shad on zooplankton community structure. Limnol. Oceanogr. **27:** 965–968.

———, S. B. TAYLOR, X. LAZZARO, AND D. KETTLE. 1984. Particle-grazing and plankton community impact of an omnivorous cichlid. Trans. Am. Fish. Soc. **113:** 397–402.

———, S. T. THRELKELD, AND M. D. McCRACKEN. 1986. Experimental analysis of the direct and indirect effects of an omnivorous filter-feeding clupeid on plankton community structure. Can. J. Fish. Aquat. Sci. **43:** 1935–1945.

GREEN, J. 1974. Parasites and epibionts of Cladocera. Trans. Zool. Soc. Lond. **32:** 417–515.

KANKAALA, P., AND P. ELORANTA. 1987. Epizoic ciliates (*Vorticella* sp.) compete for food with their host *Daphnia longispina* in a small polyhumic lake. Oecologia **73:** 203–206.

McCOMAS, S. R., AND R. W. DRENNER. 1982. Species replacement in a reservoir fish community: Silverside feeding mechanics and competition. Can. J. Fish. Aquat. Sci. **39:** 815–821.

ROSOWSKI, J. R., AND P. KUGRENS. 1973. Observations on the euglenoid *Colacium* with special reference to the formation and morphology of attachment material. J. Phycol. **9:** 370–383.

STRICKLER, J. R. 1984. Sticky water: A selective force in copepod evolution, p. 187–239. *In* Trophic interactions within aquatic ecosystems. AAAS Select. Symp. 85. Westview.

THRELKELD, S. T. 1987. Experimental evaluation of trophic-cascade and nutrient-mediated effects of planktivorous fish on plankton community structure, p. 161–173. *In* W. C. Kerfoot and A. Sih [eds.], Predation. Direct and indirect impacts on aquatic communities. New England.

WETTERER, J. K. 1989. Mechanisms of prey choice by planktivorous fish: Perceptual constraints and rules of thumb. Anim. Behav. **37:** 955–967.

WHITFIELD, P. J. 1979. The biology of parasitism. University Park.

WILLEY, R. L., AND J. G. GIANCARLO. 1986. Cell attachment in the flagellate, *Colacium* (Euglenophyceae), p. 65–78. *In* L. V. Evans and K. D. Hoagland [eds.], Algal biofouling. Elsevier.

WINER, B. J. 1971. Statistical principles in experimental design, 2nd ed. McGraw-Hill.

ZARET, T. M. 1980. Predation and freshwater communities. Yale.

Siliceous microfossil succession in Lake Michigan

Abstract—Quantitative analysis of siliceous microfossils in ^{210}Pb-dated Lake Michigan sediments shows five time zones in microfossil abundance and composition. Sediments deposited before 1885 contain low abundances comprising species associated with very oligotrophic lakes. Between 1885 and 1925 abundance increases slowly as does the ratio of planktonic diatoms to benthic diatoms and chrysophyte remains. These trends accelerate in sediments deposited between 1925 and 1964, most rapidly between 1954 and 1964. Maximal microfossil abundance occurs in sediments deposited ~1964 and numbers, particularly of oligotrophic species with summer abundance maxima, decline thereafter. This sequence appears to reflect progressive eutrophication of Lake Michigan culminating in silica limitation during summer stratification after the mid-1960s.

The role of various factors in driving changes in phytoplankton community structure in the Great Lakes remains a topic of considerable interest and debate. Some time ago we (Schelske and Stoermer 1971, 1972) advanced the hypothesis that reduction in available silica concentration was a major factor in Lake Michigan. The silica depletion hypothesis rests on two major assumptions: that increased phosphorus loading results in increased production of diatoms and other phytoplankton which require or utilize silica and that some fraction of the siliceous remains of these organisms is sequestered in sediments. In systems such as Lake Michigan where hydraulic renewal times are relatively long (~100 yr) and the lake surface constitutes a significant (~30%) portion of its total drainage basin (Schelske 1975), relatively modest increases in silica storage can result in decreased concentrations of available silica in the water column.
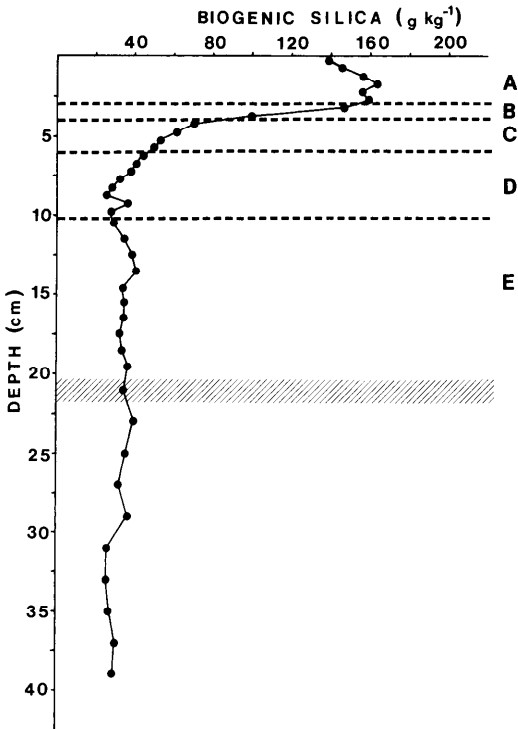
Fig. 1. Concentration of biogenic silica vs. depth in core K-34-83.

Progressive reduction in silica availability should have two successive effects. Initially it should confer competitive advantage on diatom species adapted to relatively low Si:P ratios or to growth during winter circulation. Further reductions in silica availability should limit diatom growth in summer and result in summer production mainly by phytoplankton species that do not require silica for growth. Thus resource limitation could have effects at the levels both of populations and of major physiological groups.

According to our interpretation, quantitatively analyzed cores from the Great Lakes (Frederick 1981; Schelske et al. 1983; Stoermer et al. 1985a,b,d, 1987; Wolin et al. 1988) demonstrate such effects. This interpretation is not universally shared. The main contention is based on a paper by Parker and Edgington (1976, p. 893) who concluded that "the permanent sediment does not appear to be an important sink for large quantities of biogenic silica in Lake Michigan. . . ." This conclusion was based on an apparent logarithmic decrease in quantities

of diatom remains downcore, which Parker and Edgington attributed to dissolution of diatom frustules after deposition, and on the fact that diatom remains recovered accounted for only a minor fraction of the potential flux calculated on the basis of conservative production estimates. Based on these considerations, Edgington (1984) argued that historic changes in phytoplankton community structure in Lake Michigan resulted largely from modification of communities at higher trophic levels.

We have undertaken quantitative analysis of diatoms and other siliceous microfossils in a core which extends well beyond western settlement in the Lake Michigan drainage basin to address the issue of preservation or nonpreservation of siliceous microfossils in Lake Michigan sediments. The results form the basis of the following report.

The core analyzed was lifted from station K34 (44°36.9′N, 86°321.6′W), near the deepest sounding in Lake Michigan, in June 1983 with a benthos gravity corer. The coring locality is in the northern basin, which receives the least anthropogenic nutrient loading and is the least perturbed region of the lake. Methods and procedures of analysis have been described previously (Stoermer et al. 1985b). Cluster analysis reported is based on Euclidean distance measure and the average distance clustering method (Carney 1982).

The biogenic silica profile (Fig. 1) is characterized by low and relatively constant values below 10 cm, a rapid increase in concentration to a peak between 2 and 3 cm, and declining values thereafter. Similar to chemically measured biogenic silica, total siliceous microfossil abundance is relatively low and constant below 10 cm in the section, rises to a strong peak at 2.5–3.0 cm, and then declines toward the surface (Fig. 2). The single exception is an isolated peak in abundance in the 20–22-cm sample. Planktonic diatoms are the most abundant microfossils found in all strata of the core. Chrysophyte remains are present in small numbers in all samples. Their absolute and relative abundance tends to increase with depth, although there is a good deal of variation. There seem to be long-period cycles
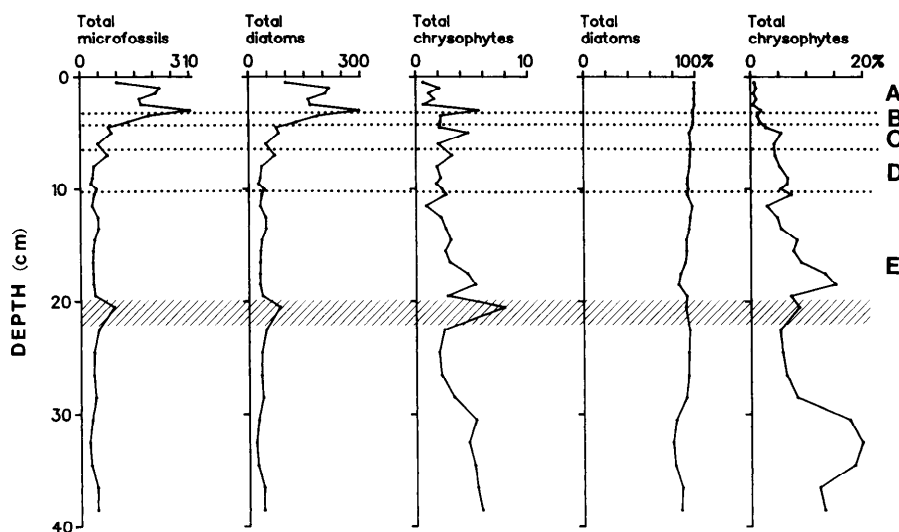
Fig. 2.   Absolute (valves or cysts × 10⁶ g⁻¹ dry wt sediment) and relative (%) abundance of major microfossil groups at depth in core K-34-83.

of relative chrysophyte abundance imposed on the generally declining trend.

Benthic diatoms (Fig. 3) are present at all levels and are proportionally more abundant in deeper samples. Benthic species range from 10 to 25% of the total microfossil assemblage in samples below 10 cm and decline in relative abundance toward the surface. The highest absolute abundance

of benthic diatoms occurs in the sample from 20 to 22 cm.

We noted 170 morphotypes of algal remains during the study. Of them, 138 are diatoms and the remainder chrysophyte remains. Chrysophyte remains consist almost entirely of cysts. Scales and other structures are very rare. Only in a few cases were we able to associate the cysts encountered with
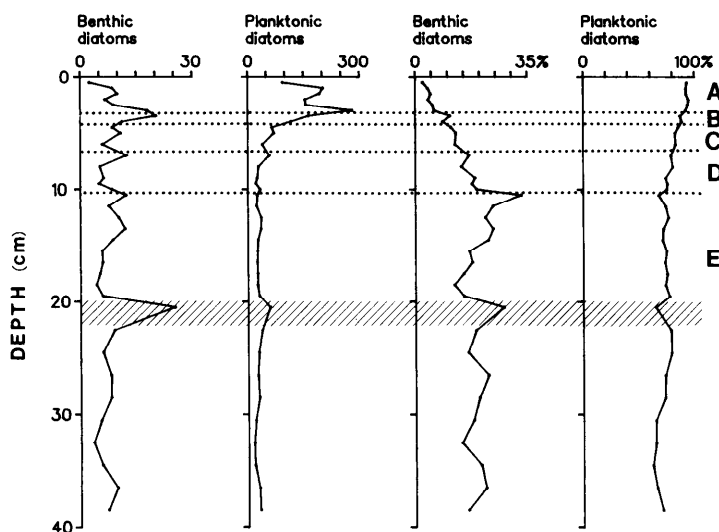

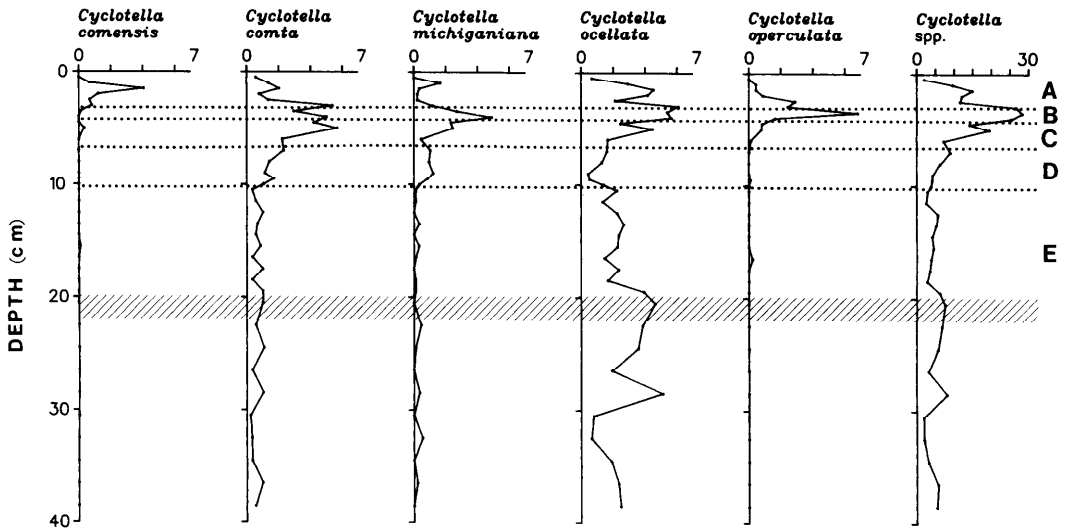Fig. 3.   As Fig. 2, but of benthic and planktonic diatoms.

Fig. 4.   As Fig. 2, but of absolute abundance of *Cyclotella* spp.

living species and they are treated as form taxa. Listings of all taxa present can be obtained from E.F.S.

All of the numerically important *Cyclotella* species are regarded as characteristic of oligotrophic lakes. In Lake Michigan they reach greatest abundance in summer (Stoermer and Ladewski 1976). Except for *Cyclotella comensis,* they were originally present throughout the Great Lakes system. *Cyclotella operculata* was present, but very rare, in all of the lakes and has become relatively abundant only in postsettlement samples from Lakes Huron and Michigan (Fig. 4). All these species of *Cyclotella* have been virtually eliminated from the floras of Lakes Ontario (Stoermer et al. 1985*b*) and Erie (Stoermer et al. 1987) but are still present and apparently increasing in abundance in Lakes Superior (Stoermer et al. 1985*d*) and Huron (Wolin et al. 1988). In our samples they, except for *C. comensis* and *C. operculata,* are present in most strata studied. The general pattern of occurrence of *Cyclotella* species is similar, with low and relatively stable abundance in the lower section of the core, an increase to maximal absolute and relative abundance above 10 cm, followed by decreasing numbers toward the sediment surface. Exceptions are *C. comensis* and *C. operculata,* which were

noted in only one sample below 10 cm, and *Cyclotella ocellata,* which was most abundant at 30 cm.

Both planktonic (Fig. 5) and benthic (Fig. 6) species of *Fragilaria* are present in samples from most levels of the core. Abundance declines markedly in the 3-cm sample and *Fragilaria* spp. are virtually absent from surficial sediments. Of major planktonic taxa, *Fragilaria capucina* is usually associated with eutrophic conditions in the Great Lakes (Stoermer 1978), *Fragilaria intermedia* var. *fallax* is usually associated with oligotrophic conditions and has apparently been eliminated from Lake Ontario (Stoermer et al. 1985*b*), and *Fragilaria crotonensis* is apparently eurytopic and common throughout the Great Lakes system. Considered together *Fragilaria* species have two striking abundance maxima, at 3.0–3.5 cm and 20–22 cm. Planktonic species, particularly *F. capucina* and *F. crotonensis,* are most important in the 3.0–3.5-cm maximum and both benthic and planktonic taxa contribute to the 20–22-cm maximum, although benthic taxa are most important at this level. The most abundant benthic taxa are widely distributed species that tend to be particularly abundant in deep-living benthic communities from large lakes, in lateglacial deposits (Haworth 1975, 1976), and
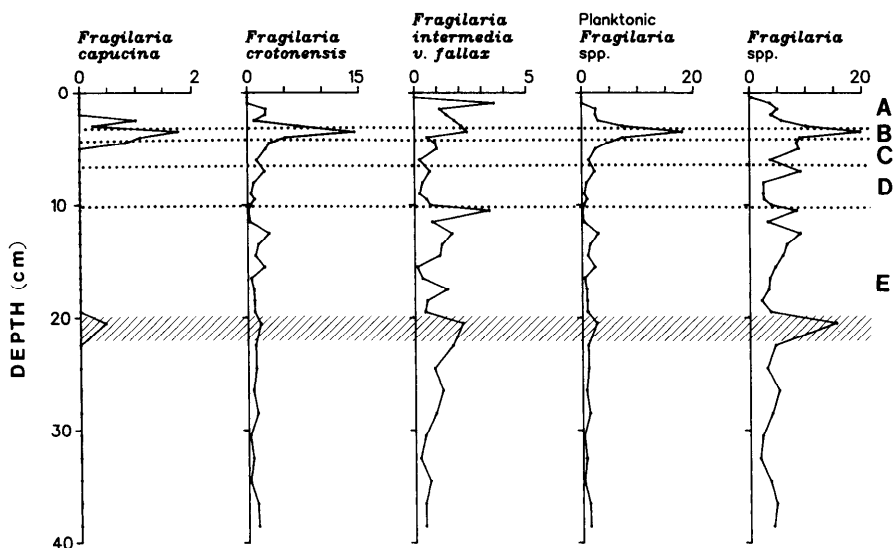
Fig. 5.   As Fig. 2, but of absolute abundance of planktonic *Fragilaria* spp.

in sediments of arctic lakes (Smol 1983). The most striking feature common to small benthic *Fragilaria* spp. is the abundance maximum in the 20–22-cm sample (Fig. 6).

Species of *Melosira* (Fig. 7) are common components of phytoplankton communities during winter circulation (Stoermer and Ladewski 1976) in the Great Lakes and are generally well represented in sedimentary assemblages (Stoermer et al. 1985*b,c,d*, 1987; Wolin et al. 1988). *Melosira* abundance is relatively low and uniform in samples below 10 cm but increases to >70% of the assemblage in surficial sediments. This increase occurs in two stages, moderate increase in samples between 3 and 10 cm and more rapid increase in samples near the sediment surface. *Melosira islandica* contrib-
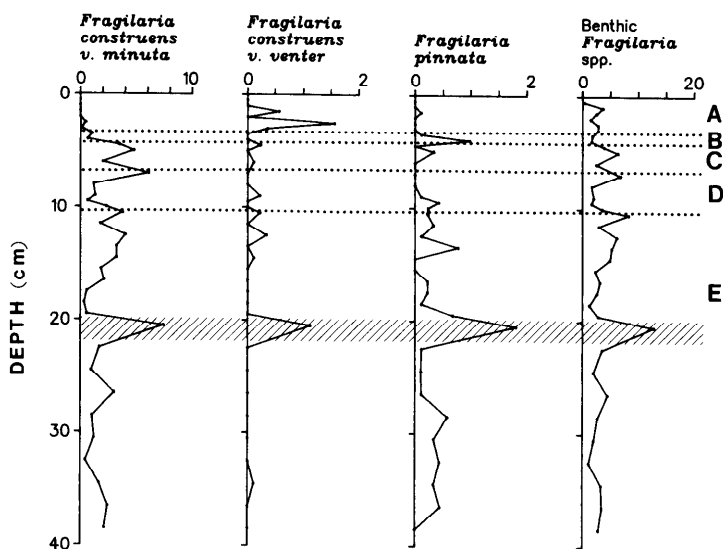

Fig. 6.   As Fig. 2, but of absolute abundance of benthic *Fragilaria* spp.
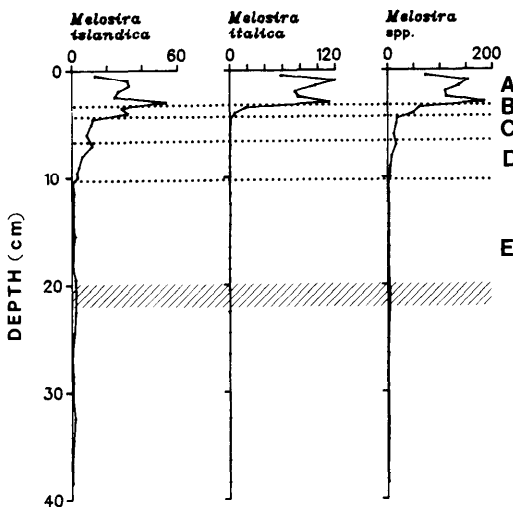
Fig. 7. As Fig. 2, but of absolute abundance of *Melosira* spp.

utes most strongly to the initial rise and *Melosira italica* becomes strongly dominant in the near-surface sediments.

Species of *Stephanodiscus* (Fig. 8) are most abundant in Lake Michigan during winter and spring circulation (Stoermer and Ladewski 1976). With the exception of *Stephanodiscus transilvanicus,* they are present throughout the Great Lakes system. Both *Stephanodiscus alpinus* and *Stephanodiscus*

niagarae are present throughout the pre- and postsettlement record in Lakes Ontario (Stoermer et al. 1985*b*) and Erie (Stoermer et al. 1987). There are no modern records of *S. transilvanicus* from the lower Great Lakes, although it was once abundant in Lake Ontario (Stoermer et al. 1985*b*).

Two main clusters are defined (Fig. 9), which distinguish samples deposited before and after ~1964. Within the latter cluster the surface sample is grouped with samples from 1.5 to 2.5 cm rather than with their nearest stratigraphic neighbors. Within the former cluster, samples deposited between 1954–1964, 1925–1964, and 1885–1925 are resolved further. All samples deposited before 1885, except the sample from 20 to 22 cm (~1735), are very similar.

Our results do not support Parker and Edgington's (1976) conclusion that decrease in siliceous microfossil abundance with increasing sediment depth results largely from dissolution. Reduction in abundance does not continue in sediments deposited in the presettlement era and even relatively fragile species such as *F. crotonensis* are preserved in the deepest sediments sampled. Further, we find no microscopic evidence of dissolution at successively greater sediment depths. It has been our consistent observation that the best microfossil preservation
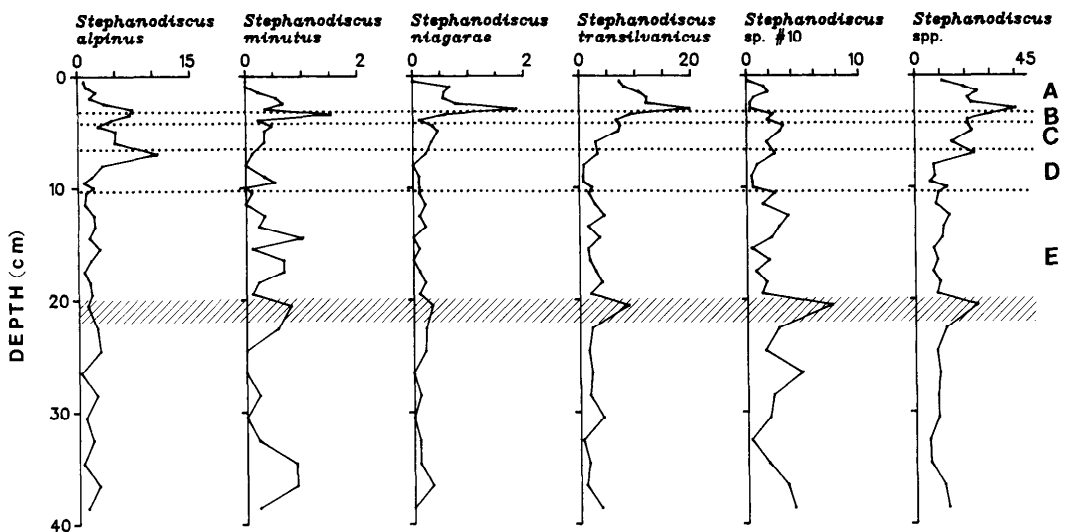

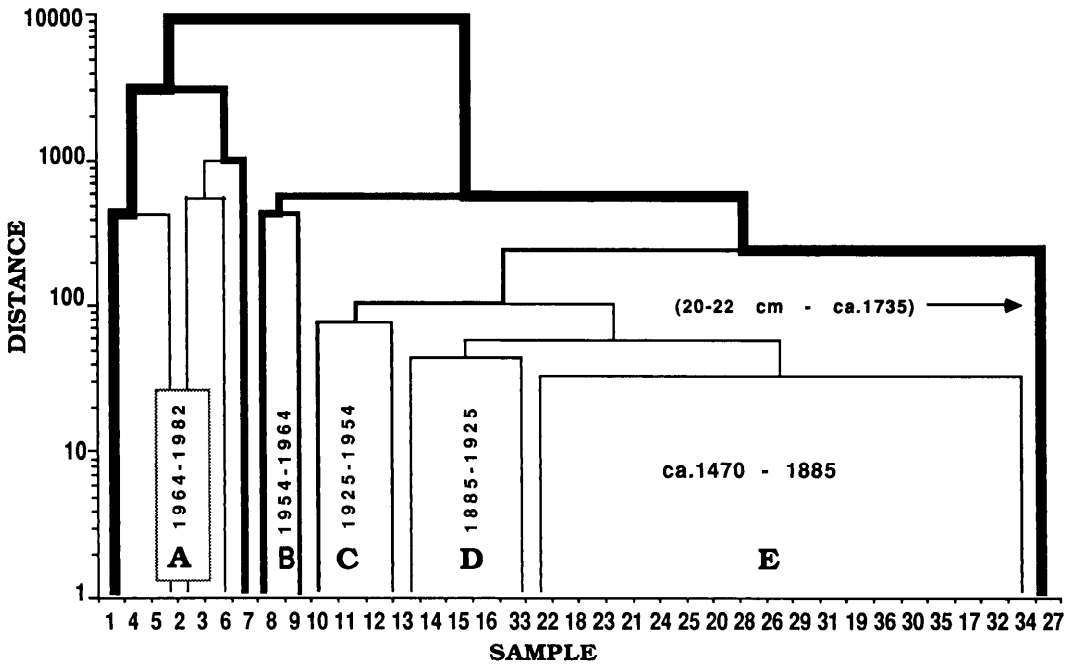Fig. 8. As Fig. 2, but of absolute abundance of *Stephanodiscus* spp.

Fig. 9. Cluster analysis based on absolute abundance of the most abundant species in core K-34-83. Date ranges shown in clusters are based on ^{210}Pb. Dates before 1880 are extrapolated based on the assumption of constant sedimentation rate and may be conservative.

is found in presettlement strata, particularly in the lower Great Lakes (Stoermer et al. 1985c).

In our opinion the most probable explanation for the obvious quantitative and qualitative changes in Lake Michigan sedimentary microfossil assemblages is anthropogenic eutrophication in the postsettlement era (Schelske et al. 1983, 1986). We infer that samples from zone E represent the natural state of the system, before substantial intervention by European settlers. Accordingly, responses in zone D result from increased nutrient fluxes brought about by forest clearance, introduction of extensive agriculture, and general human population growth. Samples in zone C reflect acceleration of these trends. The very rapid transition in zone B reflects response to introduction of phosphate-based detergents and increase in the proportion of population served by sanitary sewers in the post-World War II era. We conclude that samples from zone A reflect changes in siliceous microfossil deposition resulting from silica limitation during summer stratification. At some

level the microfossil record must also record the effects of other external forcing functions and effects of internal biotic interactions. However our results support the view that any such effects are small (Lehman 1988) compared to effects of increased phosphorus loading.

In evaluating this scenario, it should be remembered that only one core was analyzed but that it probably represents the least modified conditions in Lake Michigan. Sedimentary sequences in the southern basin of the lake might be expected to reflect both earlier and more extensive effects. For instance it is well known that severe, by the standards of the day, local sewage pollution problems occurred in the Chicago area in the 1870s and 1880s (Briggs 1872; Thomas and Chase 1881). The political response to these problems, diversion of sewage from the Chicago metropolitan region to the Mississippi drainage via the Chicago Sanitary and Ship Canal, was likely the most important factor in preserving relatively high water quality in Lake Michigan.

Granting real differences in planktonic

floras indigenous to lakes in the Great Lakes system, it is possible to arrive at an approximate comparison of present conditions in Lake Michigan to past states in the lower lakes. It is clear that Lake Michigan is in a much earlier successional stage. Comparison of population responses leads to the conclusion that Lake Michigan during the 1970s passed through the same changes that occurred in Lake Ontario (Stoermer et al. 1985*b*) ~1900. In retrospect it is somewhat ironic that our original hypothesis (Schelske and Stoermer 1971, 1972) was based on experiments carried out in Lake Michigan during the critical period. With the value of hindsight, interlake comparative experiments in the early 1970s or institution of a comprehensive routine measurement program in the 1950s and 1960s (Schelske 1988) would probably have served to clarify the situation earlier.

Although the magnitude of postsettlement changes overwhelms presettlement events, our results do not imply the presettlement environment of Lake Michigan was unchanging. We have already noted the apparent cyclic pattern of chrysophyte abundance imposed on a generally declining trend in presettlement samples. We also call attention to the exceptional relative abundance of *F. crotonensis* in samples between 11 and 16 cm (~1811–1864). Bradbury (1988) postulated that high abundance of this species is associated with limited spring circulation and high summer production. This suggestion is congruent with our observations on recent phytoplankton assemblages in Lake Michigan (Stoermer and Ladewski 1976) and Hartig's (1987) work in Lake Erie. Perhaps the most intriguing problem in our presettlement material is sample 27 (~1735). Species composition (atypical abundance of small benthic *Fragilaria* and oligostenothermal *Stephanodiscus*) suggests that Lake Michigan underwent a period of extreme low temperatures at this time. Bradbury (1988) noted a similar episode in Elk Lake somewhat earlier, but likely within dating error. Resampling and reanalysis of material from interval 27 convinces us that its outlier status does not result from a subsampling or preparation

artifact. Our data thus suggest natural perturbation events in the presettlement history of Lake Michigan, but extended sampling and analysis would be necessary to define them.

E. F. Stoermer
J. A. Wolin

Center for Great Lakes and
    Aquatic Sciences
University of Michigan
Ann Arbor 48109

C. L. Schelske

Department of Fisheries and Aquaculture
University of Florida
Gainesville 32606

D. J. Conley

Horn Point Environmental Laboratory
Cambridge, Maryland 21613

References

BRADBURY, J. P. 1988. A climatic-limnologic model of diatom succession for paleolimnological interpretation of varved sediments at Elk Lake, Minnesota. J. Paleolimnol. **1:** 115–131.

BRIGGS, S. A. 1872. The diatomaceae of Lake Michigan. The Lens **1:** 41–44.

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

EDGINGTON, D. N. 1984. Great Lakes eutrophication: Fish, not phosphates?, p. 25–31. *In* The future of Great Lakes resources. Univ. Wisconsin Sea Grant Inst. 1982–84 Biennial Rep.

FREDERICK, V. R. 1981. Preliminary investigation of the algal flora in the sediments of Lake Erie. J. Great Lakes Res. **7:** 404–408.

HARTIG, J. H. 1987. Factors contributing to development of *Fragilaria crotonensis* pulses in Pigeon Bay waters of western Lake Erie. J. Great Lakes Res. **13:** 65–77.

HAWORTH, E. Y. 1975. A scanning electron microscope study of some different frustule forms of the genus *Fragilaria* found in Scottish late-glacial sediments. Br. Phycol. J. **10:** 73–80.

———. 1976. Two late-glacial (late Devesian) diatom assemblage profiles from northern Scotland. New Phytol. **77:** 227–256.

LEHMAN, J. T. 1988. Algal biomass unaltered by food-web changes in Lake Michigan. Nature **332:** 537–538.

PARKER, J. I., AND D. N. EDGINGTON. 1976. Concentration of frustules in Lake Michigan sediment cores. Limnol. Oceanogr. **21:** 887–893.

SCHELSKE, C. L. 1975. Silica and nitrate depletion as related to rate of eutrophication in Lakes Michi-

gan, Huron and Superior, p. 277–298. *In* A. D. Hasler [ed.], Coupling of land and water systems. Springer.

———. 1988. Historic trends in Lake Michigan silica concentrations. Int. Rev. Gesamten Hydrobiol. **73:** 559–591.

———, AND E. F. STOERMER. 1971. Eutrophication, silica depletion, and predicted changes in algal quality in Lake Michigan. Science **173:** 423–424.

———, AND ———. 1972. Phosphorus, silica, and eutrophication of Lake Michigan. Am. Soc. Limnol. Oceanogr. Spec. Symp. **1:** 157–171.

———, ———, D. J. CONLEY, J. A. ROBBINS, AND R. M. GLOVER. 1983. Early eutrophication in the lower Great Lakes: New evidence from biogenic silica in sediments. Science **222:** 320–322.

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

SMOL, J. P. 1983. Paleophycology of a high arctic lake near Cape Hershel, Ellesmere Island. Can. J. Bot. **61:** 2195–2204.

STOERMER, E. F. 1978. Phytoplankton as indicators of water quality in the Laurentian Great Lakes. Trans. Am. Microsc. Soc. **97:** 2–16.

———, J. P. KOCIOLEK, C. L. SCHELSKE, AND D. J. CONLEY. 1985a. 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 sed-

iments of Lake Erie's central basin. Diatom Res. **2:** 113–134.

———, AND T. B. LADEWSKI. 1976. Apparent optimal temperatures for the occurrence of some common phytoplankton species in southern Lake Michigan. Univ. Mich. Great Lakes Res. Div. Publ. 18. 48 p.

———, J. A. WOLIN, C. L. SCHELSKE, AND D. J. CONLEY. 1985b. 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 ———. 1985c. Variations in *Melosira islandica* valve morphology related to eutrophication and silica depletion. Limnol. Oceanogr. **30:** 414–418.

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

THOMAS, B. W., AND H. H. CHASE. 1881. Diatomaceae of Lake Michigan as collected during the past 16 years from the water supply of the city of Chicago. Notarisia **2:** 328–330.

WOLIN, J. A., E. F. STOERMER, C. L. SCHELSKE, AND D. J. CONLEY. 1988. Siliceous microfossil succession in recent Lake Huron sediments. Arch. Hydrobiol. **114:** 175–198.

Temperature of limpets in the rocky intertidal zone: Effects of caging and substratum

Abstract—Depending on weather, temperatures (T_e) of intertidal limpets (*Collisella scabra*) were decreased as much as 4°C by the types of cages used in ecological studies in the rocky intertidal zone. The cages blocked 60–80% of incident solar radiation. Differences in substratum may have larger effects on T_e, however, than those introduced by cages.

Interspecific interactions in the rocky intertidal zone are perhaps the best understood of any ecological community. This situation results largely from the tractability of caging techniques, which have been used successfully in numerous studies (*see* Paine 1977). Cage experiments have generally controlled for cage effects by including "roofed" cages, open at the sides to allow access of crawling invertebrates, but presumably producing shading and hydrodynamic effects similar to those of the fully enclosed cages. Effects of caging on the physiological environment of study organisms have rarely been investigated directly. Therefore it seemed worthwhile to examine the effects of cages on the thermal environment.

Operative temperature (T_e) is a means of describing the microclimate of an area with a model of the organism as the temperature probe. T_e incorporates all the avenues of