Limnol. Oceanogr., 38(6), 1993, 1311–1316

Paleolimnological comparison of the Laurentian Great Lakes based on diatoms

Abstract—We used cluster analysis to compare records of diatom succession recorded in dated cores from offshore basins of the five Great Lakes. Most recently deposited samples from Lakes Erie and Ontario are far removed from the cluster centroid, as are samples deposited in Lakes Huron and Michigan during forest clearance. Most recently deposited samples from Lake Superior are also clearly segregated, but occupy the opposite end of the ordination. At a lower level, samples clustered by lake and time. For each lake, sample clusters from presettlement, early industrialization, and postindustrialization were identified. Relationships of cluster structure allow inferences concerning the comparative state of the lakes at different periods in their history.

During the past several years we have attempted to reconstruct ecological changes in the Laurentian Great Lakes on the basis of inferences derivable from siliceous microfossils, mainly diatoms, preserved in sediments (Stoermer et al. 1985*a,b,* 1987, 1990, 1991; Wolin et al. 1988). These studies showed considerable changes in the diatom flora of all the lakes, which we interpreted as reflecting varying levels of anthropogenic perturbation. Four zones of samples with similar diatom assemblages, which we take to infer similar ecological conditions, are present in all cores examined. Samples deposited before European settlement contain similar floras in all cases. In all cases, the diatom floras of samples deposited at about the time the drainage basins of the lakes were logged and burned are markedly different from those deposited before and after. In all cases examined, this is followed by a sequence of similar samples extending to the decade between 1940 and 1950. These zones can be variously subdivided, but the diatom assemblages present are clearly different from those deposited before and after. Samples of the most recent sediments of each lake are also clearly different from any deposited earlier in the lake's history.

Although the sequence of effects in each lake is roughly similar, the degree of effect is greatly different between lakes. We have attempted to assess the degree of difference with cluster analysis, the same multivariate technique used to compare and contrast diatom assemblages in different strata of cores from each lake. Standardized relative frequency estimates of 20 abundant and widely distributed species in 171 samples were analyzed with an average clustering algorithm and Euclidean distance measure (Carney 1982). Methods used in sample analysis are detailed in the original papers (cited above). It should be pointed out that different cores were sampled at different intervals and that sedimentation rates varied widely between cores, so that the number of cases contained in a given cluster does not necessarily infer either depth of sediment or amount of time sampled. Results of the cluster analysis are shown in Fig. 1. The clusters distinguished and estimates of dates associated with samples included in each cluster are shown in Table 1. Dates are radiometric, based on ^{210}Pb for all cases except Lake Huron which is based on ^{137}Cs. Thus, in all cases, we consider recent dates to be quite precise, with increasing uncertainty associated with dates for older sediments.

Samples from the same lake tend to cluster together, especially in the cases of Lakes Huron and Erie (Fig. 1). It also appears that lake groupings within the main cluster are aligned according to trophic status, with samples from Lake Superior, the most oligotrophic of the Great Lakes, at the top of the figure and samples from Lake Erie, the most naturally eutrophic, toward the bottom. The placement of samples from Lake Huron might appear anomalous in this regard, because its offshore waters are generally considered to be highly

Acknowledgments

We thank Mark Edlund, Gail Emmert, and Daiqing Mou for technical assistance.

Population data used here was mostly compiled as part of work under NSF grant OCE 86-14619 and EPA grant R-813831. Analysis was carried out under EPA grant R-816467 from the Office of Exploratory Research.

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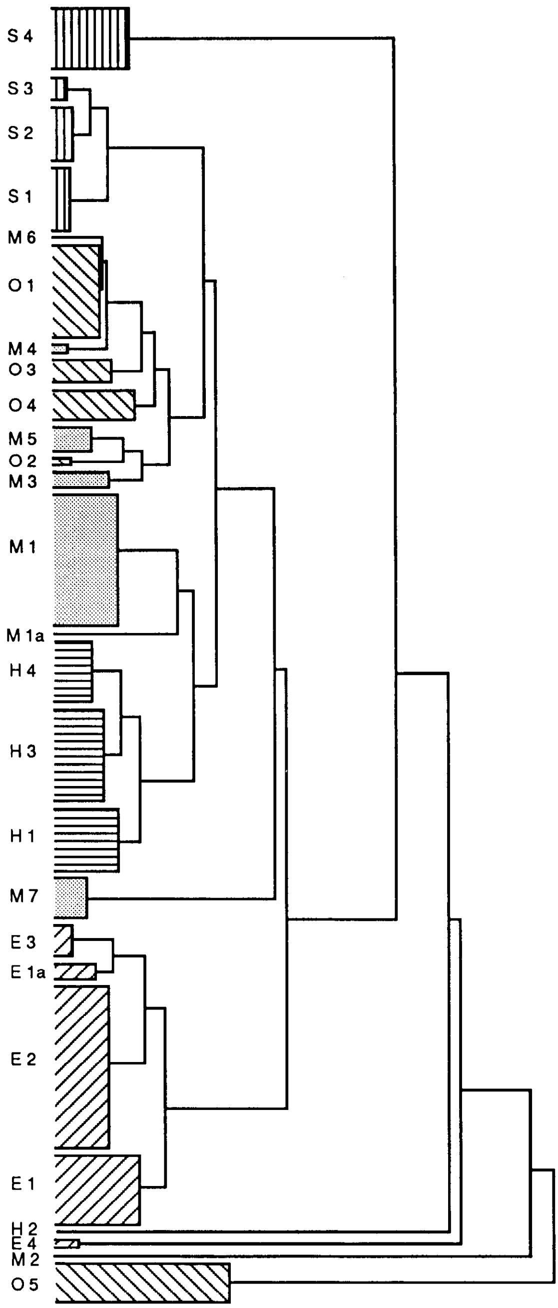

Fig. 1. Cluster dendrogram of samples in cores from the Laurentian Great Lakes. Prefix and pattern of bars indicate lake from which samples were derived: E—Erie; H—Huron; M—Michigan; O—Ontario; S—Superior. Numerical suffix indicates within-lake clusters as per Table 1.

Table 1. Dates associated with samples included in clusters shown in Fig. 1. Dates for Lake Huron core extrapolated from ^{137}Cs; all others based on ^{210}Pb.

Cluster	Lake	Dates
	Superior	
S 1		1818–1882
S 2		1884–1929
S 3		1929–1941
S 4		1945–1979
	Huron	
H 1		1752–1880
H 2		1910
H 3		1888–1946
H 4		1950–1978
	Michigan	
M 1		1470–1864
M 1a		1782
M 2		1877
M 3		1886–1911
M 4		1923–1933
M 5		1943–1954
M 6		1959
M 7		1964–1982
	Erie	
E 1		1854–1942
E 1a		1894–1907
E 2		1947–1976
E 3		1977–1980
E 4		1981–1982
	Ontario	
O 1		1704–1874
O 2		1881–1889
O 3		1896–1917
O 4		1924–1952
O 5		1957–1979

oligotrophic (Vollenweider et al. 1974). However, the waters of Saginaw Bay, on the western shore of Lake Huron are amongst the most eutrophic in the Great Lakes system (Vollenweider et al. 1974). Several studies (Schelske et al. 1974; Stoermer and Kreis 1980; Stoermer and Theriot 1985) suggest episodes of mass transport of Saginaw Bay water to the main lake basin, and Wolin et al. (1988) concluded this transport accounts for unusual diatom assemblages in the sediments of the Goderich Basin. Thus the core examined from the Goderich site may furnish a more or less accurate integration of conditions in the entire southern basin of Lake Huron.

Four outlying clusters appear at the bottom end of the dendrogram. Two of these include most recent samples from Lakes Erie and Ontario and two are single samples near the effective settlement horizons in Lakes Michigan and Huron. All of these sample groupings are far removed from the main sample sequence and relatively far removed from one another. The most distant—recent samples from Lake Ontario (O 5)—is most easily explained in that it contains diatom populations from a system that has undergone massive geochemical change (Schelske et al. 1988; Schelske and Hodell 1991) and has no analog in either modern or past conditions in the other Great Lakes. Based on comparison of species in these samples with those present in near-surface samples from Lake Erie (E 4), we believe the Lake Erie case is also a no-analog situation, but of a somewhat different type. It is our hypothesis that these samples represent partial recovery of a more naturally eutrophic system that was highly disturbed. Short cores taken from Lake Ontario containing sediments deposited after the material analyzed here show a similar transition (Wolin et al. 1991).

It is our conclusion that the single, settlement horizon samples from Lakes Huron (H 2) and Michigan (M 2) reflect the strong effects of land clearance and fires in their drainage—events which also have no apparent analogs in the previous or subsequent record. A large portion of Lake Michigan's northern drainage burned in 1871, which is in good agreement with the radiometric date of this sample. Our date for the Lake Huron sample is more recent than known major disturbances in the drainage, but dates for this core were extrapolated from ^{137}Cs, hence the window of confidence is quite large for samples this old.

It should also be noted that one or more early samples from the other lakes are placed in clusters outside their stratigraphic sequence. Samples deposited in Lake Erie between 1894 and 1907 (E 1a) are placed between samples deposited in the 1970s, rather than with their stratigraphic neighbors. Samples deposited in Lake Ontario between 1881 and 1889 (O 2) exchange positions in the stratigraphic sequence with samples deposited in Lake Michigan between 1943 and 1954 (M 5). This cluster order infers that, so far as features affecting diatom growth are concerned, conditions in Lake Ontario during the 1880s were very similar to those found in Lake Michigan during the 1940s.

The major hypothesis underlying the work presented here is that eutrophication in the Laurentian Great Lakes has been driven by increases in P loading. The sequence of P loading and its ecosystem consequences have been discussed in papers cited, but in general two inflection points related to increased loading occurred in the drainage basin. The first resulted from forest clearing and settlement by Europeans, which occurred in the mid-1800s in the Lake Ontario system and spread westward and northward ending in the 1920s in the Lake Superior drainage basin. Resulting increases in P loading were relatively small compared to the large increases in the 1940s and 1950s that followed introduction of phosphate detergents and increased population growth and expanded sewer systems. One of the major ecosystem consequences of increased P loading was increased biogenic silica production by diatoms that rapidly caused silica limitation for diatom production in Lakes Ontario, Erie, and Michigan (Schelske et al. 1986). P loadings to Lakes Huron and Superior were lower and increases in diatom production have not induced silica depletion.

The next cluster to join are most recently deposited samples from Lake Superior. These samples are placed toward the "oligotrophic" end of the ordination, but are very clearly distinguished from other samples in the entire set. Inspection of the species matrix shows that these samples contain particularly high abundance of *Cyclotella.* Their composition is similar to immediate postsettlement samples from the other lakes, but the relative abundance of *Cyclotella* is even higher than found in early samples from Lake Ontario. Species composition is also somewhat different. *Cyclotella comensis* Grun., in particular, reaches very high abundance in near-surface Lake Superior samples. This species is associated with high nitrate levels in Lake Huron (Stoermer and Kreis 1980). It is not clear what causality underlies this apparent trend. It does not appear to be nutrient limitation in the classic sense, since the data of Stoermer and Kreis (1980) show increasing abundance above 200 μg liter^{-1} to over 300 μg liter^{-1} nitrate. Large increases in abundance of *C. comensis,* concomitant with increased nitrate levels, have also been observed in large, oligotrophic inland lakes in Michigan (Fritz et al. in press).

Next to join are all samples from Lake Erie.

Samples are clustered in their stratigraphic sequence, except for the E 1a cluster, discussed above. Segregation of all samples from Lake Erie is expected, in that this lake has a much greater proportion of shallow, hence not stably stratified, water than the other lakes, and apparently has always been comparatively more productive. Its brief water residence time is unique amongst the Great Lakes, and it appears to be more immediately responsive to changes in external loading than the upper lakes. It should be emphasized that our approach of clustering based on species common to all the lakes tends to underemphasize the real degree of difference. There are a number of taxa abundant in Lake Erie, in all segments of the sedimentary sequence examined, which do not occur, or never occur in significant abundance, in the main basins of the other Great Lakes. Lake Erie, at least in the region sampled, is more similar to the Bay of Quinte (Stoermer et al. 1985*c*) and Green Bay (Stoermer et al. 1991) in some limnological characteristics and in its diatom flora.

The next cluster to join are samples from Lake Michigan deposited after 1964 (M 7). This apparently is the period during which lack of silica in the surface mixed layer limited diatom growth during summer stratification and hence modified composition of the sedimentary diatom flora.

The next level of clustering distinguishes samples from Lake Huron (H 1, H 3, H 4) and early samples from Lake Michigan (M 1, M 1a) from the remaining data. Aside from H 2, discussed previously, the Lake Huron samples are clustered in order of stratigraphic position. In the Lake Michigan case, in addition to the anomalous sample deposited ~1977 discussed previously, its stratigraphically superior neighbor (M 1a) is also an outlier to the main group of early Lake Michigan samples.

The next level distinguishes all Lake Superior samples deposited before ~1945. These samples are clustered at a lower level than sample clusters from the other lakes, implying little variation in Lake Superior diatom flora and, presumably, little variation in ecological conditions. They are also clustered in stratigraphic order, with subclusters divided at ~1885 and ~1930.

The remaining clusters all contain samples from Lakes Michigan and Ontario. These are also grouped in approximate stratigraphic order, except that the O 2 cluster of Lake Ontario samples and the M 4 cluster of Lake Michigan samples switch places in the ordination. We infer from this that, in terms of conditions resulting in modification of the diatom flora, environmental modification occurred in Lake Ontario at least 40 yr before similar effects were present in Lake Michigan.

Each of the Great Lakes has some degree of individuality in its diatom flora, and these differences are largely maintained across considerable periods of time and despite varying degrees of environmental modification. On the basis of the diatom assemblages preserved in their sediments, the lakes most different under presettlement conditions were Erie and Superior, as might be expected on the basis of their morphometry and latitude difference. Lake Erie's differentiation from the other lakes is maintained despite environmental changes, probably as a result of the same factors. Lake Michigan is the only case where the majority of samples from a particular lake do not cluster closely together. Early Lake Michigan samples are nearest to the main Lake Huron cluster and most recent Lake Michigan samples form a cluster between samples from Lakes Huron and Erie. Lake Michigan samples of intermediate age cluster with Lake Ontario samples. In particular, Lake Michigan M 4 samples (1923–1933) exchange sequence position with Lake Ontario O 2 samples (1881–1889). We infer that early successional changes in the diatom flora occurred in Lake Ontario ~40 yr earlier than they did in Lake Michigan.

Aside from the above, segregation of samples by time period in all the lakes using combined data shows essentially the same pattern as found in analysis of samples from a single lake. In all cases presettlement samples cluster together. In all cases but Lake Superior there seems to be a strong, but time-limited, effect shortly after European settlement. In all cases, this episode is followed by a period of more or less rapid eutrophication, culminating in rapid and substantial changes in the diatom flora after ~1945.

The analysis of combined data from all the lakes clarifies the relative degree of perturbation that occurred in the different lakes at various time periods. No event in the presettlement era sampled approached the magnitude of changes later in the record. This relative stability in the presettlement record implies that anthropogenic modifications of the Laurentian Great Lakes system are of much greater magnitude than changes forced by natural variations in climate or other factors.

Surprisingly large effects are associated with forest clearance and early agriculture throughout the region. Much of this effect was associated with the large-scale wild fires that followed logging over much of the region. Changes in composition of the diatom flora indicate that the effect was brought about by mobilization of large quantities of plant nutrients (particularly P and Si) and conservative elements from a mature and well-buffered landscape. This effect was of limited temporal duration and, in most cases, the lakes briefly "regressed" slightly toward their original state following initial large-scale settlement, probably as a result of revegetation and soil stabilization.

The rate and time-course of subsequent environmental change was apparently quite different in the different lakes, although all showed some signs of progressive eutrophication. It appears that Lake Ontario and probably eastern Lake Erie were affected by silica limitation during summer stratification in the immediate postsettlement era and have been so affected ever since. On the other hand, significant summer silica limitation apparently did not occur until the 1940s or early 1950s in Lake Michigan. According to our analysis (Fig. 1), diatom assemblages deposited in Lake Ontario during the 1880s are the nearest homolog of assemblages deposited in Lake Michigan between 1943 and 1954. Secondary nutrient limitation apparently has never been a factor substantially limiting diatom growth in Lake Superior or the offshore basins of Lake Huron, although transient limitation can surely occur in local regions, particularly in Saginaw Bay of Lake Huron.

In all cases, strong effects on the diatom flora occurred after the late 1940s, probably due to increased loadings resulting from human population growth, more direct delivery of pollutants to the lakes due to sewer construction, and introduction of phosphate-based detergents. Again, although timing of changes was consistent throughout the system, the precise nature of perturbations differed between lakes according to amount and history of external loadings. In the lower lakes the indigenous flora was largely replaced by species tolerant of (or capable of avoiding) silica limitation such as *Stephanodiscus binderanus* (Kütz.) Krieg. and *Actinocyclus normanii* fo. *subsalsa* (Juhl.-Dannf.) Hust. In Lake Superior the most evident change was increased production of species usually considered "indicative" of oligotrophic conditions, a stage that occurred much earlier in the lower lakes.

The most recently deposited sediments sampled in the cores we examined also show substantial departures from previous conditions. Although part of this change can be reasonably attributed to positive effects of nutrient-loading reductions, it is clear that the direction of change, at least as measured by the diatom flora, is not to return to a previous system state. Part of this difference results from the fact that nutrient ratios have not returned to previous conditions due to differences in external loading and recycle rates of major plant nutrients (Schelske 1991). For example, although concentrations of P in Lake Ontario have been reduced and N limitation has been eliminated, diatoms in the lake are still severely silica limited during most of the year.

The effects of P loading abatement are not the entire story. The most interesting and puzzling aspect of our results is the strong departure of diatom assemblages in most recently deposited Lake Superior sediments from any previous analog in the Great Lakes system. Because Superior is the headwater lake and relatively most susceptible to atmospheric loading, the most attractive hypotheses to explain this departure involve some aspect of current trends in global atmospheric contamination. Although, on the basis of a retrospective study such as this, we can only speculate as to cause, there is good evidence that levels of nitrate, most probably delivered via the atmosphere, were increasing throughout the Great Lakes during this period. It is also possible that most recent changes are at least partially reflective of other direct (e.g. increased CO_2 levels) or indirect (e.g. climatic warming) effects of the same general phenomenon.

The other possible explanation for changes in the diatom flora of the Great Lakes, particularly those occurring relatively late in the record, is that they are the result of, or at least influenced by, biotic interactions. Although it seems generally the case that changes in the diatom flora preceded large-scale modification of fish and invertebrate communities, the large-scale introduction of exotic species (Mills et al. in press), both planned and accidental, must influence composition of the algal flora to some extent. It also seems likely that some of the diatom species that have become important in the postsettlement flora (e.g. *S. binderanus*) were introduced to the Great Lakes from outside their basin and perhaps from outside North America.

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References

CARNEY, H. J. 1982. Algal dynamics and trophic interactions in the recent history of Frains Lake, Michigan. Ecology **63:** 1814–1826.

FRITZ, S. C., J. C. KINGSTON, AND D. R. ENGSTROM. In press. Quantitative trophic reconstruction from sedimentary diatom assemblages: A cautionary tale. Freshwater Biol.

MILLS, E. L., J. H. LEACH, J. T. CARLTON, AND C. L. SECOR. In press. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. J. Great Lakes Res.

SCHELSKE, C. L. 1991. Historical nutrient enrichment of Lake Ontario: Paleolimnological evidence. Can. J. Fish. Aquat. Sci. **48:** 1529–1538.

———, L. E. FELDT, M. S. SIMMONS, AND E. F. STOERMER. 1974. Storm induced relationships among chemical conditions and phytoplankton in Saginaw Bay and western Lake Huron. Proc. 17th Conf. Great Lakes Res., p. 78–91. Int. Assoc. Great Lakes Res.

———, AND D. A. HODELL. 1991. Recent changes in productivity and climate of Lake Ontario detected by isotope analysis. Limnol. Oceanogr. **36:** 961–975.

———, J. A. ROBBINS, W. D. GARDNER, D. J. CONLEY, AND R. A. BOURBONNIERE. 1988. Sediment record of biogeochemical responses to anthropogenic perturbations of nutrient cycles in Lake Ontario. Can. J. Fish. Aquat. Sci. **45:** 1291–1303.

———, E. F. STOERMER, G. L. FAHNENSTIEL, AND M. HAIBACH. 1986. Phosphorus enrichment, silica utilization and silica depletion in the Great Lakes. Can. J. Fish. Aquat. Sci. **43:** 407–415.

STOERMER, E. F., J. P. KOCIOLEK, C. L. SCHELSKE, AND N. A. ANDRESEN. 1991. Siliceous microfossil succession in the recent history of Green Bay, Lake Michigan. J. Paleolimnol. **6:** 123–140.

———, ———, ———, AND D. J. CONLEY. 1985*a*. Siliceous microfossil succession in the recent history of Lake Superior. Proc. Acad. Nat. Sci. Phila. **137:** 106–118.

———, ———, ———, AND ———. 1987. Quantitative analysis of siliceous microfossils in the sediments of Lake Erie's central basin. Diatom Res. **2:** 113–134.

———, AND R. G. KREIS, JR. 1980. Phytoplankton composition and abundance in Southern Lake Huron. Univ. Michigan, Great Lakes Res. Div., Spec. Rep. 65. 382 p.

———, AND E. C. THERIOT. 1985. Phytoplankton distribution in Saginaw Bay. J. Great Lakes Res. **11:** 132–142.

———, J. A. WOLIN, C. L. SCHELSKE, AND D. J. CONLEY. 1985*b*. An assessment of ecological changes during the recent history of Lake Ontario based on siliceous microfossils preserved in the sediments. J. Phycol. **21:** 257–276.

———, ———, ———, AND ———. 1985*c*. Post settlement diatom succession in the Bay of Quinte, Lake Ontario. Can. J. Fish. Aquat. Sci. **42:** 754–767.

———, ———, ———, AND ———. 1990. Siliceous microfossil succession in Lake Michigan. Limnol. Oceanogr. **35:** 959–967.

VOLLENWEIDER, R. A., M. MUNAWAR, AND P. STADELMANN. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. J. Fish. Res. Bd. Can. **31:** 739–762.

WOLIN, J. A., E. F. STOERMER, AND C. L. SCHELSKE. 1991. Recent changes in Lake Ontario 1981–1987: Microfossil evidence of phosphorus reduction. J. Great Lakes Res. **17:** 229–240.

———, ———, ———, AND D. J. CONLEY. 1988. Siliceous microfossil succession in recent Lake Huron sediments. Arch. Hydrobiol. **114:** 175–198.

Submitted: 13 April 1992
Accepted: 1 December 1992
Revised: 21 December 1992