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# POST-PLEISTOCENE DIATOM SUCCESSION IN DOUGLAS LAKE, MICHIGAN[1,2]

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ABSTRACT

*Analysis of fossil diatom assemblages recovered from a 12.2 m core reveals a series of distinct floristic associations. The associations present are correlated with sediment type and reflect successive stages in the development of the lake. A basal red clay sediment contains a planktonic association characteristic of large, proglacial lakes. At 10.0 m core depth, sediment type changes to fine sand containing a higher abundance of benthic species indicating reduction of water depth at the deposition site. Marl sediments begin at 9.7 m and contain an association characteristic of a small, shallow, oligotrophic lake. At 8.8 m the marl sequence is interrupted by highly organic sediment containing a eutrophic plankton association. From 8.5 to 7.6 m the sediment type grades from marl to organic, apparently reduced sediments and diatom associations present contain successively higher percentages of planktonic species associated with eutrophic habitats. By the 7.6 m level a eutrophic plankton association, similar to the modern flora, is established and remains remarkably constant to the surface of the section.*

*Key index words: diatoms; Douglas Lake; eutrophication; Holocene; species succession*

Largely because the University of Michigan Biological Station is located on its shore, Douglas Lake has been subject to more prolonged and intensive investigation than most lakes in North America. Its unusual morphometry and the effect of several basins on other limnological parameters have been intensively investigated (21–24). The composition and seasonal succession of phytoplankton has been studied (20) and considerable information on phytoplankton productivity is available (15). The composition of the benthic algal flora has also been treated in considerable detail (13). In addition to the physical studies cited above, the current structure of certain portions of the lake has been investigated by Moffett (12) and, more recently, by Gannon and Brubaker (9).

On the basis of these investigations and my own observations, the general characteristics of Douglas Lake tend to fall across the boundaries of classical schemes of lake classification. Although it is classically eutrophic and apparently has been during the history of available direct measurements (4), in the sense that the hypolimnion is completely depleted of oxygen during the summer stagnation, the algal flora of Douglas Lake retains many elements of the boreal flora which are usually associated with more oligotrophic habitats. In recent years phytoplankton succession has been characterized by successive maxima of diatoms and bluegreen algae throughout most of the year which, combined with strikingly low levels of available nitrogen following the diatom maxima, suggests that the system is N-limited.

One of the more interesting aspects of Douglas Lake and the surrounding region is the record of drastic disturbances which have occurred. The northern portion of Michigan's lower peninsula has been subjected to several events which have served to more or less wipe the successional slate "clean," at least so far as terrestrial plant communities are concerned. The entire region was covered by successive advances of pleistocene glaciers (7) and significant portions were subsequently inundated by early stages of the Laurentian Great Lakes (10,16). More recently the dominant vascular vegetation of the region was devastated by indiscriminate deforestation and fire (11). At the present time lakes in the region, because of their attractiveness as recreational property, are suffering from largely uncontrolled development and concommitant problems of nutrient addition and further landscape modification.

The record of this successional history, as recorded in the sediments of Douglas Lake, has been at least partially exposed in a remarkably ambitious and thorough series of investigations by I. T. Wilson (25, 26). In a later publication Wilson and Potzger interpreted the succession of events which have affected Douglas Lake on the basis of sedimentary stratigraphy and the pollen preserved in the sediments (27). Wilson also deposited material from his "borings" (suitable for study by specialists in other microscopic biological groups) in a number of institutions in the United States. It is this material, originally collected in 1942, that forms the basis of the present report.

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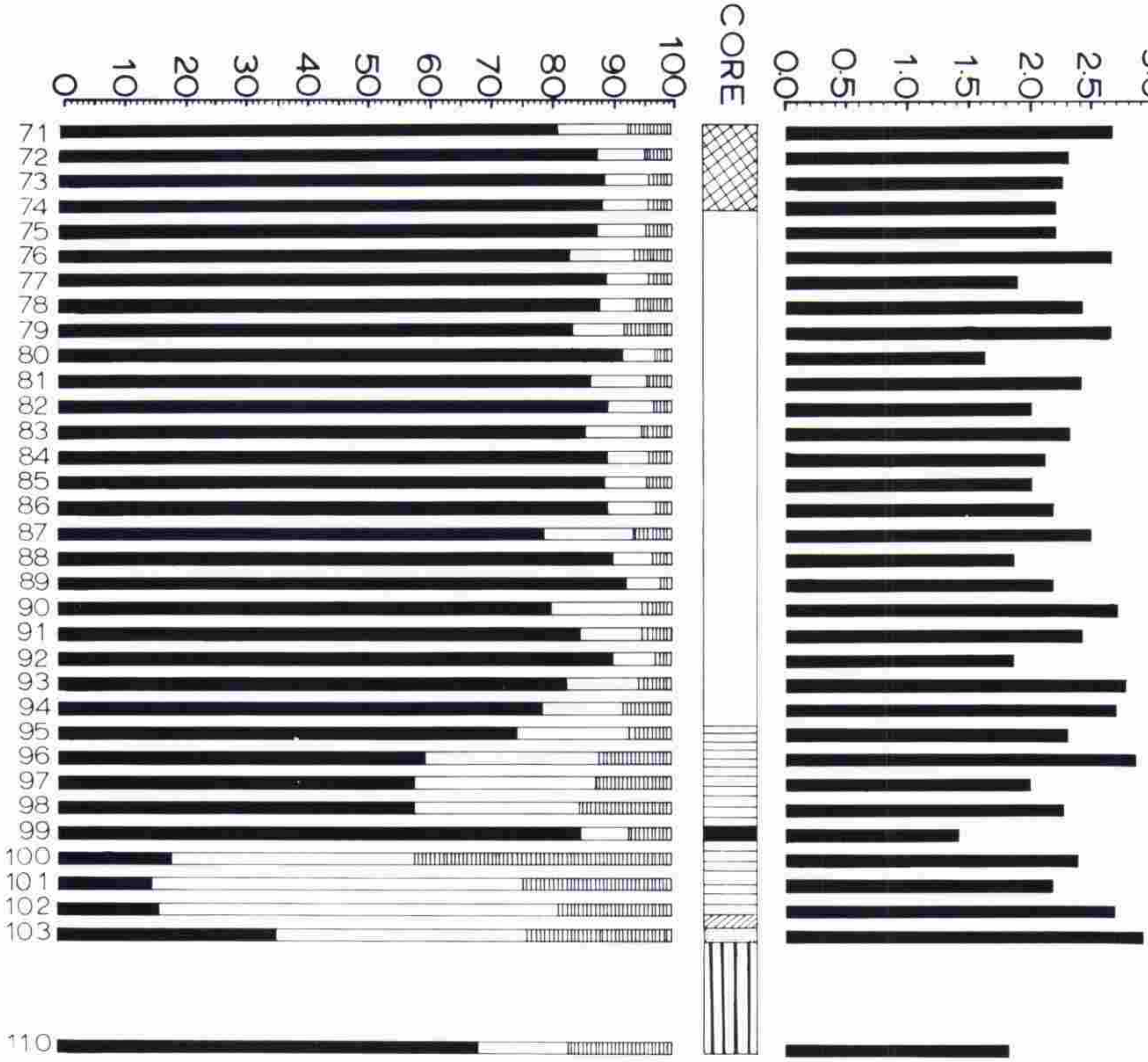


FIG. 1. Sediment and gross assemblage characteristics at levels sampled. Following terminology of Wilson (26), levels sampled at 1 ft intervals are numbered from the mud-water interface (71) downward. Left panel shows relative abundance of planktonic (filled bars), epipelic (open bars), epiphytic (hatched bars) species at each sample depth. Center panel shows sediment types in core and approximate extent: cross hatch = soft flocculent black mud; open bar = gelatinous laminated brown mud; horizontal bars = gray marl; filled bar = tough organic black mud; oblique hatch = medium fine red sand; stipple = fine white sand; vertical lined = red clay. Right-hand panel shows diversity index of assemblage in each sample.

## MATERIALS AND METHODS

The material available for study was a series of prepared diatom slides made at the Academy of Natural Sciences of Philadelphia from material deposited there by I. T. Wilson. The slides are strewn mounts of cleaned material embedded in Hyrax. The original material deposited by Wilson consisted of samples taken at 1 ft (0.3048 m) intervals from his "boring 4," located near the center of South Fishtail Bay (26). In Wilson's nomenclature, sample levels were numbered from ambient lake level. Samples from "boring 4" extended from level 71, the sediment-water interface, to level 110. Although the total length of section was 40 ft (12.2 m) only 34 samples were available for study, since intervals between 103 and 110 were apparently not sampled.

Material was examined with a Leitz Ortholux research microscope fitted with fluorite oil immersion objectives of 1.30 or greater numerical aperture. All identification and enumeration were carried out at 1250×. A total of 500 valves were counted from each sample. This sample size required scanning most of the area of the slides from the lower levels, where specimens were sparse, and more limited sectors in samples from the upper levels. Because of the wide sampling interval and uncertainties regarding the precise stratigraphic range of individual samples, more extended analysis was deemed unjustified.

## RESULTS AND DISCUSSION

A total of 248 diatom taxa were recorded from the material examined. Only those which constitute a

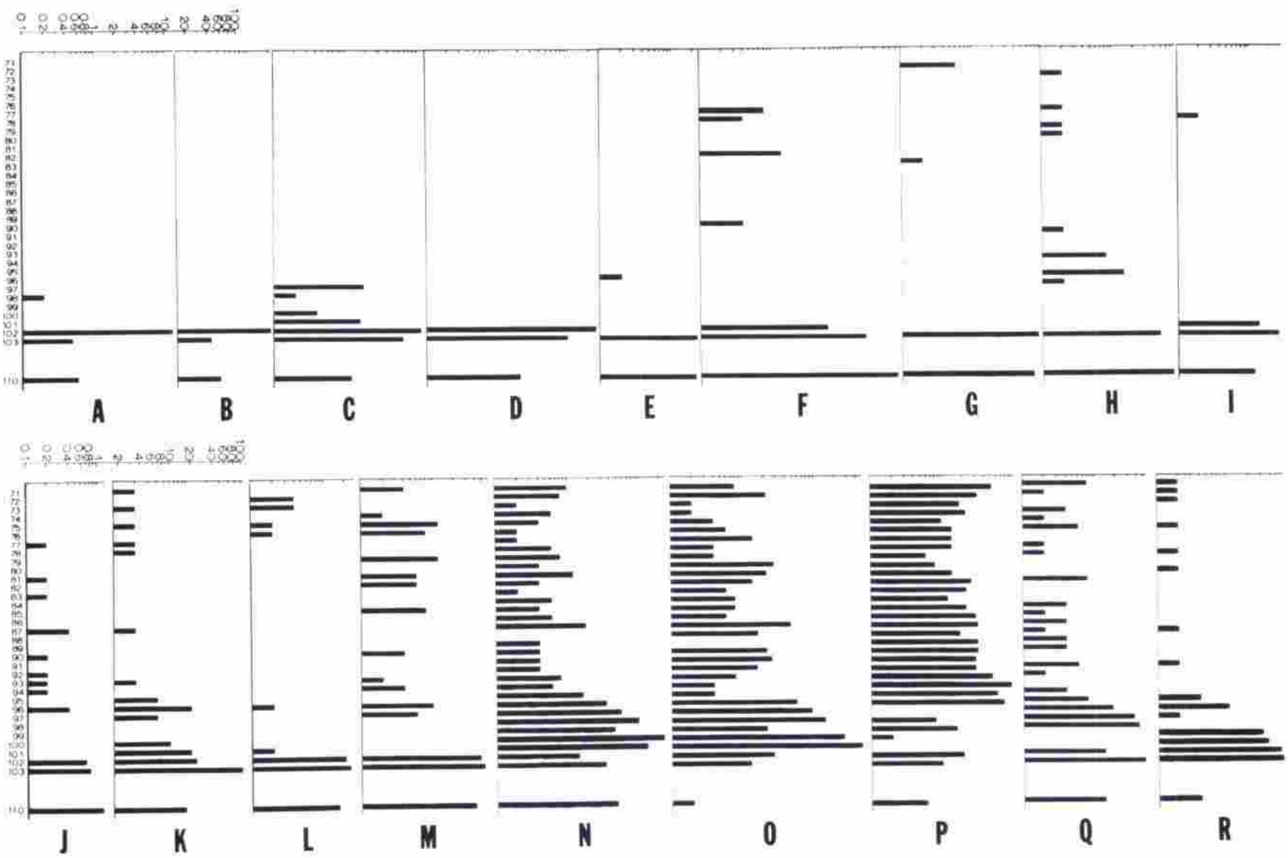


FIG. 2. Relative abundance and distribution of more abundant species. Depth intervals as in FIG. 1. A = *Melosira arenaria* Moore. B = *Achnanthes calcar* Cl. C = *Navicula cocconeiformis* Greg. D = *Cymbella sinuata* var. *antiqua* (Grun.) Cl. E = *Denticula tenuis* var. *crassula* (Näg. ex Kütz.) West & West. F = *Melosira islandica* O. Müll. G = *Cocconeis placentula* var. *euglypta* (Ehr.) Cl. H = *Stephanodiscus transilvanicus* Pant. I = *Navicula paludosa* Hust. J = *Achnanthes lanceolata* (Bréb.) Grun. K = *A. clevei* Grun. L = *A. clevei* var. *rostrata* Hust. M = *Cocconeis placentula* Ehr. N = *Amphora ovalis* var. *pediculus* (Kütz.) V. H. O = *Fragilaria pinnata* Ehr. P = *Cyclotella comta* (Ehr.) Kütz. Q = *Stephanodiscus alpinus* Hust. R = *Cocconeis diminuta* Pant.

significant fraction of the flora in at least some levels are reported in the graphic representations of species abundance. All species present were included in the diversity calculations. Raw count data are available from the Great Lakes Research Division, University of Michigan, and the physical samples are the property of and are housed at the Academy of Natural Sciences, Philadelphia.

The general characteristics of the section studied are shown in Fig. 1. The center panel of the figure gives the sediment characteristics as reported by Wilson (26). The lowermost portion of the section (levels 110 to 103) was composed of red clay with little apparent inclusion of either coarser grained sediments or organic matter. This material is overlain by clean, white, medium fine sand, covered with a veneer of reddish sand. According to Wilson's description there is relatively little intergradation between the red clay and the overlying sand layers. Immediately overlying the sand is a highly calcareous, fine grained sediment which Wilson referred to as gray marl. This material extends from level 102 through level 95. The lowermost level of this sequence apparently rests upon the sandy layers with relatively little intergradation. The upper part of the sequence, however, grades imperceptibly into the sediments above. The gray marl sequence is interrupted at level 99 by a fairly narrow band of black, gelatinous, apparently highly organic material. Beginning at level 95 the gray marl grades into the sediment type which constitutes the bulk of the core and which Wilson described as gelatinous, laminated, brown mud. This material is apparently highly organic and the mineral fraction present is largely composed of diatom frustules and other mineralized plant remains. Beginning between levels 75 and 74 this material again grades into the surficial sediment type, which Wilson described as soft, flocculent, black mud. This material, which is the modern surficial sediment type, is also highly organic and contains a relatively high proportion of identifiable phytoplankton remains. Besides mineralized diatom frustules and chrysophyte cysts, morphologically identifiable organic remains, such as the cell walls of *Pediastrum* spp., *Ceratium hirundinella*, and heterocysts and akinetes of *Anabaena flos-aquae* are common. Viable

*Melosira* (14,17) have been recovered from modern samples of this material from depths in excess of 15 cm.

The left-hand panel of Fig. 1 depicts the relative abundance of planktonic species vs. those which are found primarily in epipelic and epiphytic communities. Granted the uncertainties involved in composing arbitrary habitat preference classifications, it is quite apparent that substantial changes in the contribution of microfossils from these communities has taken place over the time sequence represented by the section. Material from the lowermost level of the core is composed primarily of planktonic species with, however, a considerable and nearly equal admixture of species which have their primary habitat in epipelic and epiphytic communities. Beginning with the sandy sediments in level 103 and particularly in the gray marl sequence immediately overlying it, the flora is dominated by epipelic and epiphytic species. The highest contribution of epipelic species found in this section occurs at level 102 and the highest contribution of epiphytic species is found at level 100. This situation is dramatically reversed in the black organic layer found at level 99, where planktonic species suddenly assume levels of abundance more characteristic of the upper segments of this section. Although epipelic and epiphytic species never again become dominant elements of the flora, they are important through the remainder of the gray marl sequence. Above level 95, however, planktonic species consistently comprise more than 75% of the specimens recovered.

The right-hand panel of Fig. 1 depicts the Shannon-Weaver diversity index calculated for all samples. This index is quite variable throughout the section and no particular trends are evident. Markedly low diversities were found at level 110 in the red clay sequence, level 99 representing the black, organic band interrupting the gray marl sequence, and at levels 92, 88, 82, 80, and 77 in the laminated, brown sediment sequence. Highest diversity was at level 103 from the sandy material containing nearly equal contributions of planktonic, epipelic, and epiphytic species.

The distributions of most abundant diatom taxa found are shown in Fig. 2–4. A number of reasonably distinct trends are evident. A few species are entirely limited to the lower levels of the section (Fig. 2A–D). Included in this group are *Melosira arenaria* (Fig. 2A) whose modern distribution is limited to boreal lakes (6) and which is considered by some authorities (5) to be an appropriate marker fossil of large, proglacial lakes. Other species with similar distribution in the core have primarily boreal modern distribution.

Several other species are abundant in the lower levels of the section but are rare or sporadic in distribution above level 102 (Fig. 2E–I). Included in this group are both common cold season plankton dominants in large oligotrophic to mesotrophic northern lakes and primarily benthic species which share the same modern distribution. *Cocconeis placentula* var. *euglypta* (Fig. 2G), is the only species having this pattern of occurrence in the core which is widely distributed in a variety of habitats in the modern flora. It and *Denticula tenuis* var. *crassula* (Fig. 2E) have been found in modern collections from Douglas Lake. The others are either absent from the modern flora or present in such low numbers that they have not been collected.

There are a number of species which are present or relatively abundant in levels 110, 102, and 103 but which become less abundant and more sporadic in occurrence in higher levels of the section (Fig. 2J–R). Included in this group are several widely distributed, primarily epiphytic species and all have been found in modern collections from Douglas Lake. Two primarily epipelic species, *Amphora ovalis* var. *pediculus* (Fig. 2N) and *Fragilaria pinnata* (Fig. 2O), have similar distributions within the section but reach their highest relative abundance in levels 100 and 101. Only 2 planktonic species occurring in level 110 have distribution similar to those discussed above in the upper levels of the core. These are *Cyclotella comta* (Fig. 2P) and *Stephanodiscus alpinus* (Fig. 2Q). Both are common in northern and alpine lakes, with *C. comta* usually being a warm season dominant and *S. alpinus* a cold season or sub-thermocline dominant. It should be noted that *C. comta* is more consistent in its occurrence above level 96, which is similar to the pattern shown by most of the major planktonic taxa discussed later.

A number of species (most of which are primarily benthic) are first noted at level 102 or 101, become most abundant in the gray marl sediment sequence, and are reduced in abundance in higher levels of the section (Fig. 3A–T). Primarily epiphytic species which have a similar pattern of distribution within the core are *Amphora michiganensis* (Fig. 3T), *Cymbella parvula* (Fig. 3I), and *Navicula scutelloides* (Fig. 3J). The pattern of occurrence of *Achnanthes trinodis* (Fig. 3U) is somewhat similar, but it is also present at level 101 and it is somewhat more consistently present in the upper levels of the section.

*Navicula seminoides* (Fig. 3A) and *N. diluviana* (Fig. 3B) were originally reported from fossil deposits. Their occurrence is restricted to the lower levels of the Douglas Lake section. However they are known to occur in modern collections from the Laurentian Great Lakes, and *N. seminoides* is particularly abundant in epipelic communities in relatively undisturbed portions of Lake Superior.

Two primarily planktonic taxa, *Cyclotella michiganiana* (Fig. 3O) and *C. kuetzingiana* (Fig. 3P), make their first appearance near level 100 but, similar to the majority of the planktonic dominants discussed later, do not become consistently abundant until level 96 and above.

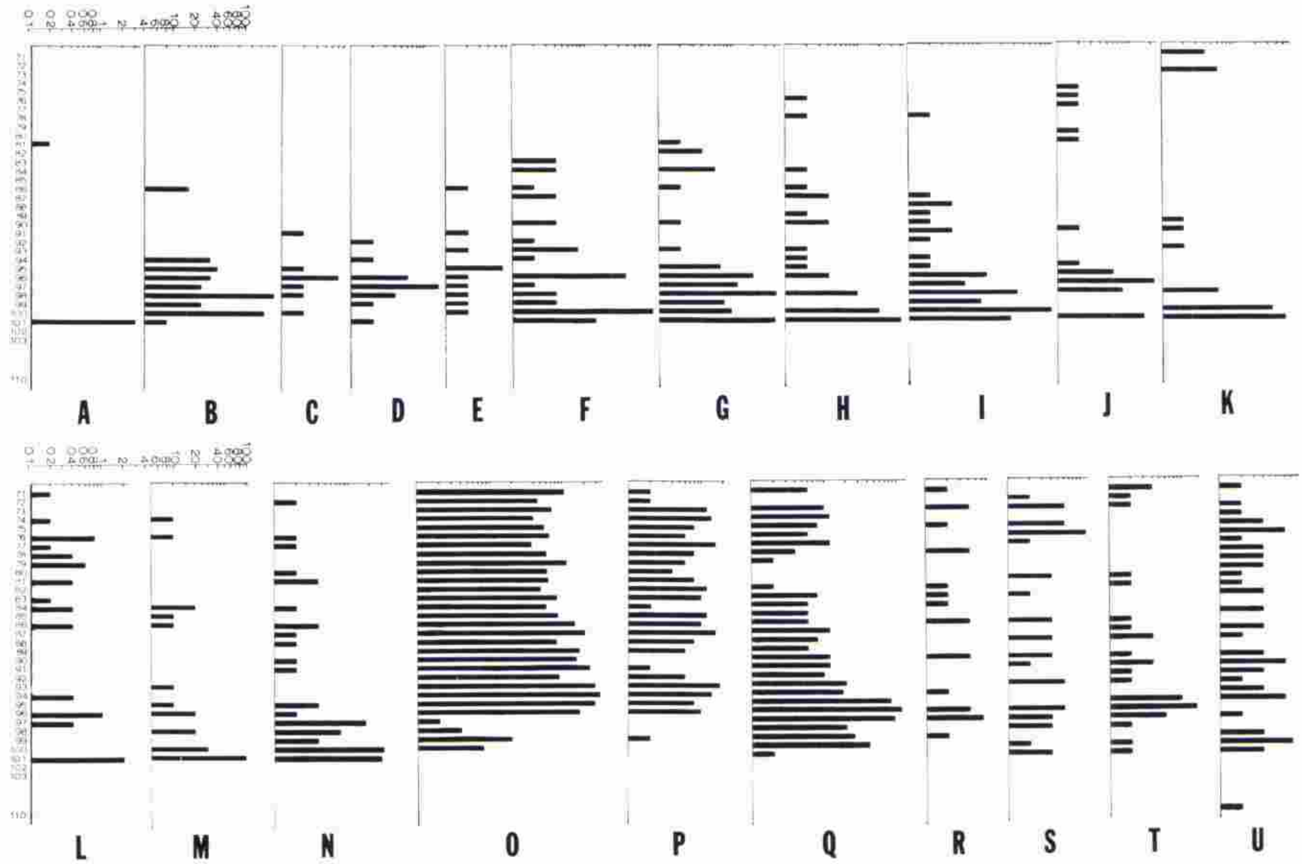


FIG. 3. Relative abundance and distribution of more abundant species. Depth intervals as in FIG. 1. A = *Navicula semenoides* Hust. B = *N. diluviana* Krasske. C = *Mastogloia smithii* var. *amphicephala* Grun. D = *Gyrosigma attenuatum* (Kütz.) Rabh. E = *Nitzschia denticula* Grun. F = *Fragilaria brevistriata* Grun. G = *F. brevistriata* var. *inflata* (Pant.) Hust. H = *F. construens* (Ehr.) Grun. I = *Cymbella parvula* Krasske. J = *Navicula scutelloides* Wm. Sm. K = *Fragilaria construens* var. *venter* (Ehr.) Grun. L = *F. construens* var. *minuta* Temp. & Per. M = *Nitzschia fonticola* Grun. N = *Achnanthes exigua* Grun. O = *Cyclotella michiganiana* Skv. P = *C. kuetzingiana* Thw. Q = *Mastogloia smithii* var. *lacustris* Grun. R = *M. grevillei* Wm. Sm. S = *Navicula seminuloides* Hust. T = *Amphora michiganensis* Stoerm. & Yang. U = *Achnanthes trinodis* (Wm. Sm.) Grun.

The plankton diatom which is most abundant in the modern flora of Douglas Lake, *Melosira granulata* (Fig. 4A), first appeared in relatively low abundance in levels 103 and 102. It declined to very low relative frequency in levels 101 and 100, then became the overall dominant element of the flora in level 99. Since that time it has undergone some fluctuations in abundance but has remained the single most abundant species in all subsequent sample levels. Species which have become established between level 99 (Fig. 4B–K) include the common mesotrophic to eutrophic plankton dominants and level 95 *M. granulata* var. *angustissima* (Fig. 4F), *Fragilaria crotonensis* (Fig. 4G), and *Cyclotella stelligera* (Fig. 4I), and a number of epiphytic species. The only member of this group which occurs below level 99 is *Cymbella microcephala*, (Fig. 4B) with a single occurrence at level 103. The only primarily epipelic taxon which was first noted in this interval was *Entomoneis ornata* (Fig. 4C). Although this species finds its primary habitat in epipelic communities, it has morphological modifications which allow it to become a successful facultative planktont and it is routinely noted in plankton collections from small lakes in the upper Great Lakes region and from the Laurentian Great Lakes (18).

Beginning at levels 95 and 94, which form the transition between the gray marl and brown laminated mud sedimentary sequences, a number of common eurytopic taxa were first noted. Included in this group are a number of modern plankton dominants (Fig. 4L–P) and 3 species (Fig. 3Q–S) which reach their greatest abundance in epipelic communities. Of this group *Navicula radiosa* (Fig. 4R) and *N. radiosa* var. *tenella* (Fig. 4S) are more abundant in plankton collections than most other members of the genus.

Only 3 species which reach significant levels of abundance make their appearance above level 99. *Nitzschia confinis* (Fig. 4T) is an apparently euplanktonic member of the genus which is abundant in certain regions of the Laurentian Great Lakes (18) but

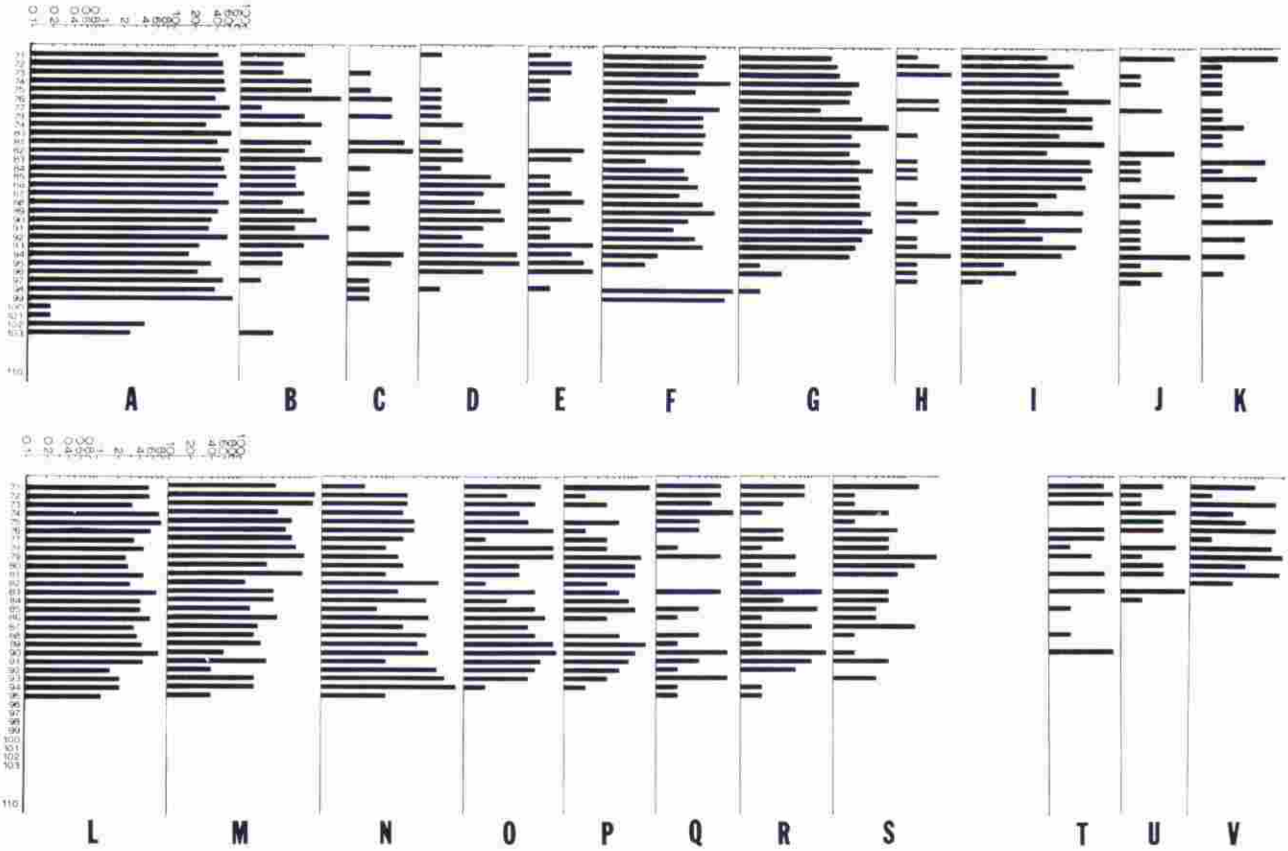


FIG. 4. Relative abundance and distribution of more abundant species. Depth intervals as in FIG. 1. A = *Melosira granulata* (Ehr.) Ralfs. B = *Cymbella microcephala* Grun. C = *Entomoneis ornata* (J. W. Bail.) Reim. D = *Cymbella delicatula* Kütz. E = *Achnanthes flexella* (Kütz.) Brun. F = *Melosira granulata* var. *angustissima* O. Müll. G = *Fragilaria crotonensis* Kitton. H = *Rhopalodia gibba* (Ehr.) O. Müll. I = *Cyclotella stelligera* (Cl. & Grun.) V. H. J = *Cymbella hustedtii* Krasske. K = *Achnanthes minutissima* Kütz. L = *Tabellaria fenestrata* (Lyngb.) Kütz. M = *Asterionella formosa* Hass. N = *Stephanodiscus niagarae* Ehr. O = *Synedra delicatissima* var. *angustissima* Grun. P = *S. ulna* var. *chaseana* Thomas. Q = *Navicula lanceolata* (Ag.) Kütz. R = *Navicula radiosa* Kütz. S = *N. radiosa* var. *tenella* (Bréb.) Grun. T = *Nitzschia confinis* Hust. U = *Surirella angusta* Kütz. V = *Stephanodiscus minutus* Grun. ex Cl. & Möll.

which has not been widely reported from inland lakes in the region. *Surirella angusta* (Fig. 4U) is a common element in epipelic communities in mesotrophic to eutrophic lakes. It is also apparently a successful facultative planktont and is an important element of winter assemblages in highly disturbed portions of the Laurentian Great Lakes (19). *Stephanodiscus minutus* (Fig. 4V) is a common winter dominant in eutrophic lakes in many parts of the world.

## CONCLUSIONS

In interpreting the results of this study, it is important to realize that the limited number of widely spaced samples available restrict resolution to the scale of major events. Andresen (2), using a short core from Douglas Lake sampled at fine intervals, has demonstrated very dramatic but relatively short time-scale changes in the diatom flora resulting from deforestation of the surrounding area. This event is not resolved at the scale available to this study, and there are undoubtedly other significant events which could be resolved from more detailed study of this section.

So far as the major events recorded in the Douglas Lake sedimentary sequence are concerned, results of the present study tend to confirm Wilson's (26) conclusions based largely on consideration of gross stratigraphy. The lowermost levels of the core—110, 103, and 102—were clearly deposited under a very large, cold water lake. Many elements of the "arenaria flora," considered by many Scandinavian workers to be indicative of deposits from proglacial lakes (1,5,6), are present. Based on the relative abundance of the taxa present, it appears that at the time level 110 was deposited the basin which now forms South Fishtail Bay of Douglas Lake was overlain by one of the high stands of the proto-great lakes. Considering the current controversy (8) regarding late pleistocene chronology in the upper Great Lakes region and the limited sample available, assignment of level 110 to a particular stage is hazardous but its deposition appears to be most likely correlated with the Algonquin stage. It is unfortunate that the rest of the samples from the red clay sequence were not preserved, since this matrial might shed some light on the current Valders controversy.

In any event, the relative dominance of euplanktonic species such as *Melosira islandica*, *Stephanodiscus alpinus*, and *S. transilvanicus* indicates primary sedimentary contribution from a planktonic community. If the material in level 110 was deposited during the Algonquin stage, the presence of a fairly large number of benthic species might be explained by the fact that the topographic high immediately to the south and west of South Fishtail Bay was not overridden by the Algonquin high stage and remained as an island which provided suitable substrates for colonization by benthic diatoms.

The marked increase in benthic species in levels 103 and 102, together with the change from fine to relatively coarse-grained sediments, indicates that these levels mark the shoaling and gradual withdrawal of proto-great lakes waters. The assemblages found in these samples are characteristic of arctic and boreal habitats, and their closest modern regional analog is found in collections from the bottom of sandy embayments in Lake Superior.

On the basis of the diatom flora present, it would appear that the direct influence of the Great Lakes had ceased before the deposition of level 101. The elements of the arenaria flora and large lake plankton dominants prominent in lower samples are absent from this level and are replaced to a large extent by species characteristic of small, shallow lakes. In some respects the flora present in levels 101 and 100 are quite similar to that recorded by Andrews (3) from the Trempealeau Valley deposit in Wisconsin.

One of the most interesting, and in many respects most puzzling, aspects of this core is the extreme change which occurred in level 99. At this time the primarily benthic flora previously present was almost entirely replaced by a planktonic flora dominated by *Melosira granulata* and *M. granulata* var. *agustissima*. Andresen's (2) work has shown large increases in these species to be associated with deforestation and, presumably, increased nutrient loading to Douglas Lake. Both are also primarily warm water species and it is tempting to postulate some major climatic event at this time. Pollen records from the same core (27) however tend to argue against this assumption, since the spruce-pine transition begins at level 103 and ends at level 99. It is also possible that the levels 101 and 100, in which the flora is dominated by benthic species, represent a low stand of Douglas Lake at least roughly contemporaneous with the Lake Stanley-Lake Chippewa low stand of the Laurentian Great Lakes. Level 99 then could represent a subsequent high stand of Douglas Lake contemporaneous with the Nipissing high stand of the Laurentian Great Lakes. The waters of Lake Nipissing apparently approached but did not occupy the Douglas Lake basin. It is possible, however, that the water level of Douglas Lake increased reflooding part of the basin and provided a more ideal habitat for euplanktonic, eutrophic species such as *M. granulata*.

Whatever the nature of the events recorded in level 99, it is apparent that conditions reached a new equilibrium during the period represented by deposition of levels 98, 97, and 96. Although *Melosira granulata* remained abundant, benthic species regained greater relative abundance and certain eurytopic, euplanktonic species such as *Cyclotella stelligera* and *Fragilaria crotonensis* reached detectable abundance. On the basis of the slight floristic shift during this period, it appears that the lake remained in approximately its present physical configuration during this time and gradually became more eutrophic.

Level 95, which lies at the boundary between the gray marl and laminated brown mud sediment sequences, also is a rather remarkable floristic boundary. A number of the eurytopic plankton dominants which are also present in the modern flora make their appearance at or immediately adjacent to this stratum. From the results of this study it appears that Douglas Lake stabilized in something very near its present trophic status at that time and has remained relatively little changed since. Although this conclusion runs counter to that of Bazin and Saunders (4), it appears plausible that this boundary marks the beginning of oxygen depletion in the bottom waters of South Fishtail Bay and that the changes in species composition associated with this level are the result of changes in mineral cycling within the system brought about by this event. Although some degree of further eutrophication may be inferred from increases in the abundance of species such as *Stephanodiscus minutus* and *Surirella angusta* at higher levels in the core, it is apparent that Douglas Lake is a remarkably resilient and stable system and that the effects of modern events have not had the profound influence on the system that previous climatic and geological events have. This conclusion is reinforced by Andresen's (2) study which demonstrated the ability of the Douglas system to return to nearly its previous status following a major ecological insult. It is quite probable that other episodes of this type would be discovered by more detailed sampling and analysis of the section whose broad general trends are presented here.

I thank the Academy of Natural Sciences, Philadelphia and particularly Curator Dr. C. W. Reimer for loan of the material used in this study. Mrs. J. J. Yang provided able assistance in the identification and analysis work. I am indebted to several colleagues for valuable insights regarding this problem and would particularly like to thank Dr. N. A. Andresen for many valuable discussions and access to his results on a more detailed study of the post-settlement segment of a core from the same locality.

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# OBSERVATIONS ON CELL DEVELOPMENT IN *CHLAMYDOMONAS SEGNIS* (CHLOROPHYCEAE) AT LOW AND HIGH CARBON DIOXIDE TENSION[1]

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ABSTRACT

*Some cell cycle events were compared in* Chlamydomonas segnis *Ettl during its development in synchronous cultures (12:12 LD) supplied with air and air enriched with 5%* $CO_2$. *In cultures bubbled with air, growth resulted in production of 2 relatively small zoospores. In cultures provided with 5%* $CO_2$, *4 large zoospores were formed but not released in darkness unless the cultures were bubbled with* $CO_2$*-free air and/or exposed to light. Respiration in zoospores was inhibited by high* $CO_2$ *tension. In cultures maintained under continuous illumination for one cell cycle, provision of 5%* $CO_2$ *led to enhanced growth, a relatively long S-phase and a 4 h delay of the second cell division. In such cultures, the DNA content of parental cells (12 h L) was insufficient to support two cell divisions. The RNA/DNA ratio of the resulting*

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