Gepp, A. & Gepp, E. S. 1905. Antarctic algae. *J. Bot.* 43:105–9.
———. 1906. A new species of *Lessonia*. J. Bot. 44:425–6.
———. 1912. Marine algae of the Scottish National Antarctic Expedition. *Scott. Natl. Antarct. Exped., Rep. Sci. Results* 3:71–83.
Lucas, A. H. S. 1919. The algae of Commonwealth Bay. *Australasian Antarct. Exped. 1911–14, Sci. Rep.* Ser. C, 7(2), 18 pp.
Moe, R. L. & Silva, P. C. 1976. Taxonomic position of the Antarctic brown algae *Himantothallus, Phaeoglossum,* and *Phyllogigas*. *J. Phycol.* 12(suppl.): 27–8.
———. 1977a. Antarctic marine flora: uniquely devoid of kelps. *Science* 196: 1206–8.
———. 1977b. Sporangia in the brown algal genus *Desmarestia* with special reference to Antarctic *D. ligulata*. *Bull. Jap. Soc. Phycol.* 25(suppl.): 159–67.
Neushul, M. 1963. Reproductive morphology of Antarctic kelps. *Bot. Mar.* 5: 19–24.
Reinsch, P. F. 1890. Zur Meeresalgenflora von Süd-Georgien. *Internatl. Polarforsch. 1882–1883, Dtsch. Exped.* 2:366–449.
Schmitz, K. & Lobban, C. S. 1976. A survey of translocation in Laminariales (Phaeophyceae). *Mar. Biol.* 36:207–16.
Skottsberg, C. 1907. Zur Kenntnis der subantarktischen und antarktischen Meeresalgen. I. Phaeophyceen. *Schwed. Südpolar-Exped. 1901–1903, Wiss. Ergebn.* 4(6), 172 pp.
——— 1941. Communities of marine algae in subantarctic and antarctic waters. *K. Svenska Vet. Akad. Handl.* ser. 3 [i.e. 5], 19(4), 92 pp.
Skottsberg, C. & Neushul, M. 1960. *Phyllogigas* and *Himantothallus*. Antarctic Phaeophyceae. *Bot. Mar.* 2:164–73.
Zinova, A. D. 1958. [Composition and character of the algal flora near the shores of the Antarctic continent and in the vicinity of the Kerguelen and Macquarie islands.] (In Russian.) *Inform. Byull. Soviet Antarkt. Eksped.* 3:47–9.
———. 1959. [On two brown algae from the Antarctic—*Phyllogigas* and *Himantothallus*.] (In Russian.) *Bot. Zhurn.* 44: 372–9.

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# QUANTITATIVE DIFFERENCES BETWEEN BENTHIC ALGAL COMMUNITIES ALONG A DEPTH GRADIENT IN LAKE MICHIGAN[1,2]

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ABSTRACT

*This study analyzes the impact of conditions associated with depth upon benthic algal communities in Lake Michigan. Diatom abundance was greater at 9.1 and 14.6 m depths than 6.5, 22.6 and 27.4 m. Shallow (6.5 m), mid-depth (9.1 and 14.6 m) and deep (22.6 and 27.4 m) zones were distinguishable on the basis of community composition, structure and abundance. Dominance of benthic species, high diversity and low abundance in shallow communities probably resulted from substantial substrate disturbance by wave action in this productive zone. Dominance of benthic species, high diversity and high abundance characterized mid-depth communities where less wave disturbance enabled algal accumulation. Preponderance of living planktonic taxa, low diversity and low abundance delineated deep communities where planktonic algae accumulated and low light levels reduced growth of benthic species.*

*Key index words: algal methods; depth effects; diatoms; epipsammic algae; Lake Michigan; population abundance*

Benthic microscopic algae are commonly neglected in phycological investigations of lentic habitats. Substantial spatial heterogeneity has been observed in lentic benthic algal communities. Determination of factors causing this heterogeneity will aid in establishing the contribution of benthic algae to the energy budget of the total ecosystem and their impact on the distribution of organisms in other trophic levels.

This study describes species composition and population abundance changes in the living component of naturally occurring benthic algal communities resulting from different physicochemical conditions along a depth gradient. Qualitative documentation of vertical distributions of algal populations in marine environments has been made by Aleem (1950), Simonsen (1962) and Edsbagge (1965). The impact of depth upon epilithic standing crop and productivity on plexiglass or glass slides has been quantified in a high mountain lake (Maciolek and Kennedy 1964), a small southeastern Michigan lake (Newcombe 1950), in Czechoslovakian artificial reservoirs (Sládečková 1966) and in a lake in northwestern Ontario (Stockner and Armstrong 1971). Neal et al. (1967) monitored algal community development upon polyethylene tape at various depths in a waste water impoundment. Meschkat (1934), Rehbronn (1937) and Szczepańska (1968) discussed the dynamics of freshwater littoral benthic algal assemblages. Round (1961) documented the seasonal abundance of epipelic algae at various depths in two

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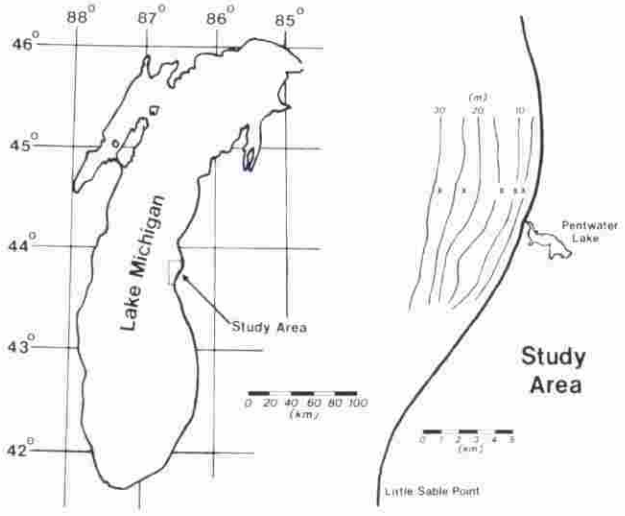


FIG. 1. Sampling locations (×) on the depth gradient transect in the Lake Michigan study area.

lakes of the English Lake District. Fox et al. (1969) described epilithic communities at shallow depths in Lake Superior.

An important part of our study was the development of a technique for examining live diatoms in a mounting medium of high refractive index. Distinguishing algae that were living (containing protoplasm) at the time of sampling from those that were dead is essential for precisely characterizing a community. Residual frustules of dead diatoms come from many spatially and temporally divergent sources and if abundant, mask the true assemblage character (Pryfogle and Lowe 1979).

## MATERIALS AND METHODS

*Sample Collection and Preparation.* The central portion of the eastern shore of Lake Michigan provides an environment with substantial light penetration and uniform substrate to a considerable depth that enabled characterization of benthic algal community changes as depth varied. A 5 km sampling transect perpendicular to the shore one mile north of Pentwater was chosen (Fig. 1). It was positioned in the mid-lake coastal region between southern and northern circulation gyres.

Duplicate samples were collected July 26, 1978 by divers at 5 depths: 6.5, 9.1, 14.6, 22.6 and 27.4 m. The samples were 8 cm deep cores from the sand substrate. The coring apparatus was 67 mm I.D. PVC tubing. A line was scribed 8 cm from the bottom of the tubes so that divers could assure a uniform core length. Rubber stoppers were placed in each end to seal the core after collection. Two holes near the top, just below the stopper, allowed for release of pressure when the second stopper was placed in the tube bottom. Tubes were kept vertical to prevent loss of any sample. The samples were placed in Mason jars and immediately fixed with paraformaldehyde and subsequently with glutaraldehyde (Lazinsky and Sicko-Goad 1979).

Laboratory procedures were designed to quantify populations of live algae that were found on these substrates. Silt and sand particles obscuring the observation of algae during counting made removal of the algae from the silt and sand necessary. Benthic algae were removed from the sand by vigorously swirling an added 100 mL of distilled water and the 280 mL of sand in a 2L beaker with a metal spatula. Rinsing the sand from sides of the beaker after swirling allowed adequate time for settling of the coarser particles. The algal suspension was immediately decanted into a beaker. This three step procedure was repeated eight times. The abundance of algae in the decanted suspension decreased sharply after the third decantation. No live algae were observed in the processed sand upon completion of the eight rinses.

FIG. 2. Vapor substitution chamber used to prepare algae for mounting in a toluene based medium.

Algae in the suspension were concentrated to ca. 50 mL by settling. A volume to 10 ppm acid fuchsin solution equal to the volume of the highly concentrated algal suspension was added to provide a general cytoplasmic stain. Staining was necessary because solvents in subsequent dehydration steps extracted chlorophyll, making it difficult to distinguish living from dead cells. Cells were stained for 6 h. Excess stain was removed by washing and decanting.

In order to achieve good optical quality it is necessary to mount the algae on a cover glass in a medium with a high refractive index. Since most desirable mounting media are toluene soluble, this necessitated dehydration. To prevent possible loss of material during processing, dehydration was accomplished by vapor substitution (Sanford et al. 1969).

The concentrated, stained, algal suspension was diluted to an appropriate cell density and 1.0 mL of the suspension was evenly distributed on a 484 mm² cover glass positioned on supports in the vapor substitution chamber. This chamber is a modification of the design used by Meyer (1965). It consists of a metal cake pan covered by a pane of glass with stopcock grease applied to the pan lip to provide an airtight seal. Corks topped by metal washers, to provide a level surface, are used as support pedestals. The assembly is attached to a wooden base to provide stability. Drainage holes drilled through the foundation and the bottom of the pan allow removal of excess solvents. The apparatus is shown in Fig. 2.

After placement of the 1 mL of algal suspension on the coverslip, the chamber was left uncovered to allow evaporation of most, but not all, of the water of the suspension. Only a film of water remained. This allowed a greater dilution by ethyl alcohol which was then placed in dishes in the chamber. The chamber was covered immediately. After 3 days the dishes of alcohol were removed and excess alcohol mopped from accessibile areas of the chamber bottom. The chamber again was left uncovered to allow evaporation of most, but not all, of the alcohol on the coverslips. Dishes of toluene were then placed in and the cover placed on the chamber for 3 days.

Coverslips were then mounted on slides in a high refractive index, toluene soluble mounting medium such as HYRAX or CUMAR-9. To prevent dessication and plasmolysis of algal protoplasm, a film of toluene was left on the coverslips. Material on the coverslips was then inverted into mounting medium on slides. Low heat was applied to the slides for 2 h to volatilize the solvent.

It proved critical that each solvent be replaced as completely as possible by subsequent solvents used in the vapor chamber

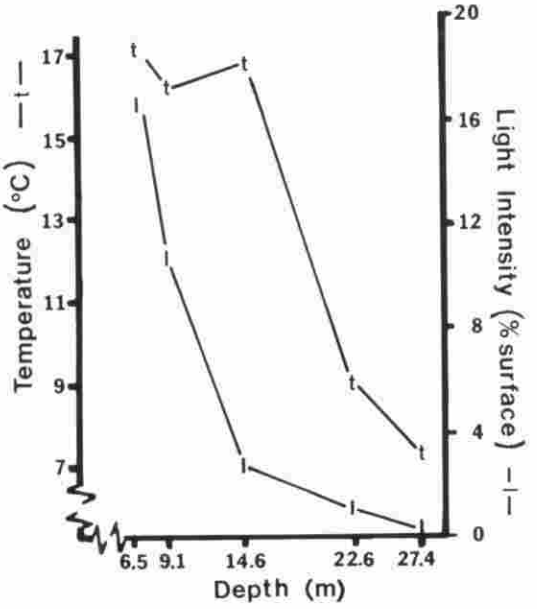


FIG. 3. Temperature (t) and percent of surface incident light intensity (l) at the sampled depths.

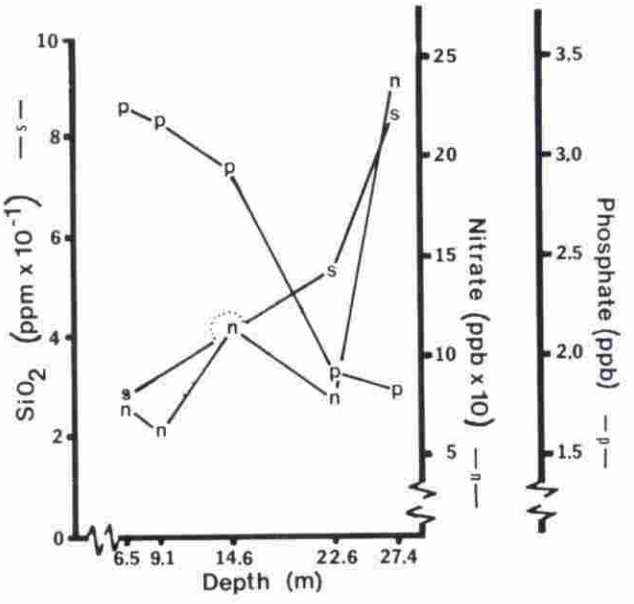


FIG. 4. Silicate (s), nitrate (n) and phosphate (p) concentrations at the sampled depths.

processing. Incomplete replacement prevented toluene, and then HYRAX, from penetrating the algal cells.

Two transects per slide and two slides per sample were counted from each of the five depth locations to check for error caused by sample preparation. Transect enumeration totals averaged about 250 organisms, 1000 organisms per sample. Only organisms that were alive at the time of collection were counted using a Leitz Ortholux microscope with an oil immersion objective and condenser system of 1.32 numerical aperature, providing 1200× magnification.

Water temperature was measured by divers at the substrate surface. Acid-rinsed polyethylene bottles were filled with water from within 20 cm of the substrate surface at each depth for subsequent chemical analyses. Dissolved reactive silica and nitrate were analyzed with the Technicon Auto Analyzer II according to Davis and Simmons (1979). Water transparency, measured with a white secchi disc, was converted to percent of surface incident light reaching the substrate with the calculations of Ladewski and Stoermer (1973).

*Statistical Methods.* For statistical analyses, slide enumerations were called subsample communities. The average of two slide enumerations from one sample was designated as a sample community. The average of the two sample communities of a location was designated as a location community. Analysis of variance and Tukey pairwise comparisons (Scheffé 1959) were used to identify differences in community population abundance between depths.

Species diversity (Shannon and Weaver 1949) was calculated averaging subsample community values of each sample. Some values were exceptionally low because of large abundances of extremely variable and colonial blue-green algae. These values were eliminated from the averaging.

Distributions of the most abundant diatom taxa were characterized by polynomial regression analyses (Neter and Wasserman 1974) that provided descriptive functions of their distributions. Population abundances were normalized by subtracting the minimum and dividing by the range, so as to provide coefficients that were comparable between taxa. The equation utilized is detailed in Table 1 below.

Cluster analysis using euclidian distances and a centroid algorithm (Sneath and Sokal 1973) was employed to group the sample communities and provide quantitative estimates of dissimilarity between communities. Principle components analysis was used to investigate the major population differences among sample communities. The 46 more common taxa with low variances between replicate samples were chosen as characteristic components of the assemblages. The abundances of these taxa were used as variables in both analyses as standardized values. The division of abundance by its standard deviation more heavily weights rare taxa because of their disproportionally lower variances. Unstandardized abundances weight common taxa more heavily. Analysis with both data forms provides valuable information. Abundant taxa are important in characterizing the community because of their numerical dominance, presumed to result from greater stimulation of production of specific populations by certain environmental conditions. However, some rare taxa may have inherently lower biotic potentials and changes of the same proportion as those observed of common taxa may be just as significant in analysis of community dynamics.

## RESULTS

*Physicochemical Conditions of Study Area.* Changes in temperature (Fig. 3) indicated the sampled habitats extended from the epilimnion into the metalimnion of Lake Michigan. Silica values increased from about 0.2 ppm at 6.5 m to greater than 0.8 ppm at 27.4 m (Fig. 4). Temperature decreased from 17 to 6° C as depth increased, as did phosphate concentrations which fell from >3.0 to <2.0 ppb. Nitrate concentrations were highest at the greatest depth, 242 ppb, and were substantially lower at the 4 shallower depths, averaging about 100 ppb. Percent of surface irradiance reaching the substrate ranged from 17% at 6.5 m to 1% at 22.6 m and 0.4% at 27.4 m.

Chemical and physical conditions measured at the time of sampling are representative of average July measurements at the depths sampled along this region of the Lake Michigan coast (Great Lakes Re-

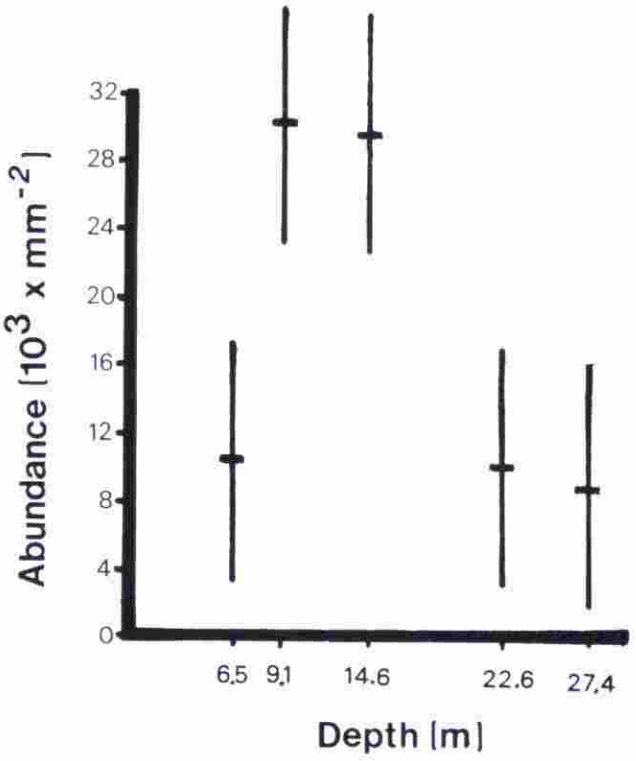


FIG. 5. Diatom abundance (±95% C.I.) at the various sampled depths.

search Division, unpublished data). Any inferences concerning a causal relationship between the conditions measured and floristic development should be approached cautiously because of the extreme variability of this habitat. The region is subject to summer upwellings (Strong et al. 1974) so that all communities are periodically subjected to the same nutrient and temperature conditions. The most consistent differences associated with depth are light level and exposure to the mechanical effects of water motion.

*Community Analysis.* There was generally a very diverse algal assemblage with 255 taxa representing 36 genera from the following divisions: Bacillariophyta, Cyanophyta, Chlorophyta, Chrysophyta, Cryptophyta, and Pyrrophyta. The benthic algal communities studied were dominated by diatoms.

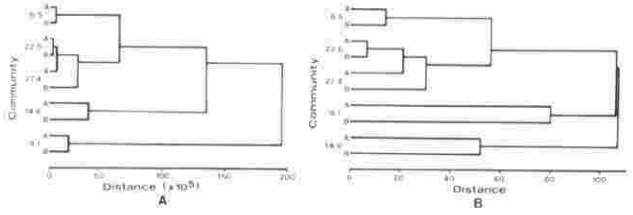


FIG. 6. Cluster analysis of the ten sample communities from five depths using the 46 more common taxa abundances as characters, euclidian distances and a centroid algorithm. A. Unstandardized abundances. B. Standardized abundances.

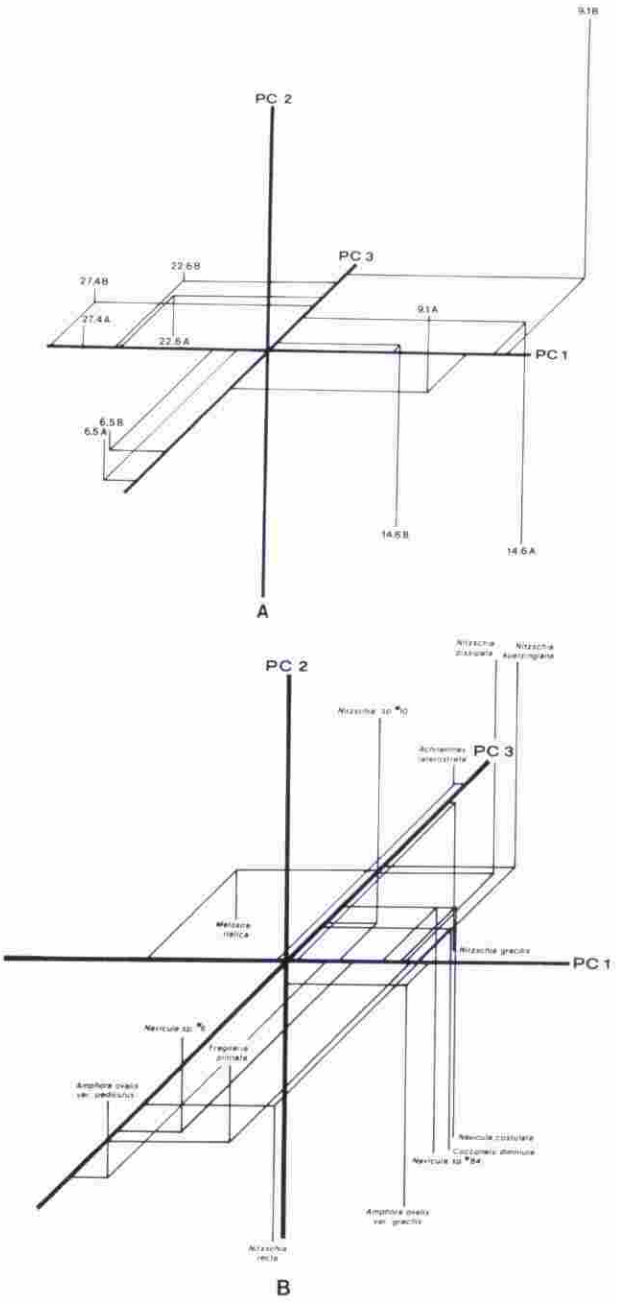


FIG. 7. Principle components analysis results of standardized population abundances and ten sample communities from five depths (2 replicates each). A. Scores of the communities plotted along the first three principle components axes. B. Loadings of important taxa plotted along the first three principle components axes.

Substantial numbers, but low biovolumes of blue-green algae were also present. Diatom abundance averaged $1.80 \times 10^4$ cells/mm² and was statistically significantly greater (ANOVA, Tukey allowances; $P < 0.05$) for the two mid-depth locations at 9.1 and 14.6 m than at 6.1, 22.6 and 27.4 m (Fig. 5). Polynomial regression defined a significant ($P < 0.05$) negative relationship between species diversity and

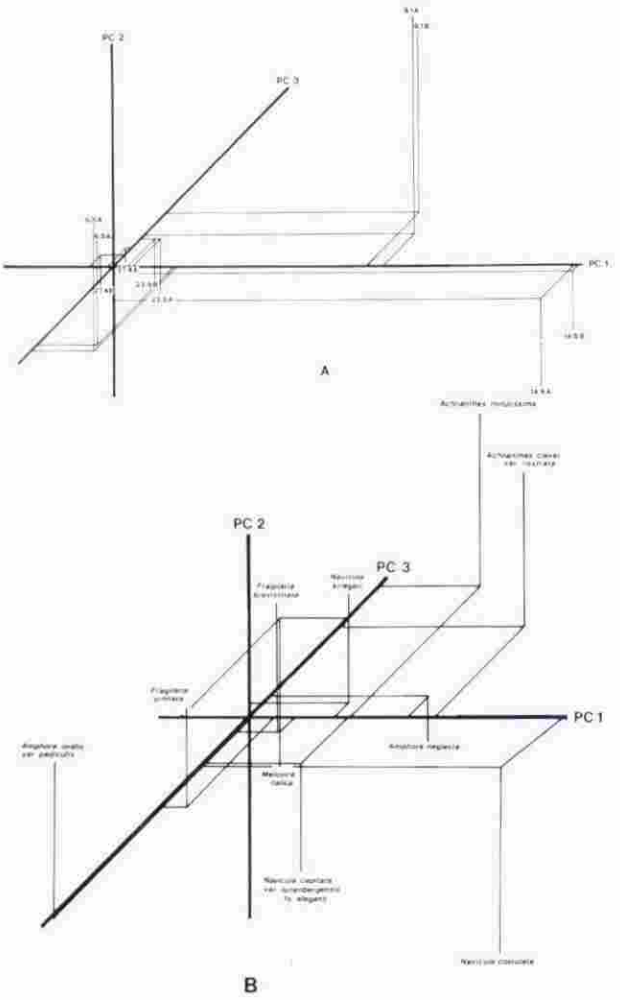


FIG. 8. Principle components analysis results of unstandardized population abundances and ten sample communities from five depths (2 replicates each). A. Scores of the communities plotted along the first three principle components axes. B. Loadings of important taxa plotted along the first three principle components axes.

depth. Species diversity decreased from about 3.4 at 6.5 m to about 2.8 at 27.4 m.

Cluster analyses of the sample communities at the first levels grouped replicate sample communities (Fig. 6A, B), except at the two deepwater locations. All four of the communities at the two deepwater locations were very similar. Composition of the location assemblages was substantially different and singly joined the main cluster which started as the two deepwater locations. The 6.5 m communities linked first, followed by 14.6 or 9.1 m communities, depending upon whether standardized or unstandardized population abundance values were used.

The even loadings of standardized taxa abundances on the first principal components axis (PCA) indicate that total community abundance is the important factor along this axis which separates the 6.5 m and two deepest location communities from

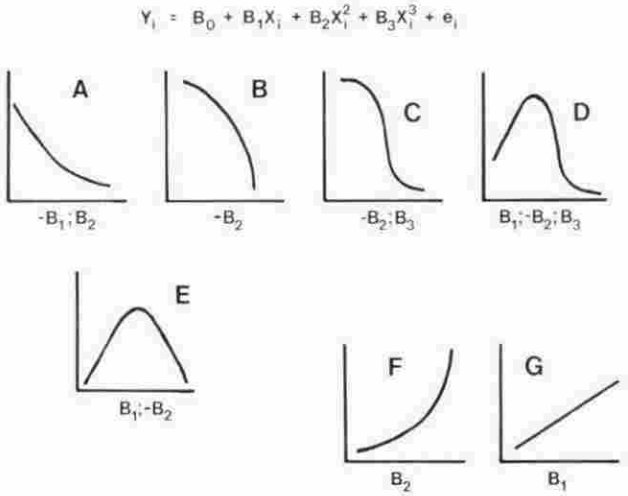


FIG. 9. Model and seven basic curves of population distribution defined by the significance of three polynomial regression coefficients associated with three levels of the independent variable depth and the dependent variable population abundance. Abundance, $Y_{ij}$, is plotted along the ordinate and depth, $X_i$, along the abscissa. Significant coefficients and their sign are indicated below each curve.

the two mid-depth location communities (Fig. 7A, B). The two mid-depth location assemblages separated on the second PCA with negative loadings of several species of *Navicula, Cocconeis diminuta* Pant. and a variety of *Amphora ovalis* that produced negative scores for the replicate sample communities from 14.6 m. Positive loadings of several species of *Nitzschia* produced more positive scores for the communities from 9.1 m. On the third PCA with standardized abundances, negative scores of the 6.5 m

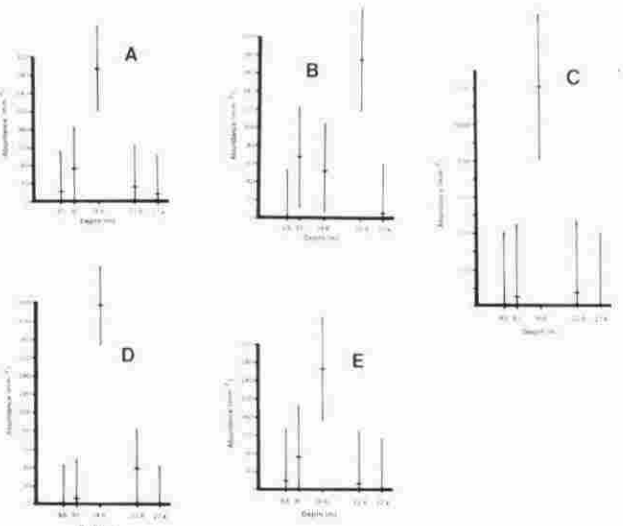


FIG. 10. Population abundances (±95% C.I.; Tukey allowances) at five depths. A. *Cocconeis diminuta* Pant.; B. *Achnanathes laterostrata* Hust.; C. *Navicula capitata* var. *lunenbergensis* fo. *elegans* Østr.; D. *Navicula* sp. #84; E. *Stauroneis acutiuscula* M. Perag. et Hérib.

TABLE 1. *Descriptions of population abundance distributions of dominant taxa utilizing the following polynomial regression model:*

$$Y_{ij} = \beta_0 + \beta_1 X_i + \beta_2 X_i^2 + \beta_3 X_i^3 + e_{ij}$$

*Where $Y_{ij}$ is the population abundance (cells/mm², not normalized) of the $j^{th}$ replicate sample community of the $i^{th}$ depth, $\beta_0$–$\beta_3$ are regression coefficients, $X_i$ is the $i^{th}$ depth and $e_{ij}$ is the residual of the $ij^{th}$ population abundance. Significance ($\alpha$) and coefficient of determination ($r^2$) of the regression equation are also listed. The taxa are listed in order of most distinct specificity for a given zone as defined by the magnitude of the regression coefficient in the model of normalized population abundances.*

| Zone of greatest abundance<br>Taxon | $\alpha$ | $r^2$ | Regression coefficients<br>0 | 1 | 2 | 3 |
|---|---|---|---|---|---|---|
| Shallow zone | | | | | | |
| *Amphora ovalis* var. *pediculatus* (Kütz.) V.H. | 0.003 | 0.82 | 2,995.3 | −259.22 | 5.7266 | |
| *Fragilaria pinnata* Ehr. | 0.000 | 0.92 | 924.24 | | −3.7946 | 0.093273 |
| *Amphora ovalis* var. ? | 0.008 | 0.60 | 93.77 | | −0.11194 | |
| *Achnanthes lapponica* (Hust.) Hust. | 0.009 | 0.60 | 183.81 | | −0.22708 | |
| *Navicula submuralis* Hust. | 0.008 | 0.61 | 436.40 | | −0.52762 | |
| *Navicula oppugnata* Hust. | 0.027 | 0.48 | 102.38 | | −0.11903 | |
| *Fragilaria brevistriata* Grun. | 0.012 | 0.57 | 737.96 | | −0.79119 | |
| Mid-depth zone | | | | | | |
| *Amphora perpusilla* (Grun.) Grun. | 0.002 | 0.91 | −20,877 | 4,939.9 | −278.02 | 4.5352 |
| *Navicula kriegeri* Krasske | 0.031 | 0.75 | −1,664.0 | 386.02 | −21.707 | 0.35506 |
| *Achnanthes clevei* var. *rostrata* Hust. | 0.001 | 0.93 | −6,390.2 | 1,607.9 | −93.309 | 1.5549 |
| *Navicula menisculus* Schum. | 0.004 | 0.88 | −1,799.7 | 425.44 | −23.825 | 0.38622 |
| *Navicula radiosa* var. *tenella* (Bréb.) Cl. and Moll. | 0.016 | 0.80 | −824.91 | 193.00 | −10.772 | 0.17477 |
| *Nitzschia hantzschiana* Rabh. | 0.005 | 0.87 | −527.71 | 132.37 | −7.6847 | 0.12800 |
| *Amphora neglecta* Stoerm. and Yang | 0.004 | 0.88 | −5,596.1 | 1,246.4 | −67.299 | 1.0620 |
| *Achnanthes minutissima* Kütz. | 0.046 | 0.71 | | 1,027.0 | −61.237 | 1.0432 |
| *Amphora* sp. #14 | 0.021 | 0.78 | −1,425.8 | 331.51 | −18.041 | 0.28479 |
| *Navicula costulata* Cl. and Grun. | 0.017 | 0.80 | −10,297. | 2,257.4 | −119.29 | 1.8421 |
| *Achnanthes clevei* var. *clevei* Grun. | 0.028 | 0.76 | −2,131.5 | 537.75 | −31.257 | 0.52276 |
| *Cocconeis* sp. #2 | 0.009 | 0.84 | −1,813.4 | 466.09 | −27.337 | 0.45901 |
| *Navicula pupula* Kütz. | 0.040 | 0.60 | | 56.047 | −1.5878 | |
| Deep zone | | | | | | |
| *Nitzschia lauenbergiana* Hust. | 0.002 | 0.73 | | | 0.0879 | |
| *Melosira italica* subsp. *subarctica* O. Müll. | 0.002 | 0.71 | | | 1.3975 | |
| *Stephanodiscus* sp. #10 | 0.006 | 0.64 | | | 3.3580 | |
| *Synedra ostenfeldii* (Krieger) Cl.-Euler | 0.003 | 0.70 | 79.885 | | 0.23876 | |
| *Stephanodiscus minutus* Grun. | 0.018 | 0.52 | | | 0.58399 | |
| *Synedra filiformis* Grun. | 0.009 | 0.60 | | 9.0840 | | |

communities isolated it from other assemblages and strongest negative loadings were for *Amphora ovalis* var. *pediculus* (Kütz.) V.H., *Navicula* sp. #6 and *Fragilaria pinnata* Ehr.

Using unstandardized taxa abundances, principle components analysis indicated a first axis most positively loaded by *Navicula costulata* Cl. and Grun. and *Achnanthes clevei* var. *rostrata* Hust., which produced high scores for the two mid-depth communities (Fig. 8A, B). The second PCA separated communities of the two shallowest from the three deepest locations with positive scores for shallower communities correlating most strongly with *Achnanthes clevei* var. *rostrata* and *A. minutissima* Kütz. and *Amphora ovalis* var. *pediculus*. *Melosira italica* (Ehr.) Kütz. and *Navicula costulata* were negatively loaded on the second PCA which defined negative scores for the three deeper location assemblages. The third PCA again isolated the 6.5 m communities by loadings of *Amphora ovalis* var. *pediculus* and *Fragilaria pinnata*.

*Population Analysis.* Stepwise backward regression of the polynomial model selected seven basic curves, defined by the significance of coefficients of levels of depths, that described the various distributions of algal populations along the depth gradient (Fig. 9). The first five curves peaked in the three shallower depth locations (Fig. 9A–E). Abundances of mono- and biraphid, and a few araphid pennate diatom populations, generally characteristic of benthic habitats, significantly ($P < 0.05$) fit the first five curves (Table 1). Three of the first five curves had peaks at the shallowest station, whereas the other two peaked at the mid-depth locations. The remaining two curves (Fig. 9F, G) showed increasing abundances as depth increased and were significant ($P < 0.05$) for araphid pennate and centric diatom taxa, which are generally characterized as planctonic (Table 1).

Several taxa were very restricted in distribution, had no significant regression line, but did demonstrate significantly greater (ANOVA, Tukey allowances; $P < 0.05$) abundances at a single depth (Fig. 10). *Cocconeis diminuta*, *Navicula capitata* var. *lunenbergensis* fo. *elegans* Ostr., *Navicula* sp. #84, and *Stauroneis acutiuscula* M. Perag. et Herib. were most

abundant at 14.6 m. A variety of *Achnanthes laterostrata* Hust. was uniquely most abundant at 22.6 m.

Four abundant taxa, two benthic and one planctonic *Fragilaria*, and a "nearshore" planctonic *Stephanodiscus*, showed no distinguishable distributions.

## DISCUSSION

The distributions of the benthic algae along the depth gradient studied were extremely varied. Some populations remained relatively unchanged, whereas others were restricted to a single depth. The selectivity of taxa for specific depths has been observed by earlier investigators (Aleem 1950, Round 1961, Simonsen 1962, Edsbagge 1965, Fox et al. 1969, Stockner and Armstrong 1971). Three zones were recognized along the depth gradient. These zones were not discrete, but were part of a continuum. Their definition facilitated interpretation and communication of population dynamics of the benthic algal communities. The shallow zone corresponded to the 6.5 m location and was characterized by lower diatom abundance, higher species diversity and algae generally classified as those from benthic habitats. Higher light intensity, temperature and phosphorus concentrations with low nitrate and silica concentrations indicate a habitat of high productivity. Smaller standing crop abundances were probably the result of wave action disturbing the substrate and preventing accumulation (Fox et al. 1969, Stockner and Armstrong 1971). Indications of substrate disturbance by substantial benthic algal contamination of shallow-water planktonic communities have been regularly observed in samples analyzed in our laboratory. Bodoy and Plante-Cuny (1980) attributed lower benthic algal proportion of total littoral algal productivity to substrate disturbance.

The mid-depth zone included the 9.1 and 14.6 m depth assemblages and was characterized by large diatom abundances as a result of accumulation and high productivity. Minimal wave disturbance enabled accumulation of algae, and adequate light and nutrients and higher temperatures encouraged productivity in this regime.

There were, however, substantial differences in species composition of the communities of the two depths within the mid-depth zone. Greater abundances of epipsammic *Achnanthes* at 9.1 m than 14.6 m implied greater wave disturbance of the substrate at the shallower mid-depth zone depth. Substrate disturbance at 9.1 m was probably less than at 6.5 m because of the much lower total abundances at 6.5 m. The decreased abundances of epipsammic *Achnanthes* taxa at the deeper locations were probably caused by decreased grain size of the substrate. The finer substrate texture of deeper locations would have altered community composition from taxa competitive in epipsammic habitats to those adapted to epipelic habitats.

The deep zone at 22.6 and 27.4 m was characterized by low abundances, low species diversity and uniform species composition. Low light, less than or equal to 1% of surface intensities, probably reduced productivity. Viable standing crop was dominated by planctonic species of *Melosira* spp., *Stephanodiscus* spp. and *Synedra* spp. deposited from the longer water column in the deeper water.

Species composition differences as a function of depth probably resulted from the following interacting factors: wave disturbance of the substrate, the quantity and quality of light reaching the substrate, and sedimentation altering the physical character of the substrate (epipsammic vs. epipelic) and associated physicochemical conditions. The ability of small *Fragilaria*, *Achnanthes* and *Amphora* taxa to inhabit the crevices of sand grains enabled maintenance of these populations at depths of substrate disturbance by reducing their susceptibility to abrasion. Taxa more capable of movement through the finer textured substrate replaced the epipsammic taxa mentioned above at deeper locations.

The effects of nutrient and temperature conditions are more difficult to evaluate. It is clear that the degree of variability decreases with depth, and the floristic changes observed may reflect the ability of particular organisms to deal with environmental variation. In the case of chemical parameters, this problem is compounded by the fact that the actual growth habitat of the communities studied may be modified by chemical fluxes from the sediments which are extremely difficult to quantify by conventional measurement techniques. The actual variation in chemical conditions experienced by the organisms sampled may actually be less than indicated by our chemical measurements which leads us to emphasize the importance of light and mechanical disturbance in regulating algal growth in these communities.

Attenuation of light and greater transmittance of shorter wavelengths in deeper water may have enhanced the competitive abilities of selected taxa in various light regimes. More mobile taxa capable of heterotrophic nutrition would have gained a competitive advantage in deeper habitats of greater sediment accumulation. Abundance peaks of most of the *Navicula* and *Nitzschia* taxa in the mid-depth zone supported the latter argument. Admiraal and Peletier (1979) demonstrated *Nitzschia* and *Navicula* taxa growth rates were supplemented by heterotrophic growth at low light levels. We measured neither the spectral quality of light at various depths nor efficiencies of different taxa to utilize selected intensities and wavelengths of light. Likewise organic content of the substrate and heterotropic abilities of different taxa were not studied. These mechanisms for determining population abundance and community composition should be subjects for further research.

In reference to community standing crop, substrate disturbance apparently reduced benthic algal

abundance at shallower sites and low light levels at deep locations inhibited productivity. The mid-depth communities had the largest standing crops which probably resulted from minimal wave disturbance and adequate light.

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Admiraal, W. & Peletier, H. 1979. Influence of organic compounds and light limitation on the growth rate of estuarine benthic diatoms. *Br. Phycol. J.* 14:197–206.

Aleem, A. A. 1950. Distribution and ecology of British marine littoral diatoms. *J. Ecol.* 38(1):75–106.

Bodoy, A. & Plante-Cuny, M.-R. 1980. Évaluation simultanée des biomasses et productions primaires phytoplanctonique et microphytobenthique en milieu côtier. *C.R. Acad. Sci. Paris* 290:667–70.

Davis, C. O. & Simmons, M. S. 1979. Water chemistry and phytoplankton field and laboratory procedures. Univ. Michigan, Great Lakes Res. Div. Spec. Rep. No. 70.

Edsbagge, H. 1965. Vertical distribution of diatoms. *Sv. Bot. Tidskr.* 59(4):463–8.

Fox, J. L., Odlaug, T. O. & Olson, T. A. 1969. The ecology of periphyton in western Lake Superior. Part I—Taxonomy and Distribution. *Bull. Water Resour. Res. Center, Univ. Minnesota.* 14:1–97.

Ladewski, T. B. & Stoermer, E. F. 1973. Water transparency in southern Lake Michigan in 1971 and 1972. *Proc. 16th Conf. Great Lakes Res.* 1973:791–807. *Int. Assoc. Great Lakes Res.*

Lazinsky, D. & Sicko-Goad, L. 1979. Paraformaldehyde-glutaraldehyde as a routine phytoplankton fixative. *Micron* 10:49–50.

Maciolek, J. A. & Kennedy, H. D. 1974. Spatial variation in periphyton production in a mountain lake at fall overturn. *Verh. Int. Verein. Limnol.* 15:386–93.

Meschkat, A. 1934. Der Bewuchs in den Röhrichten des Plattenseen. *Arch. Hydrobiol.* 27:436–521.

Meyer, R. 1965. *Morphology, Cytology and Life History of Certain Chrysophytes.* Ph.D. Thesis. University of Minnesota, Minneapolis.

Neal, C. E., Patten, B. C. & DePoe, C. E. 1967. Periphyton growth on artificial substrates in a radioactivity contaminated lake. *Ecology* 48(6):918–24.

Neter, J. & Wasserman, W. 1974. *Applied Linear Statistical Models.* Richard D. Irwin, Inc., Homewood, Ill., 842 pp.

Newcombe, C. L. 1950. A quantitative study of attachment materials in Sodon Lake, Michigan. *Ecology* 31(2):204–15.

Pryfogle, P. A. & Lowe, R. L. 1979. Sampling and interpretation of epilithic lotic diatom communities. *In* Wetzel, R. L. [Ed.] *Methods and Measurements of Periphyton Communities: A Review.* ASTM STP 690, American Society for Testing and Materials, 77–89.

Rehbronn, F. 1937. Das natürliche Nahrungsangebot, insbesondere der Aufwuchs, und die Ernährung der Fischnährtiere in Litoral eines eutrophen Sees. *Z. Fisch.* 35:372–9.

Round, F. E. 1961. Studies on the bottom-living algae in some lakes of the English Lake District. Part VI. The effect of depth on the epipelic algal community. *J. Ecol.* 49:245–54.

Sanford, G. R., Sands, A. & Goldman, C. R. 1969. A settle-freeze method for concentrating phytoplankton in quantitative studies. *Limnol. Oceanogr.* 14:790–4.

Scheffé, H. 1959. *The Analysis of Variance.* John Wiley & Sons, Inc., New York, 477 pp.

Schelske, C. L., Feldt, L. E. & Simmons, M. S. 1980. *Phytoplankton and Physical-Chemical Conditions in Selected Rivers and the Coastal Zone of Lake Michigan, 1972.* Univ. Michigan, Great Lakes Res. Div. Publ. 19, 162 pp.

Shannon, C. E. & Weaver, W. 1949. *The Mathematical Theory of Communication.* University of Illinois, Urbana, 125 pp.

Simonsen, R. 1962. *Untersuchungen zur Systematik und Ökologie der Bodendiatomeen der westlichen Ostsee.* Akad.-Verl. Berlin.

Sládečková, A. 1966. The significance of the periphyton in reservoirs for theoretical and applied limnology. *Verh. Int. Verein. Limnol.* 16:753–8.

Sneath, P. H. A. & Sokal, R. R. 1973. *Numerical Taxonomy.* W. H. Freeman and Co., San Francisco, 573 pp.

Stockner, J. G. & Armstrong, F. A. J. 1971. Periphyton of the Experimental Lakes Area, Northwestern Ontario. *J. Fish. Res. Bd. Canada* 28:215–29.

Strong, A. E., Stumpf, H. G., Hart, J. L. & Pritchard, J. A. 1974. Extensive summer upwelling on Lake Michigan during 1973 observed by NOAA-2 and ERTS-1 satellites. *Proc. 9th Int. Symp. on Remote Sensing of Environment.* Environmental Research Institute of Michigan, Ann Arbor, MI, 923–32.

Szczepańska, W. 1968. Vertical distribution of periphyton in the Lake Mikolajskie. *Pol. Arch. Hydrobiol.* 15:177–82.