 53-79.

Krammer, K. and H. Lange-Bertalot. 1986. Süßwasserflora von Mitteleuropa, II:2 Bacillariophyceae. 1. Teil: Naviculaceae. Gustav Fischer Verlag Jena: New York, NY.

Krammer, K. and H. Lange-Bertalot. 1991. Süßwasserflora von Mitteleuropa, II:2 Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. Gustav Fischer Verlag: NY, New York.

Krammer, K. and H. Lange-Bertalot. 1997. Süßwasserflora von Mitteleuropa, II:2 Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. Gustav Fischer Verlag Jena: New York, NY.

Landrum, P.F. and T.F. Nalepa. 1998. A review of the factors affecting the ecotoxicology of *Diporeia* spp. J. Great Lakes Res. 24:889-904.

Lund, J.W.G., C. Kipling and E.D. LeCren. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11:143-170.

Merritt, R.W. and K.W. Cummins. 1996. An Introduction to the Aquatic Insects of North America. 3rd ed. Dubuque IA: Kendall/Hunt Publishing Company.

Milbrink, G. 1973. On the use of indicator communities of Tubificidae and some Lumbriculidae in the assessment of water pollution in Swedish lakes. Zoon 1:125-139.

Milbrink, G. 1983. An improved environmental index based on the relative abundance of oligochaete species. Hydrobiologia 102:89-97.

Nalepa, T.F. and P.F. Landrum. 1988. Benthic invertebrates and contaminant levels in the Great Lakes: Effect, fates, and role in cycling. In Toxic Contaminants and Ecosystem Health: A Great Lakes Focus. ed. M.S. Evans, pp. 77-102. John Wiley & Sons, New York, NY.

Nalepa, T.F. and Thomas, N.A. 1976. Distribution of macrobenthic species in Lake Ontario in relation to sources of pollution and sediment parameters. J. Great Lakes Res. 2:150-163.

Nalepa, T.F., 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.H.

Ojaveer, L.A. Kuhns, R.P. Barbiero and M.L. Tuchman. 2001. Distribution and population characteristics of *Cercopagis pengoi* in Lake Ontario. J. Great Lakes Res. 27:10-18.

Patrick, R. and C.W. Reimer. 1966. The Diatoms of the United States, Exclusive of Alaska and Hawaii. Volume One: Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaceae. Philadelphia, PA: The Academy of Natural Sciences.

Patrick, R. and C.W. Reimer. 1975. The Diatoms of the United States, Exclusive of Alaska and Hawaii. Volume Two, Part One: Entomoneidaceae, Cymbellaceae, Gomphonemaceae, Epithemiaceae. Philadelphia, PA: The Academy of Natural Sciences.

Prescott, G.W. 1962. Algae of the Western Great Lakes Area. Koenigstein, Germany: Otto Koeltz Science Publishers.

Rivier, I.K. 1998. The Predatory Cladocera (Onychopoda: Podonidae, Polyphemidae, Cercopagidae) and Leptodorida of the World. Leiden, Netherlands: Backhuys Publishing.

Schelske, C.L. and Roth, J.C. 1973. Limnological survey of lakes Michigan, Superior, Huron and Erie. Great Lakes Research Div. Pub. No. 17. University of Michigan, Ann Arbor, MI.

Scott, W.B. and E.J. Crossman. 1973. Freshwater Fishes of Canada. Bull. Fish. Res Board Can. 184.

Shrivastava, H. 1974. Macrobenthos of Lake Huron. Fish. Res. Bd. Canada, Tech. Rpt. No. 449.

SOLEC (State of the Lakes Ecosystem Conference). 1999. Selection of Indicators for Great Lakes Basin Ecosystem Health. Draft for Review, v. 3. U.S. EPA, Chicago, IL.

Stemberger, R.S. 1979. A guide to rotifers of the Laurentian Great Lakes. U.S. Environmental Protection Agency, Rept. No. EPA 600/4-79-021, 185 pp.

Teter, H.E. 1960. The bottom fauna of Lake Huron. Trans. Am. Fish. Soc. 89:193-197.

U.S. Department of the Interior. 1968. Water Quality Investigations, Lake Michigan Basin: Biology. FWPCA, U.S. Dept. of the Interior, Chicago, IL, 41 p.

Wiederholm T. 1983. Chironomidae Of The Holarctic Region: Keys & Diagnoses, Part 1. Larvae. Ent. Scand. Suppl. No. 19.

Wilhm, J.L. and T.C. Dorris. 1968. Biological parameters for water quality criteria. BioScience 18:477-481.

Wright, S. 1955. Limnological survey of western Lake Erie. U.S. Fish and Wildlife Serv., Ann Arbor, Michigan. Spec. Sci. Rep., Fish. 139.

Tables

Table 1. Average lakewide biovolume (μm^3 ml^{-1}) of dominant (>5% biomass at any site) phytoplankton taxa, spring, 1999.

	Superior	Michigan	Huron	Erie	Ontario
BACILLARIOPHYTA					
Asterionella formosa Hass.	6,018	2,834	8,620	6,106	19,222
Aulacoseira subarctica (O. Mull.) Haworth	408	64,780	15,070	0	0
Cymatopleura solea (Breb. & Godey) W. Sm.	0	1,746	2,087	0	7,113
Diatoma tenue var. *elongatum* Lyngb.	6	8,172	1,065	1,169	310
Fragilaria crotonensis Kitton	2,368	13,231	25,017	31,488	2,984
Aulacoseira islandica O. Mull.	13,060	266,857	132,554	789,661	326,446
Nitzschia gracilis Hantz.	263	14,532	800	767	6,431
Stephanodiscus alpinus Hust.	1,129	10,345	1,716	50,645	12,170
Stephanodiscus binderanus (Kutz.) Krieg.	0	131	0	14,434	70
Stephanodiscus hantzschii f. *tenuis* Hak. & Stoerm.	32	352	7	66,996	709
Stephanodiscus niagarae Ehr.	1,806	2,679	1,769	5,831	0
Stephanodiscus subtransylvanicus Gasse	1,911	8,897	3,902	1,748	66
Synedra filiformis Grun.	418	14,141	1,806	273	193
Synedra ulna var. *chaseana* Thomas	291	15,521	4,018	1,657	0
Tabellaria flocculosa (Roth) Knud.	3,897	6,484	121,219	4,637	14,272
CHRYSOPHYTA					
Dinobryon cylindricum Imhof	0	0	4,489	0	0
Dinobryon divergens Imhof	0	0	2,147	288	0
Dinobryon sociale var. *americanum* (Brunnth.) Bachm.	355	80	1,814	0	0
Haptophyceae	3,500	2,736	3,586	6,903	8,471
Mallomonas spp.	1,408	4,215	1,970	837	2,761
Unidentified coccoid ovoid (Chrysophyta)	911	1,107	844	3,164	892
Unidentified flagellate #5	8	128	10		1,309
CRYPTOPHYTA					
Cryptomonas curvata Ehr.	364	2,899	1,114	0	0
Cryptomonas erosa Ehr.	4,359	9,339	6,631	2,242	17,625
Cryptomonas erosa var. *reflexa* Marss.	1,758	2,480	3,111	260	7,569
Cryptomonas ovata Ehr.	1,256	3,431	3,575	318	2,900
Cryptomonas pyrenoidifera Geitl.	1,503	3,516	2,635	732	2,712
Rhodomonas minuta Skuja	2,475	4,174	2,948	3,773	8,570
Rhodomonas minuta var. *nannoplanctica* Skuja	904	2,136	1,134	4,229	3,942
CYANOPHYTA					
Anacystis montana f. *minor* Dr. & Daily	3,282	3,631	4,122	3,514	2,435
Oscillatoria spp.	2,067	0	0	0	0
Oscillatoria tenuis C.A. Ag.	0	0	3,632	0	0
PYRROPHYTA					
Glenodinium spp.	1,536	2,841	2,816	104	2,924
Gymnodinium helveticum Pen.	0	9,085	0	514	0
Gymnodinium helveticum f. *achroum* Skuja	0	6,249	4,131	0	25,648
Gymnodinium spp.	2,506	3,912	2,499	12,244	4,126
Peridinium spp.	0	598	1,066	951	0

Table 2. Average lakewide biovolume (μm^3 ml^{-1}) of dominant (>5% biomass at any site) phytoplankton taxa, summer, 1999.

	Superior	Michigan	Huron	Erie	Ontario
BACILLARIOPHYTA					
Cyclostephanos tholiformis Stoerm. Hak. & Ther.	0	0	0	25,781	179
Cyclotella comensis Grun.	13,189	4,923	1,765	13,324	3,190
Cyclotella comensis var. 1	1,075	21,147	12,942	76	3,717
Cyclotella comta (Ehr.) Kutz.	147,021	16,773	82,284	0	7,060
Cyclotella delicatula	21,541	2,333	10,304	133	618
Cyclotella ocellata Pant.	5,880	324	651	41,858	787
Diatoma tenue var. *elongatum* Lyngb.	75	0	227	0	17,180
Fragilaria crotonensis Kitton	10,676	59,414	25,054	35,872	89,675
Aulacoseira islandica O. Mull.	0	0	127	11,427	0
Aulacoseira italica (Ehr.) Kutz.	0	0	0	90,455	0
Stephanodiscus niagarae Ehr.	0	0	0	23,795	0
Synedra delicatissima var. *angustissima* Grun.	1,144	0	2,214	426	0
Tabellaria flocculosa (Roth) Knud.	18,369	275	2,932	1,949	15,762
CHLOROPHYTA					
Cosmarium depressum (Nag.) Lund	1,307	1,183	810	2,786	5,826
Eudorina elegans Ehr.	0	3,505	0	0	0
Gloeocystis planktonica (W. & G.S. West) Lemm.	356	902	1,985	4,801	1,637
Micractinium pusillum Fres.	0	0	0	6,100	0
Mougeotia sp.	0	0	0	70,700	0
Pediastrum duplex var. *gracillimum* W. & G.S. West	0	0	0	1,846	0
Pediastrum simplex (Meyen) Lemm.	0	0	0	2,214	0
Pediastrum simplex var. *duodenarium* (Bail.) Rabh.	0	0	3,886	2,113	0
Scenedesmus bijuga (Turp.) Lag.	134	1,036	715	7,241	1,870
Tetraspora lacustris Lemm.	0	0	4,015	617	0
Ulothrix sp.	306	0	0	1,465	51,713
CHRYSOPHYTA					
Chrysophycean coccoids	480	6,502	755	193	1,371
Chrysosphaerella longispina Laut. emend. Nich.	26	7,646	34,788	308	0
Dinobryon bavaricum Imhof	9,190	785	14,907	894	0
Dinobryon bavaricum var. *vanhoeffenii* (Bachm.) Krieg.	4,432	0	0	0	0
Dinobryon divergens Imhof	6,567	9,036	10,599	4,515	15,029
Dinobryon sertularia Ehr.	7,230	0	922	0	0
Dinobryon sertularia var. *protuberans* (Lemm.) Kreig.	4,389	0	3,239	0	0
Dinobryon sociale Ehr.	14,459	2,481	2,294	3,908	674
Dinobryon sociale var. *americanum* (Brunnth.) Bachm.	6,276	284	1,643	5,018	626
Mallomonas sp.	857	4,720	4,025	5,999	564
CRYPTOPHYTA					
Cryptomonas curvata Ehr.	0	5,177	0	0	0
Cryptomonas erosa Ehr.	8,248	25,842	13,556	22,652	48,437
Cryptomonas erosa var. *reflexa* Marss.	4,771	23,510	4,572	9,189	29,126
Cryptomonas obovata Skuja	153	0	0	0	4,797
Cryptomonas ovata Ehr.	0	2,475	3,175	8,021	9,800
Cryptomonas phaseolus Skuja	0	1,104	824	56,042	4,387

Table 2. (cont.)

	Superior	Michigan	Huron	Erie	Ontario
Cryptomonas pyrenoidifera Geitl.	0	582	347	8,446	4,402
Rhodomonas minuta Skuja	6,731	6,757	4,477	8,688	14,706
Rhodomonas minuta var. *nannoplanctica* Skuja	2,030	6,388	3,919	18,028	38,630
CYANOPHYTA					
Agmenellum quadruplicatum (Menegh.) Breb.	96	1,024	89	5,397	8,964
Agmenellum thermale (Kutz.) Dr. & Daily	0	0	0	8,910	0
Anabaena circinalis Rabh.	0	13,281	0	2,545	0
Aphanothece clathrata W. & G.S. West	2,201	7,044	1,805	4,783	4,144
Gomphosphaeria lacustris Chod.	292	526	4,396	948	1,157
Lyngbya sp. #1	1,198	0	0	104	0
Oscillatoria limnetica Lemm.	19	417	0	13,977	9,648
PYRROPHYTA					
Ceratium hirundinella (O.F. Mull.) Schr.	0	273,162	27,759	101,948	76,541
Gymnodinium helveticum Pen.	3,896	0	0	0	7,775
Gymnodinium sp.	2,661	7,219	4,808	2,757	16,233
Peridinium sp.	5,062	21,128	11,571	23,184	14,051

Table 3. Average lake-wide densities (individuals m^{-2}) of crustacean zooplankton taxa during spring survey, 1999. Numbers in parenthesis indicate volumetric densities (# m^{-3}). Densities for the three basins of Lake Erie (W=western, C=central, E=Eastern) are shown separately.

	SU	MI	HU	ER W	ER C	ER E	ON
Cladoceera							
Holopedium gibberum		20					
Daphnia galeata mendotae	35		102	1	210	2	
Daphnia longiremis					7		
Daphnia retrocurva		48			5		
Eubosmina coregoni	6		529	138	2,702	21	1,755
Alona spp.				1			
Chydorus sphaericus					5		
Leydigia spp.						5	
Bosmina longirostris	45	85	793	182	1,352	17	565
Total Cladocera	86	153	1,424	322	4,280	45	2,321
	(1)	(2)	(19)	(43)	(228)	(1)	(25)
Copepoda							
Calanoida							
Senecella calanoides	68	4	25	1			
Senecella copepodites	134		49				
Limnocalanus macrurus	755	10,578	368	19			2,662
Limnocalanus copepodites	13,874	26,207	14,138				31,982
Epischura copepodites	6						
Diaptomus ashlandi		16,680	132,033	1,636	55	2	
Diaptomus minutus		16,474	93,021	1,903	598	57	64
Diaptomus sicilis	59,455	8,817	34,113	627			3,209
Diaptomus siciloides				2	12		
Diaptomus oregonensis		1,304	2,389	36	3,620	12	1,261
Diaptomus copepodites	1,459	145,745	186,962	451	267	44	46,378
Total Calanoid	75,751	225,809	463,097	4,675	4,552	115	85,556
	(765)	(2,329)	(5,866)	(602)	(231)	(3)	(890)
Cyclopoida							
Acanthocyclops vernalis						2	
Cyclops bicuspidatus thomasi	42,327	93,960	250,318	752	7,908	43	195,855
Diacyclops nanus						9	
Eucyclops agilis				1			
Cyclops copepodites	15,471	157,042	111,836	3,292	28,656	1,804	57,042
Mesocyclops edax						3	
Mesocyclops copepodites						15	
Tropocyclops prasinus mexicanus	9	2,889	2,107	34	2,449	434	268
Tropocyclops copepodites			53				
Total Cyclopoid	57,807	253,891	364,313	4,080	39,013	2,310	253,164
	(583)	(2,674)	(4,795)	(539)	(1,996)	(52)	(2,673)

Table 4. Average lake-wide densities (individuals m^{-2}) of crustacean zooplankton taxa during summer survey, 1999. Numbers in parenthesis indicate volumetric densities (# m^{-3}). Densities for the three basins of Lake Erie (W=western, C=central, E=Eastern) are shown separately.

	SU	MI	HU	ER W	ER C	ER E	ON
Cladocera							
Bythotrephes cederstroemi	56	148	314		229	937	
Cercopagis pengoi							16,521
Leptodora kindti		101		2,294	1,297	2,904	574
Polyphemus pediculus		412					111
Diaphanosoma birgei		78		9,463	42,323		111
Holopedium gibberum	19,268		110		1,239		5,829
Ceriodaphnia spp.				37			1,559
Daphnia galeata mendotae	14,434	268,328	275,148		28,372	51,479	
Daphnia longiremis					7,134	1,921	
Daphnia retrocurva	13		112	1,916	6,126		448,322
Eubosmina coregoni		4,229	15,639	10,223	22,432	979	
Alona spp.				5			
Bosmina longirostris	2,113	474,717	109,030	22,284	395,268	177,036	
Bosmina spp.	126		238,176				627,660
Total Cladoceran	36,011	748,013	638,529	46,222	504,420	235,255	1,100,686
	(12,204)	(24,642)	(7,600)	(8,861)	(7,745)	(361)	(4,888)
Copepoda							
Calanoida							
Senecella calanoides	666	79	158				
Senecella copepodites	35						
Limnocalanus macrurus	23,919	13,077	12,518				30,454
Limnocalanus copepodites	156	159	263		47		1,342
Epischura lacustris	228	3,473	4,009	59	4,113	15,063	
Epischura copepodites	35	13,189	6,144	204	16,773	38,858	
Eurytemora affinis		222		57			111
Diaptomus ashlandi	48	42,763	77,862		1,351	1,154	
Diaptomus minutus	23	36,348	67,193	1,477	36,537	49,515	
Diaptomus reighardi				200			
Diaptomus sicilis	17,903	7,351	6,605				4,896
Diaptomus siciloides				2,588	309	445	
Diaptomus oregonensis		2,278	3,172	85	64,069	68,000	2,401
Diaptomus copepodites	264,254	331,007	695,792	11,180	186,626	416,460	32,745
Total Calanoid	307,269	449,946	873,716	15,852	309,827	589,494	71,950
	(743)	(14,989)	(2,352)	(11,653)	(4,737)	(3,086)	(12,736)

Table 4. (cont.)

	SU	MI	HU	ER W	ER C	ER E	ON
Cyclopoida							
Acanthocyclops vernalis		359		1,157		743	
Cyclops bicuspidatus thomasi	33,970	156,189	23,379	5	16,680	28,779	794,900
Eucyclops agilis						354	
Cyclops copepodites	57,302	576,338	422,900	51,748	149,083	397,994	862,980
Mesocyclops edax			284	40,079	60,983	34,214	
Mesocyclops copepodites			112	65,945	70,673	13,814	
Tropocyclops prasinus mexicanus		41,661	1,069	494	2,241	21,109	
Tropocyclops copepodites		18,178	172	72	264	1,977	
Total Cyclopoid	91,272	792,725	447,916	159,500	299,925	498,984	1,657,880
	(17,323)	(14,768)	(21,901)	(5,755)	(8,142)	(917)	(11,057)