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A STUDY OF PHYTOPLANKTON DYNAMICS IN LAKE FAYETTEVILLE AS A MEANS OF ASSESSING WATER QUALITY

by

Richard L. Meyer
Principal Investigator
Department of Botany and Bacteriology
University of Arkansas
Fayetteville, Arkansas 72701

ARKANSAS WATER RESOURCES RESEARCH CENTER
University of Arkansas
Fayetteville 72701

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Phytoplankton community was analyzed for seasonal and vertical distribution in Lake Fayetteville. This northwest Arkansas reservoir maintains a stable water level and chemical input with a relatively constant, slow overflow. Its source is groundwater seepage through a calcareous substrate with little contribution from the limited drainage basin. Phytoplankton community development with its associations and assemblages, chlorophylls -a, -b and c, and biomass distribution are described. The seasonal cycles of the chemical parameters NH_4-N, NO_2-N, NO_3-N, ortho-phosphate, silicon, pH, HCO_3- and total-alkalinity plus oxygen are described and discussed. The physical parameters of temperature, light and climate are included. The interaction of these parameters and other factors are related to phytoplankton dynamics.

Analysis of the phytoplankton data indicates the presence of four distinct structural regimes. Intermediate populations intergrade between the regimes. The winter regime is dominated by a diatom-association which includes a well developed phytomonad component. A transition flora of green algae and chrysomonads occur in the spring prior to stratification. The chrysophycean-association ends abruptly with the spring regime. The spring regime or Aphanizomenon-association is characterized by Aphanizomenon, Microcystis, and Coleosphaerium. This association gradually intergrades into the summer flora. The summer period contains three vertical components: green algae occupy the epilimnetic zone while cryptomonads and euglenoids dominate the metalimnetic zone. Oscillatoria

and Merismopedia populations develop in the hypolimnetic zone. These blue-green algae, plus euglenoids, migrate to the upper waters with destratification and become the principal component in the fall or cyanophycean-association. Merismopedia gradually disappears from the hypolimnion prior to destratification. The transition period between fall and winter regimes occurs during destratification with the development of a green algal flora similar to the winter-spring transition.

Certain phytoplanktors, their development and distribution correspond to temperature profiles. Thermal stratification and associated physico-chemical parameters are important in the development of specific populations, while certain other phytoplanktors are limited by chemical factors. Chlorophyll-a, -b and -c levels are related to the phytoplankton community composition and concentration. Biomass data corresponds to the distribution and number of phytoplanktors while oxygen is related to the metabolic balance between photosynthesis and respiration. The relationship between each of the chemical parameters and phytoplankton association is discussed. Particular attention is given to limiting factors, eg. silicon, and also the role of nitrogen and phosphorus based ions.

DESCRIPTORS: Phytoplankton, Algae, Diatoms, Aphanizomenon, Oscillatoria Cyanophyta, Cryptophyta, Chrysophyta, Oxygen, Temperature, Nitrogen, Phosphorus, Silicon, pH, Annual Cycles, Productivity, Arkansas

IDENTIFIERS: Phytoplankton, Algae, Water Chemistry, Reservoirs, Productivity, Ecology, Eutrophication, Limnology

A STUDY OF PHYTOPLANKTON DYNAMICS IN LAKE FAYETTEVILLE AS A MEANS OF ASSESSING WATER QUALITY

INTRODUCTION

Linear relationships between increase in fresh weight, chlorophyll and production rate during the spring phytoplankton pulse have been described by Rodhe, et al (1958) for Lake Erken, Sweden. Later studies on the same lake by Neuwerk (1963) and Pechlaner (1970) provide information of community structure and production. Few studies, however, have analyzed the total phytoplankton complement with regard to the qualitative, quantitative and spatial aspects. Research on Lake Fayetteville describes the seasonal distribution, succession of major associations, and community composition of the phytoplankton in relation to certain physico-chemical parameters. In addition to biomass, a detailed analysis of the biochromes, chlorophyll-a, -b and -c, are employed to describe the vertical and spatial distribution of the phytoplanktors.

The reservoir, Lake Fayetteville, Fayetteville, Washington County, Arkansas was previously studied by Hulsey (1956) in its first year of impoundment and Browne (1967) after fifteen years. Hulsey's study recorded the initial chemical, physical and biological features of Lake Fayetteville and noted the presence of various algal genera. Lake Fayetteville is a moderately eutrophic reservoir in the Ozark highlands of northwestern Arkansas, lying about 380 m above sea level. The lake covers an area of approximately 420 ha., with a maximum depth of 10.5 m and a mean depth of 4.3 m. At maximum capacity the lake contains about 3×10^6 m^3 of water. Its primary source is ground water seepage, springs

and two small vernal streams (fig. 1). The reservoir maintains a stable water level and chemical input with relatively constant, slow overflow. Intermittently, the reservoir will be drawn down about 1 m for municipal water use. The underlying geological strata are calcareous with an overlay of mix clay and broken sandstone. Detailed lake morphometry and drainage basin structure are recorded by Hulsey (1956).

A two year analysis of the phytoplankton composition and the succession of regimes is given in this report. Selected factors related to the succession of phytoplankton regimes are examined. The data obtained from this study suggests a simple methodology by which the composition, size of the standing crop and its photosynthetic potential can be determined. Prior methods of analyzing the phytoplankton population by indices and quotients are compared to a more detailed sampling program. In addition, this study suggests that certain organisms, representing different seasonal regimes, could be selected as "indicators." These indicator or marker organisms might be utilized for more intensive studies as to their physiological requirements and tolerances with respect to water quality and productivity.

A detailed analysis of the data will be presented in the Ph.D. Thesis of J. H. Wheeler, the graduate assistant working on this project. However, this report presents a summary of the seasonal trends and the interrelationship between certain physico-chemical parameters and phytoplankton distribution. A review of the applicability of phytoplankton and compound phytoplankton quotients (Nygaard, 1949) is discussed. These indicator quotients as well as selected organisms, i.e. Desmidiaceae (Brook, 1965), diatoms (Patrick, 1948), others recommended by Rawson (1956) are considered with regard to their ability to reflect the eutrophic state of reservoirs.

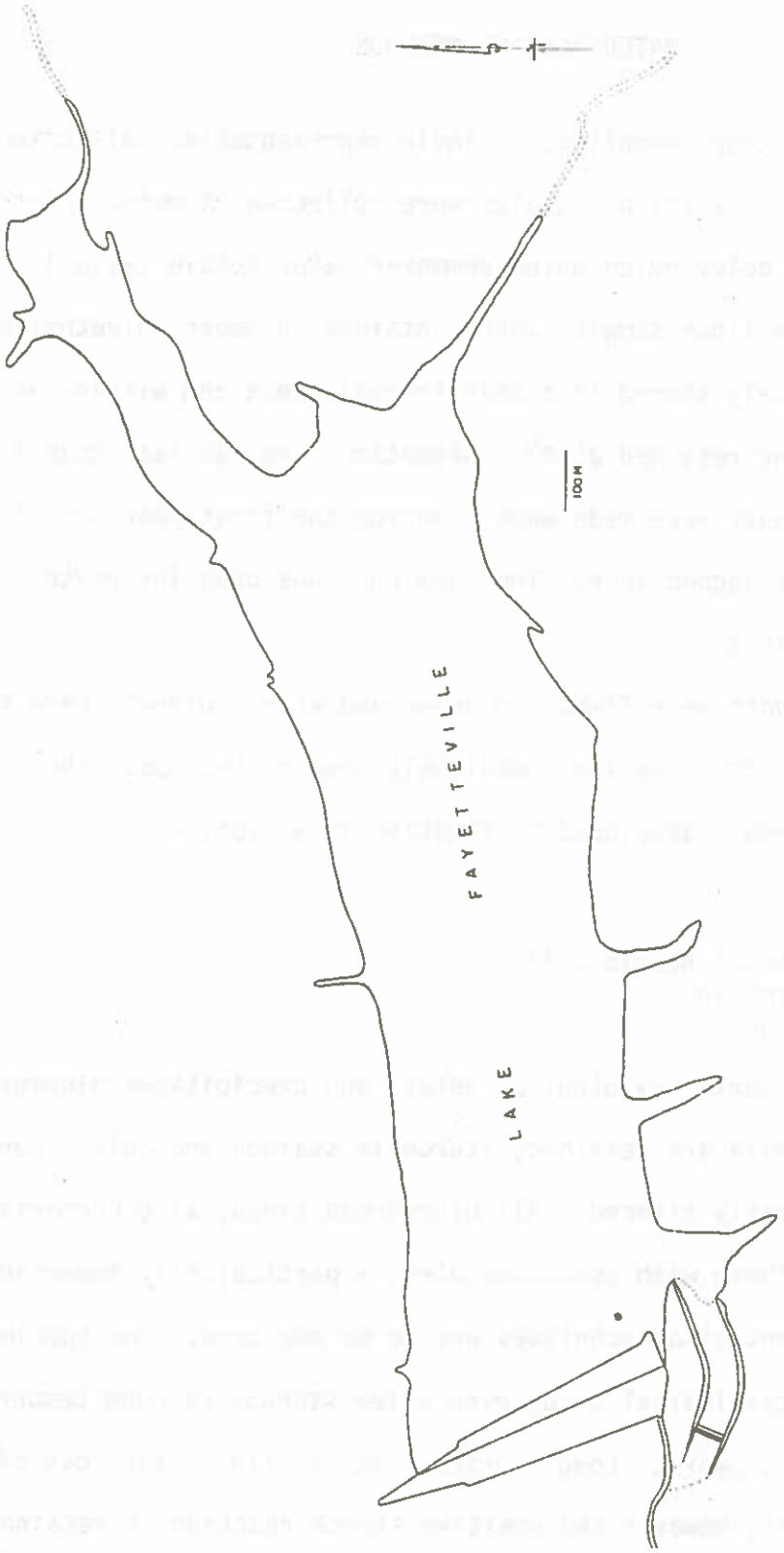

Fig. 1. Outline map of Lake Fayetteville
(● = Standard sampling site)

MATERIALS AND METHODS

After exploratory sampling, a single representative collection site was selected. Vertical samples were collected at meter intervals with a 2.2 liter polyvinylchloride kemmerer water bottle (Wildlife Supply Co.). One liter samples were contained in amber polyethylene bottles, immediately stored in a cold thermal chest and within one hour either filtered or retained at 4^{o}. Retention time was less than 12 hours. Measurements were made weekly during the first year and bi-weekly during the second year. The remainder was used for phyto-plankton identification.

Sample aliquots were fixed and preserved with "Volvox" (Cave & Pocock, 1956) or "M^3" fixative immediately upon collection. The formula for the newly developed M^3 fixative is as follows:

1 g I_2
0.5 g KI
5 ml Glacial Acetic Acid
25 ml Formalin
100 ml Water

This fixative preserves cytological detail and precipitates blue-green algae. The flagella are retained, starch is stained and cell dimensions are not significantly altered. All blue-green algae, also bacteria, sink, including those with pseudovacuoles; a particularily important feature if sedimentation techniques are to be employed. The specimens can be used for cytological study even after storage at room temperature for greater than 5 years. Long storage time results in the loss of the yellow iodine tint, however the positive starch reaction is retained.

Oxygen was measured polarigraphically with a calibrated YSI Model 54 Oxygen Meter. All readings were corrected for altitude and tempera-

ture. Temperatures were obtained from the thermister readout on the instrument. Light readings were determined with a Secchi disc. Alkalinity was determined by using 0.02 N sulfuric acid titrated to pH 8.3 and 4.3 with a Corning Model 7 pH meter (APHA, 1965). Biomass was determined by filtration of a known sample volume through dry preweighed and reweighed Millipore HA membrane filters; zooplankton were removed after filtration. The membranes were dried in a vacuum desiccator. The filtered water was retained for chemical analysis. Chemical determinations were performed with a Bauch and Lomb Spectronic 70 spectrophotometer. The analysis procedures were as follows: Ammonia-nitrogen with Nessler's reagent, nitrite-nitrogen using NitriVer* powder, nitrate-nitrogen with NitraVer* powder, ortho-phosphate with stannous chloride method, and silicon by the molybdosilicate method. Plastic ware was used for silicon analysis, since a significant level of contamination was noted when using glassware.

Biochrome analysis procedures were similar to those of Richards with Thompson (1952) except that Whatman GF/A glass filter discs were employed. The filtrate was immediately lyphalized to retard pigment degradation. The filter was eluted for at least 12 hours in cold 90% Acetone and the extract analyzed with a Perkin-Elmer 202 dual-beam recording spectrophotometer. Chlorophyll concentrations were calculated with the trichrometric equations of Parsons and Strickland (1963).

The phytoplankton was identified from a 1 liter concentrate and a vertical tow sample. One liter of the collection was filtered through a 25 mesh plankton net. A species inventory was prepared for each depth and the integrated vertical sample. These determinations were made

*Available from Hach Chemical Co., Ames, Iowa

with a Zeiss Photoscope II. Phytoplankton counts were made from the fixed samples via the sedimentation technique of Utermohl (1958) and a Wild inverted microscope.

RESULTS

The descriptions and conclusions are based upon data from approximately 700 sampling points taken between March 1969 and March 1971. A detailed presentation of the interrelationships between temperature, oxygen, biochromes, biomass and phytoplankton distribution has previously been presented by Meyer (1971_a) for the first year of this study. Meyer (1969, 1971_b) and Meyer, et al (1971) present an inventory of the algae from Lake Fayetteville and other aquatic systems. These authors include algae from the epiphytic, epilithic, epipelic, neustonic, and metaphytic subcommunities, as well as, the euplanktonic subcommunity.

Lake Fayetteville is a dimictic temperate lake (fig. 2) with thermal stratification beginning in April and destratification in November. An inverse stratification may develop under the ice, ie. January 2, 1970, with a minimum of 2.8^{o} immediately under the ice and a bottom temperature of 3.7^{o}. The lake is ice free by mid- to late-February. Slight warming of the entire water column occurs during March. Stratification develops rapidly; in early April the temperature difference in the ten meter water column is only 1.5^{o} but by mid-April the difference has increased to $7.6 - 7.8^{o}$. A thermocline is well developed between 4 and 5 m in mid-April. By mid-July the water attains a maximum surface temperature of $32 - 35+^{o}$. The bottom water temperature during the period rapidly raised to 12^{o} where it remains most of the summer. This

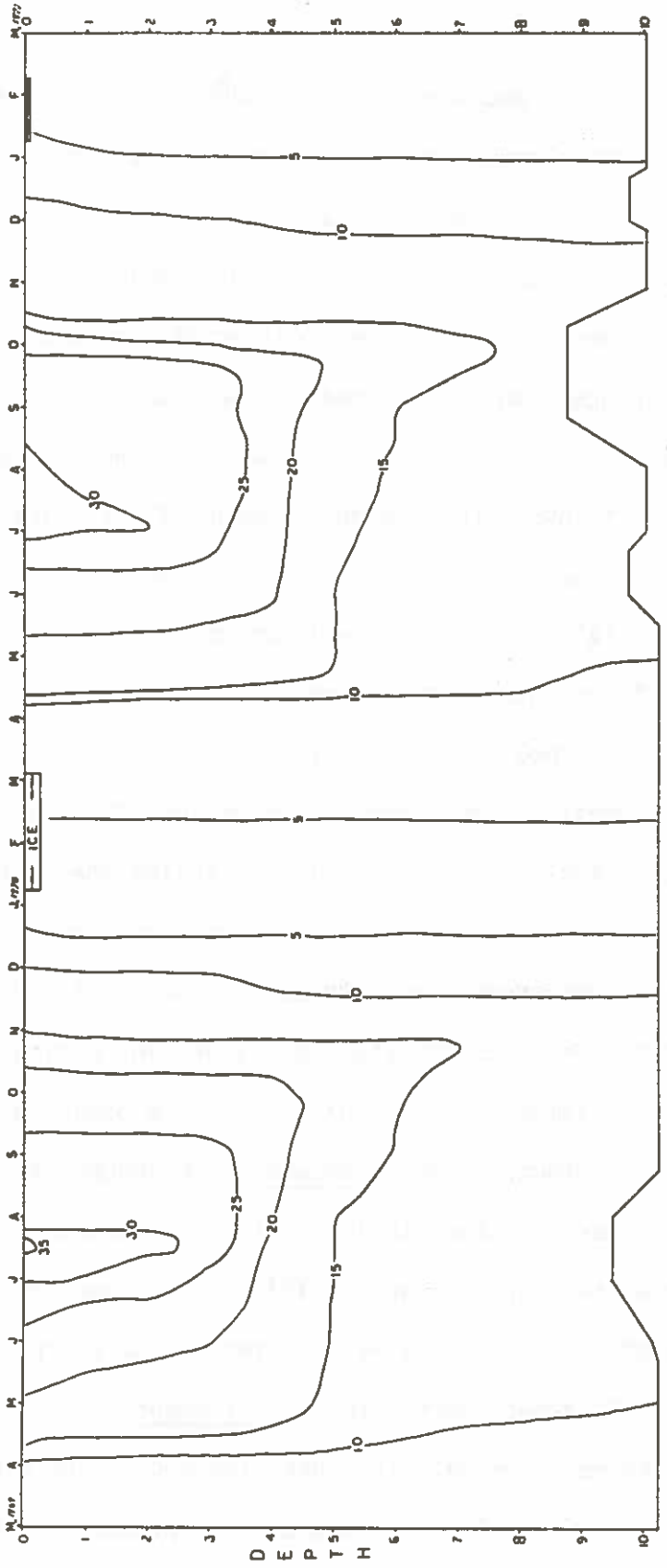

Figure 2. Changes in distribution of temperature (^{o}C)

lower region attains its maximum (13.8 - 14.8°) during destratification. Destratification proceeds slowly from mid-September through early November. Near isothermal conditions are developed by late November at a temperature of approximately 11°. True isothermal conditions are established by mid-December with a vertical profile of 5.2°.

Slight differences can be observed in the rate of destratification between years 1969 and 1970. The mild autumnal weather of 1969 resulted in a gradual heat loss. The extended summer of 1970 plus cool autumn produced a delayed destratification and a more rapid heat loss. This resulted in a 14° change in the epilimnion between 15 September and 15 October, as well as intrusion of warm water at greater depths. The bottom temperature reached a higher level in 1970 (14.8°) than in 1969 (13.0°). The 1970 maximum was temporary incursion of warmer upper waters.

Annual oxygen isopleths (fig. 3) closely follow the thermal gradients with certain modifications. March and April profiles are essentially of the orthograde type with concentrations 11± 0.6 mg/l. A well established clinograde distribution is present during the thermally stratified summer period. Oxygen maximum occurs during the spring phytoplankton bloom of Aphanizomenon where concentrations as great as 25.4 mg/l were recorded in 1969. A lower maximum of 13 mg/l was recorded during the spring bloom of 1970. This lower maximum demonstrates the effect of several late winter storms disrupting the bloom. Following its growth burst, the Aphanizomenon-association rains down into the upper metalimnion. This decaying population depresses the metalimnetic oxygen levels from June until September or October. A well developed oxygen gradient is present during the summer stratification period. Gradients of 9 mg/l are detectable between the 3

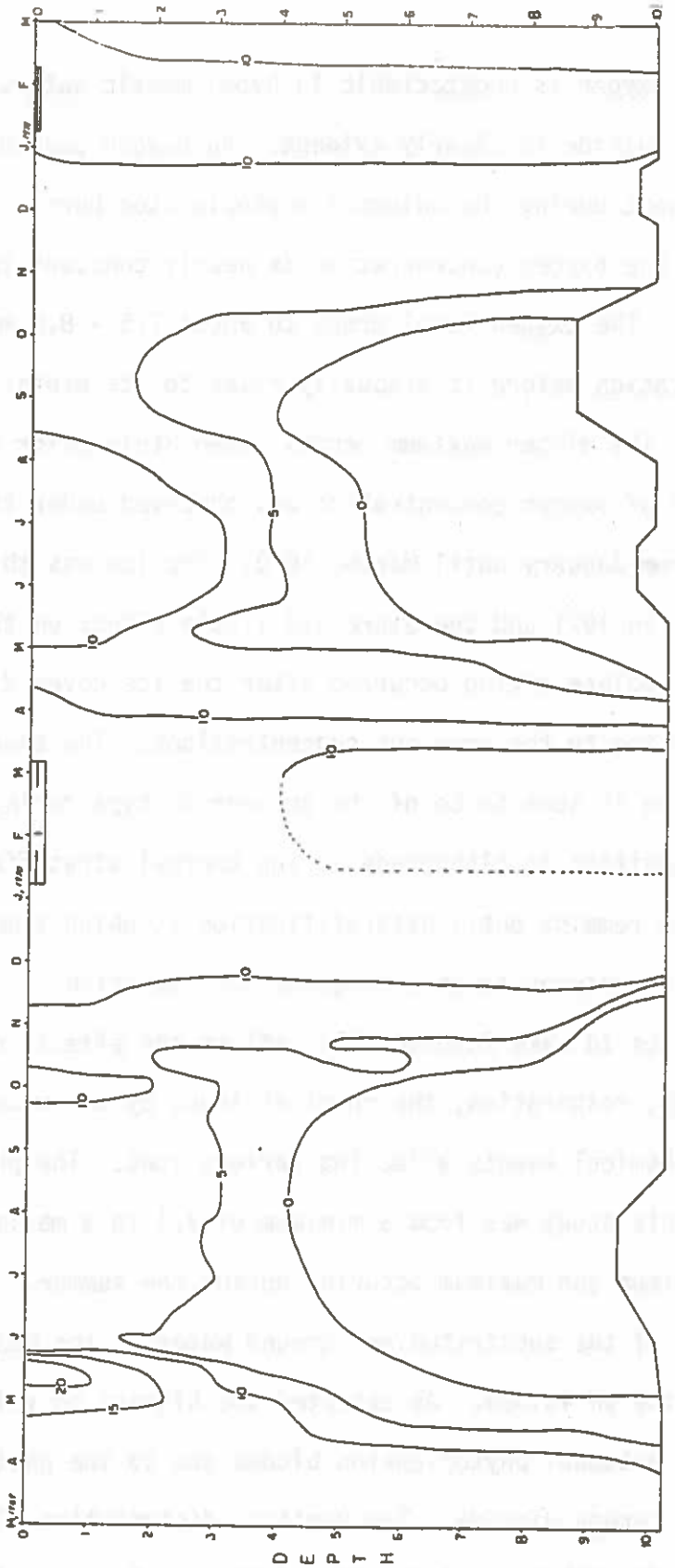

Figure 3. Variations in oxygen (mg/l) concentrations.

and 4 m levels. Oxygen is undetectable in hypolimnetic waters and the odor of hydrogen sulfide is clearly evident. An oxygen peak of 11.2 - 11.3 mg/l is present during the autumnal phytoplankton burst. With destratification the oxygen concentration is nearly constant throughout the water column. The oxygen level drops to about 7.5 - 8.0 mg/l after destratification before it gradually rises to its winter maximum of 11 $\pm$ .4 mg/l. The winter maximum occurs immediately prior to freeze-over. Depression of oxygen concentration was observed under the ice and snow cover from January until March, 1970. The ice was thin and lacked snow cover in 1971 and therefore had little effect on the oxygen concentration. Complete mixing occurred after the ice cover disappeared with oxygen returning to the previous concentrations. The annual oxygen distribution is seen to be of the orthograde type during the spring with a transition to clinograde during thermal stratification. This configuration remains until destratification at which time the oxygen distribution returns to an orthograde configuration.

The pH profiles in Lake Fayetteville reflect the effects of photosynthetic activity, respiration, the chemical input by the water supply and the complex chemical events affecting various ions. The pH range observed during this study was from a minimum of 7.1 to a maximum of 9.1, both the minimum and maximum occuring during the summer. The calcareous nature of the substratum and ground water as the major aquifer is, reflected in the pH values. As expected the highest pH values occur during spring and autumnal phytoplankton blooms due to the photosynthetic removal of carbon dioxide. The vertical distribution of pH (fig. 4) corresponds with thermal events and the development of phytoplankton associations. During thermal destratification the pH profiles

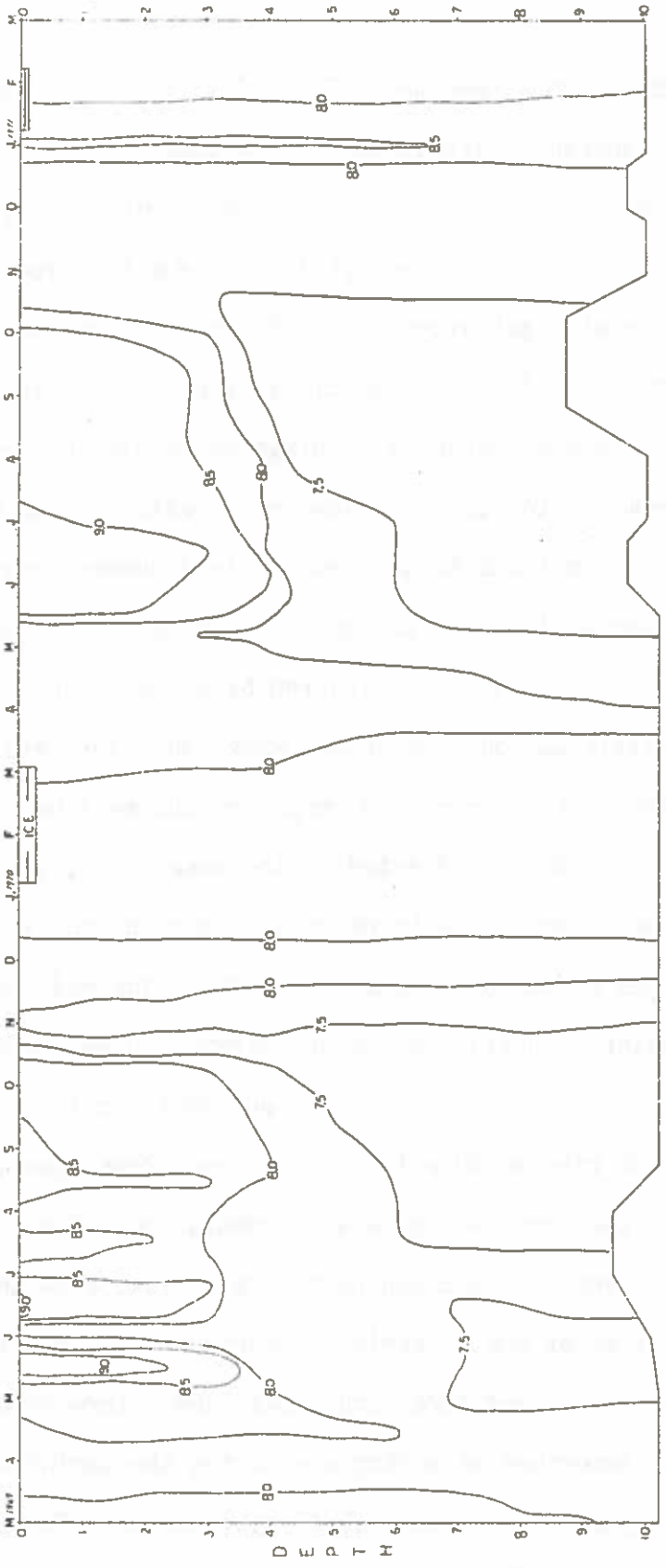

Figure 4. Distribution of the Hydrogen ion (pH).

are nearly vertical with a mean pH of 7.7 $\pm$ 0.1. With the fallout of the winter phytoplankton (diatoms) population there is a slight bacterial activity. The pH gradually rises to a peak during the spring Aphanizomenon bloom. This maximum certainly is due to carbon dioxide uptake by photosynthetic activity. This effect of the bloom is more evident in 1969 than in 1970. The percipitous decline of this bloom and the parallel increase bacterial respiration result in a sharp decrease in pH from 9.2 to 7.5. The lowered pH extends from May through the summer. The pH continues to decrease in late summer, reaching a minimum of 7.1 immediately prior to destratification. The decreased pH is probably due to anaerobic respiration by bacteria and blue-green algae. With destratification, the bottom water and flora are brought into the photic zone where there is a temporary autumnal burst of algae. This rapid growth is reflected in increase of pH, again through the uptake of carbon dioxide. With decreasing photoperiod and incident light there is a net reduction in photosynthesis. The reduced photosynthesis and greater solubility of carbon dioxide in cold water have the net effect of gradually decreasing the pH under the ice. However, there may be a sharp rise in pH prior to ice cover development because of the activity of the dense winter diatom population. The phytoplankton population and its photosynthetic activities, plus the respiratory activities of the bacteria, appear to be important factors in influencing pH. Employing Abreg and Rodhe (1942) terminology, the pH profiles can be described as orthograde during the spring with a transition to clinograde during thermal stratification. The clinograde profiles remain until autumnal destratification, at which time the profiles return to an orthograde configuration. The pH profiles closely

fit those of oxygen demonstrating an obvious relationship between oxygen evolution and removal of carbon dioxide through photosynthesis.

Total alkalinity (fig. 5) date reflects major changes in photosynthetic and respiratory activities within the ecosystem. Minimum total alkalinities are reached during blooms of algae as a result of carbon dioxide and bicarbonate ion uptake. The minimums 24 and 38 mg/l as $CaCO_3$ were detected during the fall blooms in 1969 and 1970 respectively. The total alkalinity remained relatively low in the epilimnetic zone during the summer. In the hypolimnion a gradual increase is noted, with the maximum of 141 - 155 mg $CaCO_3$ mg/l being attained immediately before destratification. The metalimnion is a transition zone reflecting a region of compensation between photosynthesis and respiration. During the destratified winter period the total alkalinity values are typically of the orthograde type. The slightly higher winter value of 1969 as compared with 1970 reflects decreased photosynthetic activity due to the longer, thicker ice and snow cover. Minor differences are noted between the two sample years, reflecting the range in variation from one year to the next; however, the basic patterns remain.

"Phenolphthalein" alkalinity (fig. 6) was measured in 1970. Only during the spring, summer and fall was there sufficient photosynthetic activity to raise the pH above 8.3. The spring algal burst, with its dense concentrations of Aphanizomenon, caused the "p" alkalinity maximum of 24 mg $CaCO_3$/l. With the die-off of the spring algal bloom "p" alkalinity rapidly decreased. The summer algal flora was photosynthetically active in the uptake of carbon dioxide. The shift in CO_2 - HCO_3^- - CO_3^- balance results in a gradual increase of "p" alkalinity. A second, but lower, maximum occurred during the autumnal blue-green algal

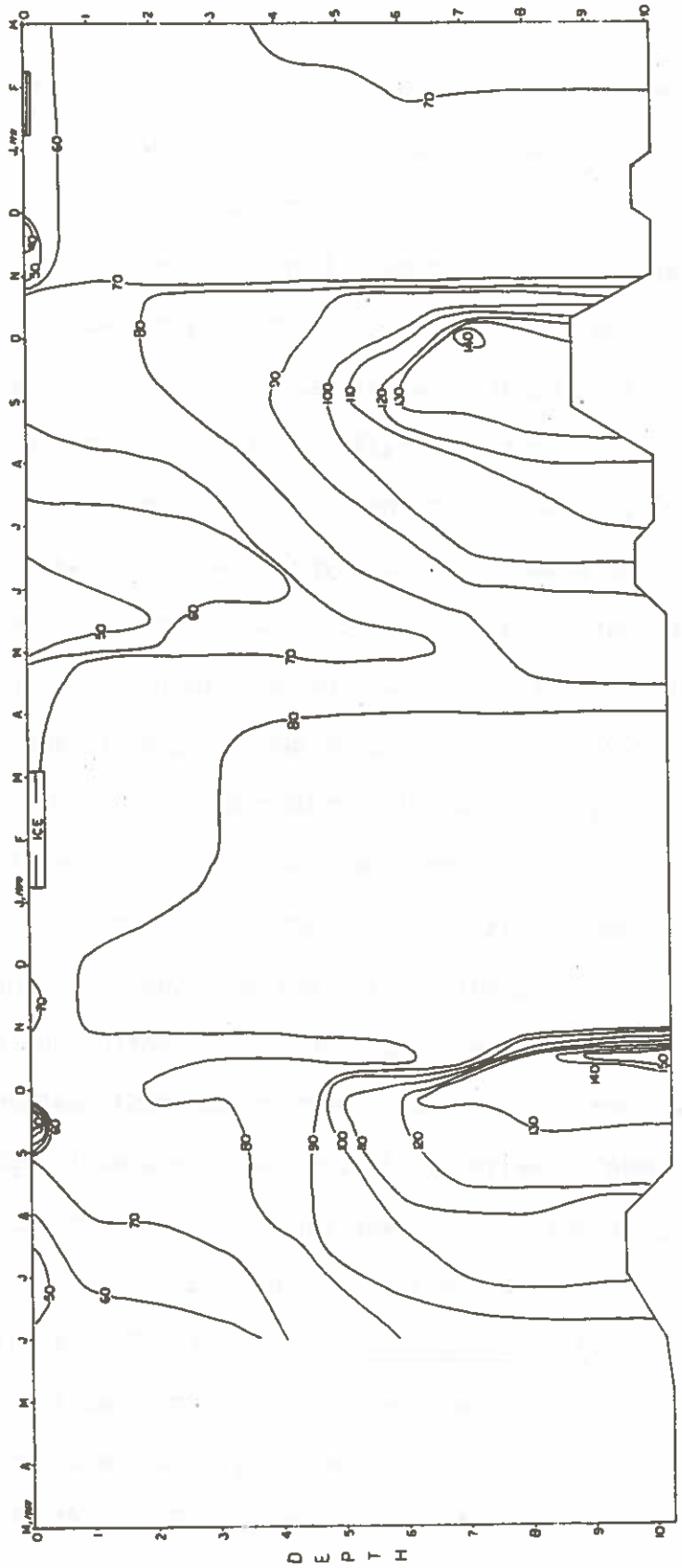

Figure 5. Diagram of Total-Alkalinity (mg $CaCO_3$/ l)

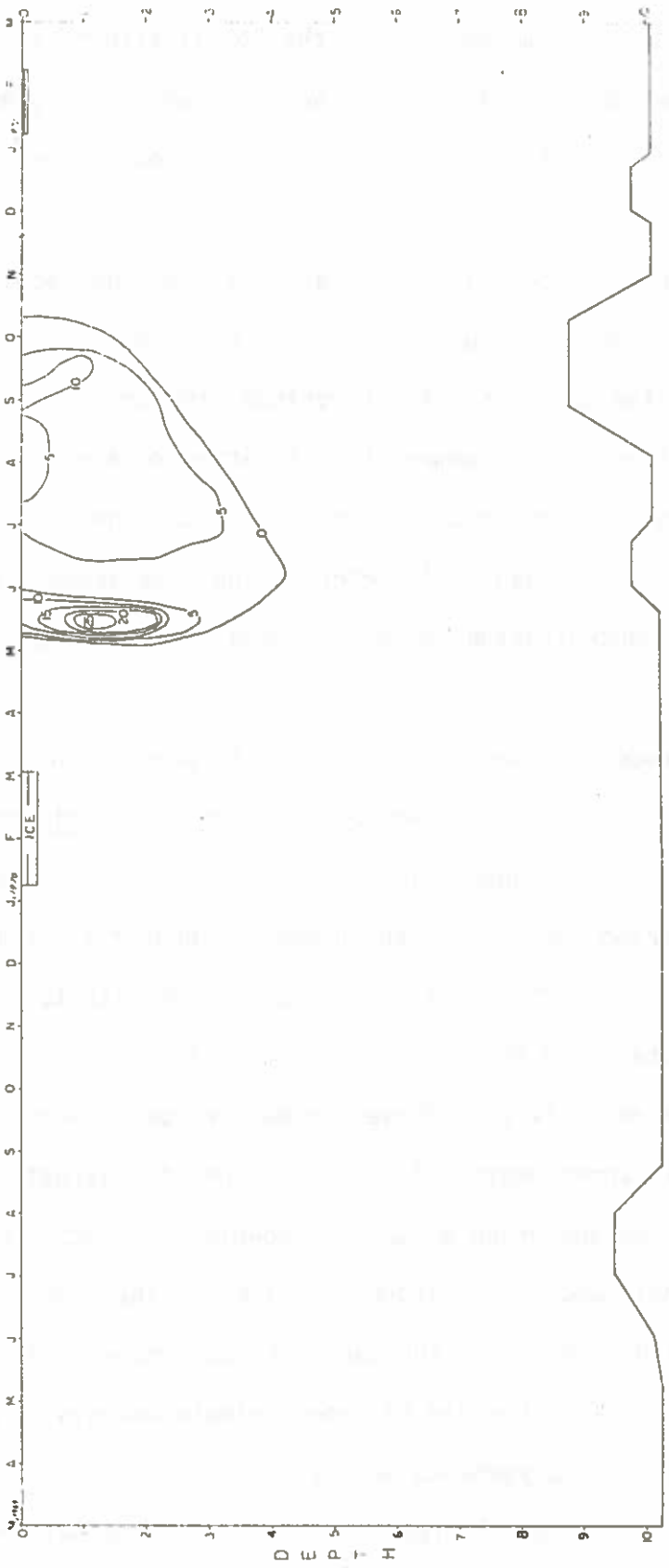

Figure 6. Distribution of Phenolphthalein-Alkalinity (mg $CaCO_3$/l).

peaks. It should be noted that all of the "p' alkalinity values are recorded from the upper 3 - 4 m of the water column. This, of course, reflects effects of insolation and the interrelations between photosynthesis and respiration.

Ammonia-nitrogen (fig. 7) varies markedly from undetectable amounts in the summer epilimnion to 16.1 mg/l in the hypolimnion. At vernal and autumnal circulation and, also winter periods, the ammonia-nitrogen is very low; 1 $\pm$ 0.5 mg/l. As summer stratification develops ammonia may disappear from the epilimnion and accumulate in the anaerobic hypolimnion. The accumulation is the result of bacterial and blue-green algae activity on debris. This concentration decreases immediately upon destratification.

Nitrite-nitrogen, as shown in figure 8, is present in signficant concentrations only after the die-off of the spring Aphanizomenon bloom; the buildup occurs in the anaerobic bottom water. This accumulation parallels an observed increase in the number of bacteria. A maximum of 0.064 ug/l is recorded within the debris rain. The nitrite found in the summer surface waters and from November through February is the result of the phytoplankton activity. These maxima are much lower than the hypolimnetic peak, approximately 1/4 - 1/5 as great. Syrett (1962) reports that diatoms and green algae are capable of reducing nitrate to nitrite in unpolluted, well oxygenated waters. The observed increase during the winter diatom regime substantiate Hutchinson's (1967) conclusions that it is reasonable to expect minute amounts of nitrite to occur in unpolluted and oxygenated waters.

Nitrate-nitrogen (fig. 9) profiles do not disclose patterns of stratification. Only during the month of May, 1969, are any zones of

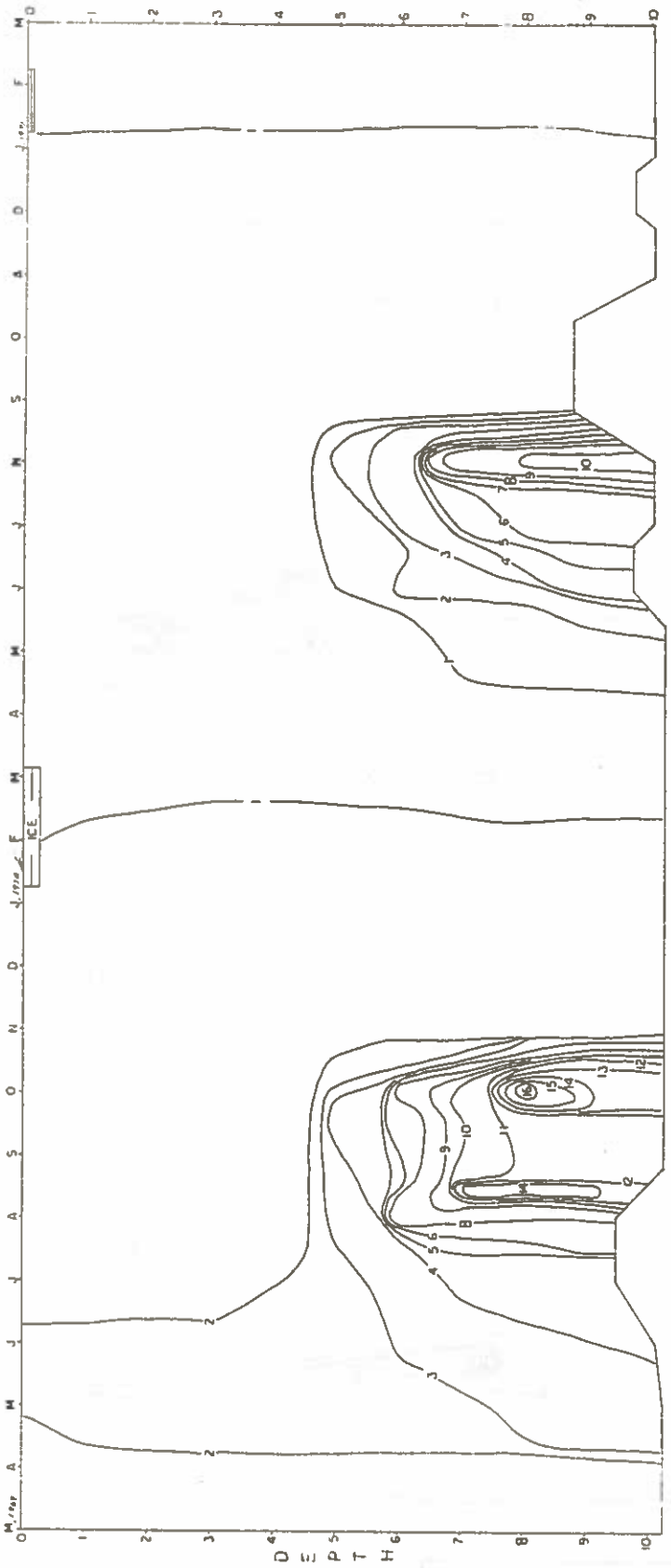

Figure 7. Variations in Ammonium-Nitrogen (mg/l) distribution.

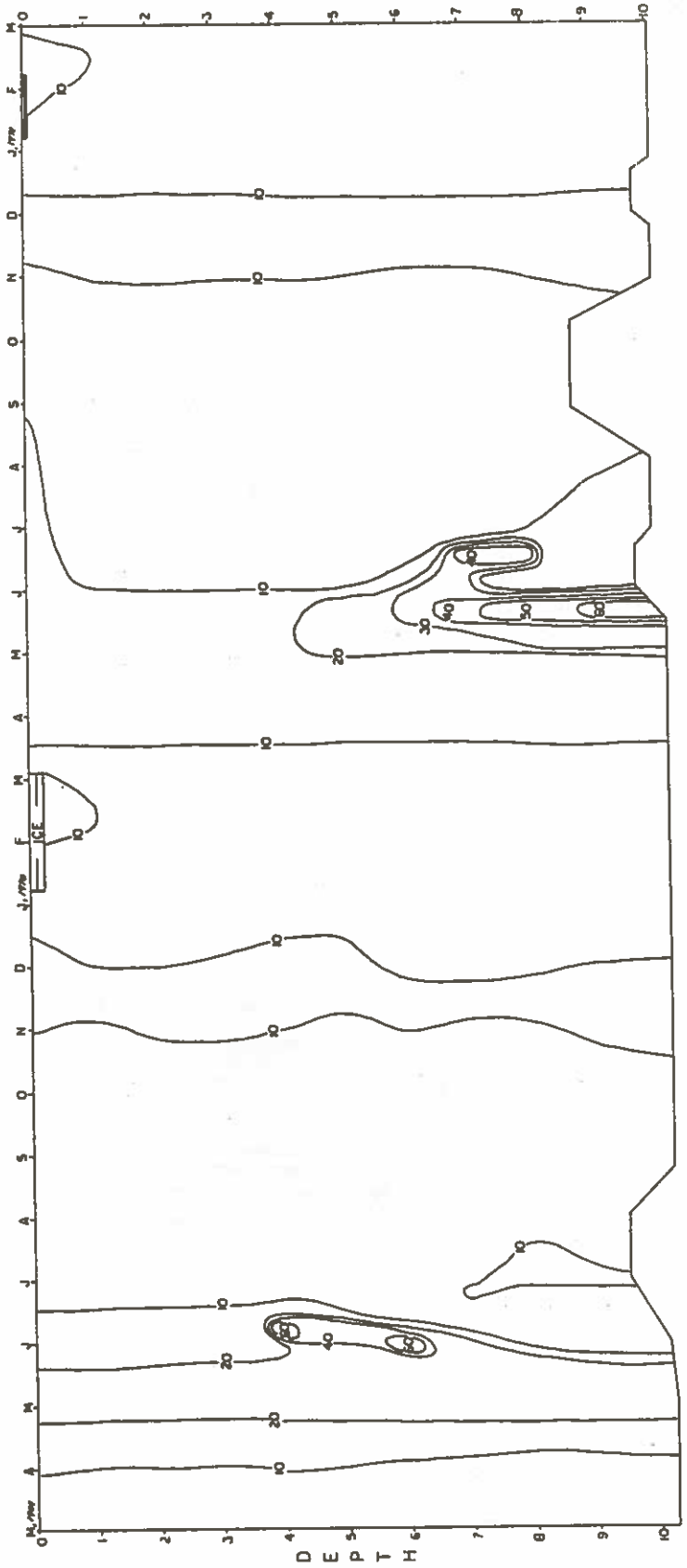

Figure 8. Nitrite-Nitrogen (µg/l) distributional pattern.

are capable of withstanding temperature above 35^{o} and intense insolation. Thus thermal enrichment may provide sufficient stress to select more desirable populations. Chlorophyll -a and -b data indicates that most of the population is near the surface receiving the greatest thermal and light stress. The nitrogen and phosphorus levels are not effected by this association. The metalimnetic flora consists of three distinct subassociations or assemblages. These subassociations are primarily composed of heterotrophic euglenoids and cryptomonads. Similar assemblages are found in a lake in northern Sweden and in Class B lakes in the Experimental Lake Area of Canada (Schindler and Holmgren, 1971). Pigmented and colorless genera are present. These organisms are osmotrophic; certain species may be phagotrophic. Thus they live on the organic milieu resulting from the decay of the spring bloom. Indications of the decay are evident by the drop in pH, increasing bicarbonate, and the accumulation of nitrite and ammonium ions. The biomass data also suggests the presence of these succeeding subassociations. Biochrome (figs. 13, 14, 15) analysis indicates the photosynthetic capacity and the taxonomic position of the planktons. Microscopic examination is necessary in order to differentiate the contribution of the debris and/or colorless organisms to the biomass. The hypolimnion has very little algae present in its early development as indicated by the almost total absence of chlorophyll. The early phases contain high levels of ammonium and phosphate which have accumulated by degradation of the debris rain from the spring bloom. As the summer progresses, a blue-green algal population develops which is capable of living under anaerobic conditions. The development of this population can be observed in the increase in biochromes. The increase in

chlorophyll -b and -c indicates the presence of certain green algae and diatoms. Ammonium continues to accumulate as does phosphate and silicon while nitrate and nitrite are little changed. The hypolimnetic, along with the metalimnetic flora, is distributed throughout the water column at thermal destratification. It is interesting to note that the blue-green algae in this association have little effect on phosphate level.

An Oscillatoria-association develops in the autumn following thermal destratification. Its extensive growth is probably limited by low light levels, cold temperatures and turbulence. The water is thermally unstable and susceptible to circulation by the wind. Members of the association are quickly transported to lower, more stable depths below the photic zone. The composition of this association can be deduced from the biochrome data. Figures 13, 14, and 15 disclose that chlorophyll-a is the major pigment present with only trace amounts of chlorophylls -b and -c. Nitrates tend to increase during the autumnal bloom and there is little, if any, change in the phosphate level. Again a blue-green algal flora has essentially no effect on the phosphate concentration.

The winter diatom-association develops after the decay of the Oscillatoria-association. This change in phytoplankton composition is clearly reflected in the rapid increase in chlorophyll-c (fig. 15). Two ions, ammonium and silicate, are utilized during the growth of the diatom population. The pH, alkalinity, phosphorus and nitrate are unaffected. There is however, an increase in the nitrates to 1.25 mg/l by spring.

The basic pattern of the phytoplankton in Lake Fayetteville is that of four seasons: winter, spring, summer and fall. A review of phyto-

plankton in several world lakes is discussed by Lund (1965) and Hutchinson (1967). These sources plus the information derived from this study suggest a certain basic pattern from which notable deviations are known. These exceptions are usually the result of human intervention. The "typical" small lake is usually described as one which contains the following pattern: a winter diatom bloom followed by a chrysophyte-chlorophycean spring flora and the development of a blue-green bloom in late summer or early fall. Schleinsee in Bavaria (Vetter, 1937), Lake Erken in Sweden (Perchlaner, 1970), Lake Mendota in Wisconsin, USA, (Hasler, 1947) and Experimental Lakes Area of Canada (Schindler and Holmgren, 1971) are representative of a diverse series of lakes from which a basic pattern can be derived. I would suggest that the "typical" lake type is one of a series of generalized lake types. These generalized lake types follow a longitudinal gradient which reflects the integrated effects of duration and intensity of insolation, thermal properties, etc. Arctic lakes possess a long term diatom association followed by a chrysophycean peak. Subarctic lakes contain the above components plus a dinoflagellate and green algal component. North temperates are characterized by a winter diatom peak followed by an enlarged chrysophycean-association mixed with green algae and dinoflagellates. The assemblages intergrade into a late summer maximum of blue-green algae. Frequently Aphanizonemon, Anabaena, Microcystis, Coleosphaerium, Merismopedia and others dominate the bloom. Temperate lakes contain four pulses as previously described for Lake Fayetteville. South temperate or sub-tropical lakes tend to have diminished diatom and chrysophycean associations and expanded green and blue-green associations. Few tropical lakes have been well studied but an expansion

of the summer green algal flora might be expected. This summary suggests that arctic and subarctic lakes contain only portions of the total cycle; the diatom, chrysophycean- and chlorophycean-associations. The north-temperate lakes include, in addition to the above associations, both the vernal and autumnal cyanophycean peaks. However, these peaks are combined into a single broad bloom. Temperate lakes contain an epilimnetic green algae flora which separates the two blue-green peaks. It is interesting to note that the blue-green peaks occur at nearly the same temperatures in north-temperate and temperate lakes. The temperate lakes reach higher summer temperatures for a longer period of time, thus permitting a unique summer flora to develop. More tropical lakes lose the winter and spring fraction of the cycle resulting in alternating peaks of green and blue-green algae.

The annual phytoplankton cycle is based upon the availability of certain chemical and physical parameters. Quantitative increases or decreases will result in a greatly modified cycle. As previously noted algae have specific nutrient and physical requirements and deviations from these requirements places stress on population causing the loss of certain members and the development of others. Manipulation of certain parameters provides a means by which specific populations can be selected or eliminated. In contrast to other reports orthophosphate-P appears to have little impact on blue-green algal blooms. With certain blue-green populations nitrate-nitrogen concentration has minor impact. Conversely, with the lysing of these blooms there is an apparent increase of these ions, however, no regrowth was noted. These particular ions are taken up readily by the subsequent green algal population. As previously

noted, control of the temperature regime may be of great value in selecting desirable photoplankton.

The various phytoplankton quotients are apparently of minor use. The quotient values vary markedly with season, the quotient used and the sampling technique. In addition, a thorough knowledge of the algal species and their habits is a pre-requisite. The use of a single indicator organism or class of organisms contains the same problems. This research indicates that many species are in extremely low numbers or absent most of the year and would be missed by many sampling routines and therefore, only those organisms that are perennial should be used as indicators or in the computation of quotients.

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