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A Study of Phytoplankton Dynamics in Lake Fayetteville as a Means of Assessing Water Quality

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A Study Of Phytoplankton Dynamics In Lake Fayetteville As A Means Of Assessing Water Quality

by

RICHARD L. MEYER

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ARKANSAS WATER RESOURCES RESEARCH CENTER

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AS A MEANS OF ASSESSING WATER QUALITY

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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 $\text{NH}_4\text{-N}$, $\text{NO}_2\text{-N}$, $\text{NO}_3\text{-N}$, 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 chrysoomonads 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 $3 \times 10^6 \text{ m}^3$ 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.

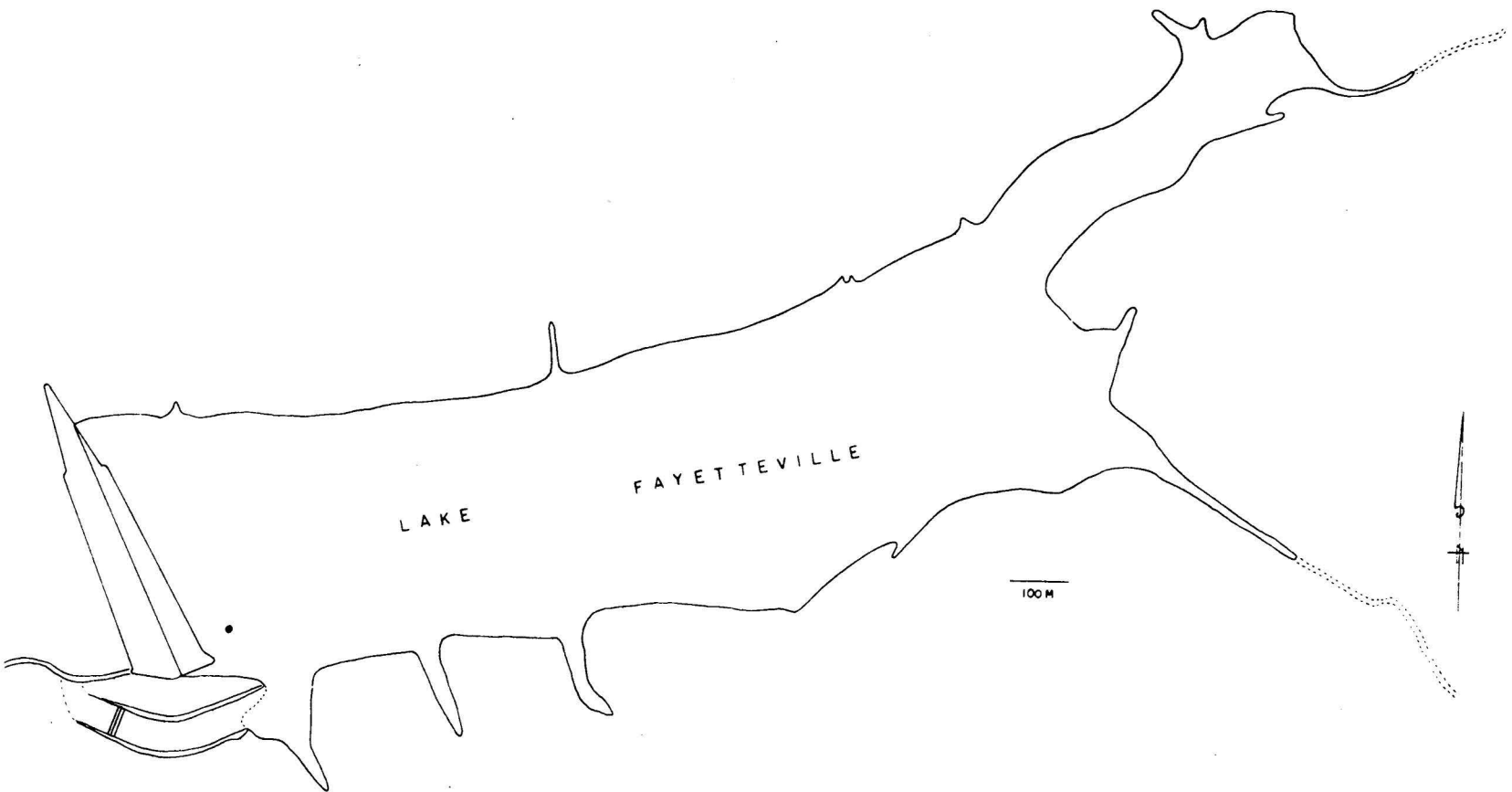


Fig. 1. Outline map of Lake Fayetteville
(● = Standard sampling site)

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 4⁰. 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 phytoplankton identification.

Sample aliquots were fixed and preserved with "Volvox" (Cave & Pocock, 1956) or "M³" fixative immediately upon collection. The formula for the newly developed M³ fixative is as follows:

1 g I₂
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 particularly 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 trichromatic 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, epipelagic, 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 2.8⁰ immediately under the ice and a bottom temperature of 3.7⁰. 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 1.5⁰ but by mid-April the difference has increased to 7.6 - 7.8⁰. 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 - 35⁰. The bottom water temperature during the period rapidly raised to 12⁰ where it remains most of the summer. This

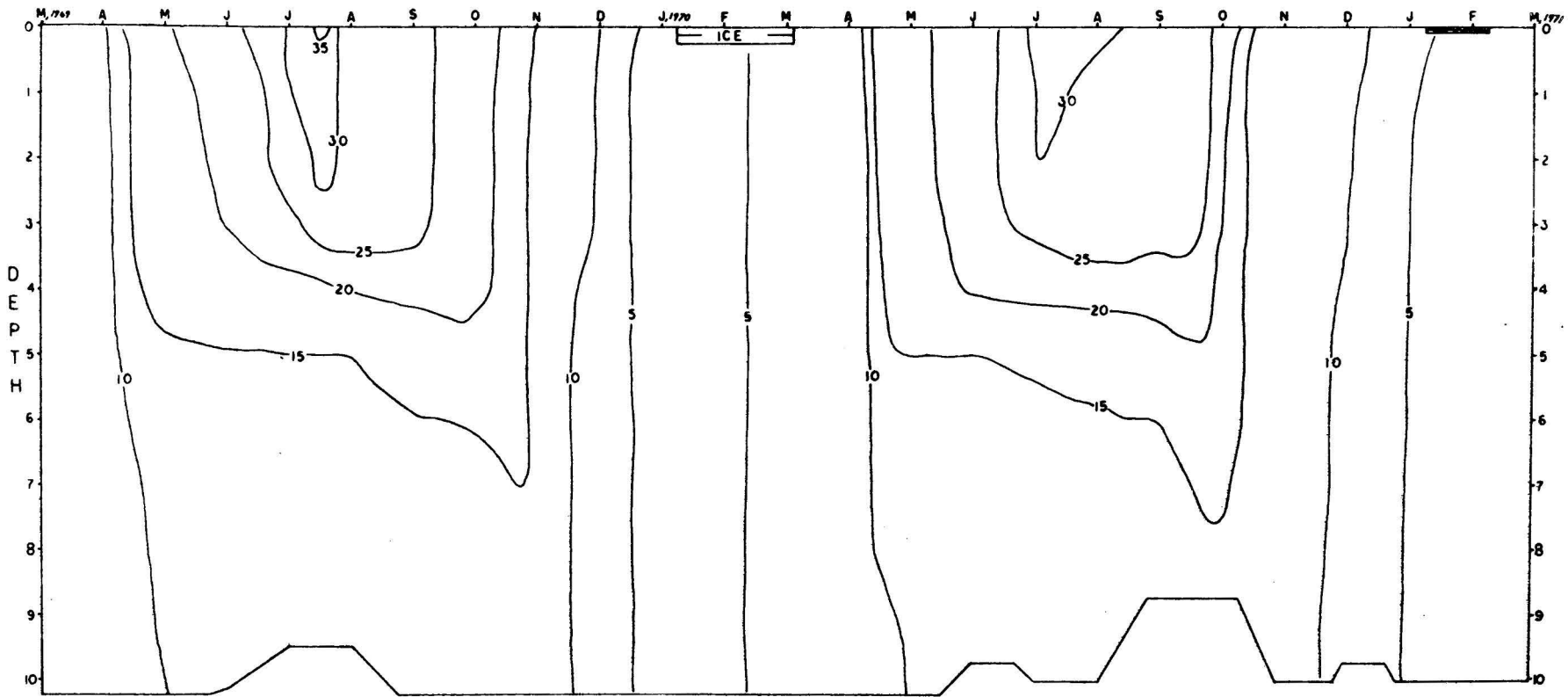


Figure 2. Changes in distribution of temperature ($^{\circ}\text{C}$)

lower region attains its maximum (13.8 - 14.8⁰) during destratification. Destratification proceeds slowly from mid-September through early November. Near isothermal conditions are developed by late November at a temperature of approximately 11⁰. True isothermal conditions are established by mid-December with a vertical profile of 5.2⁰.

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 14⁰ 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 (14.8⁰) than in 1969 (13.0⁰). 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

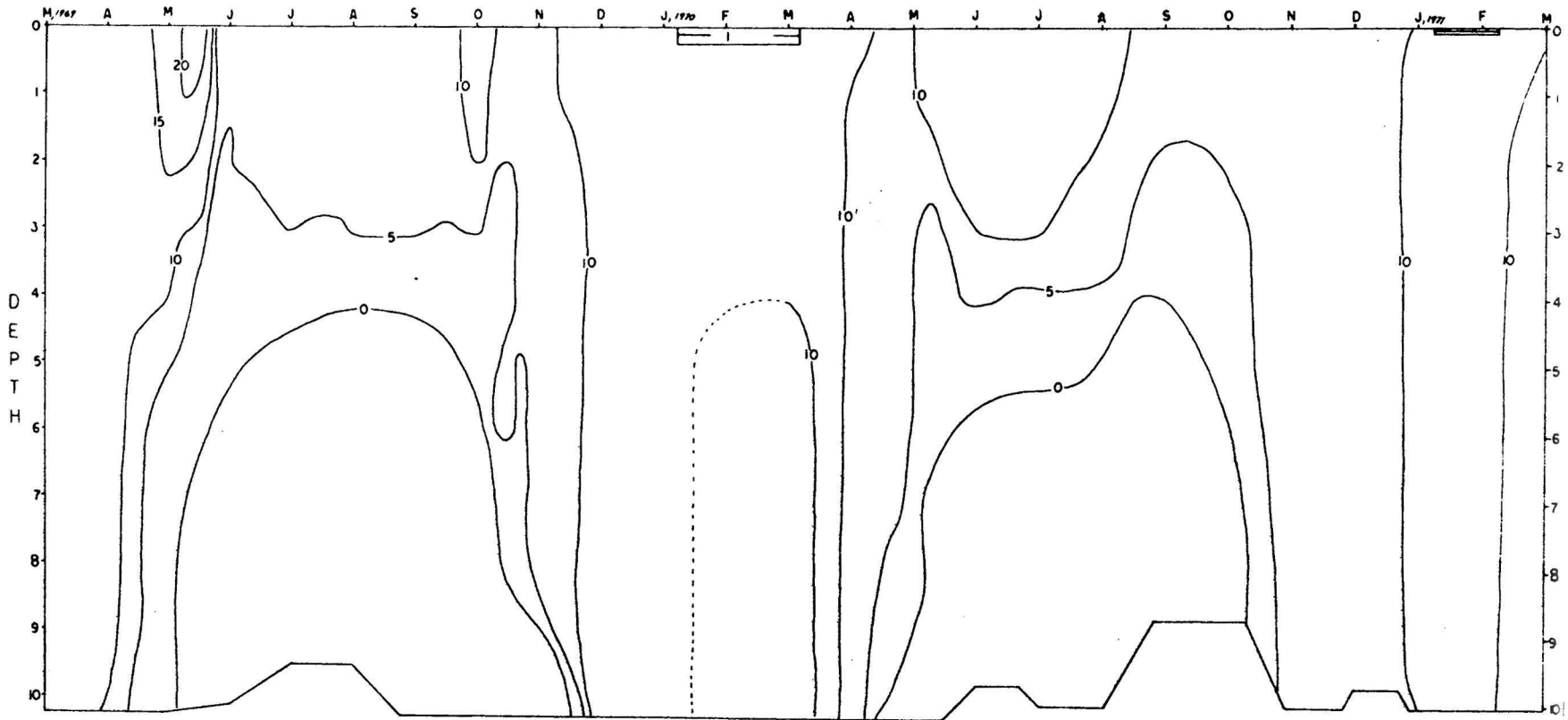
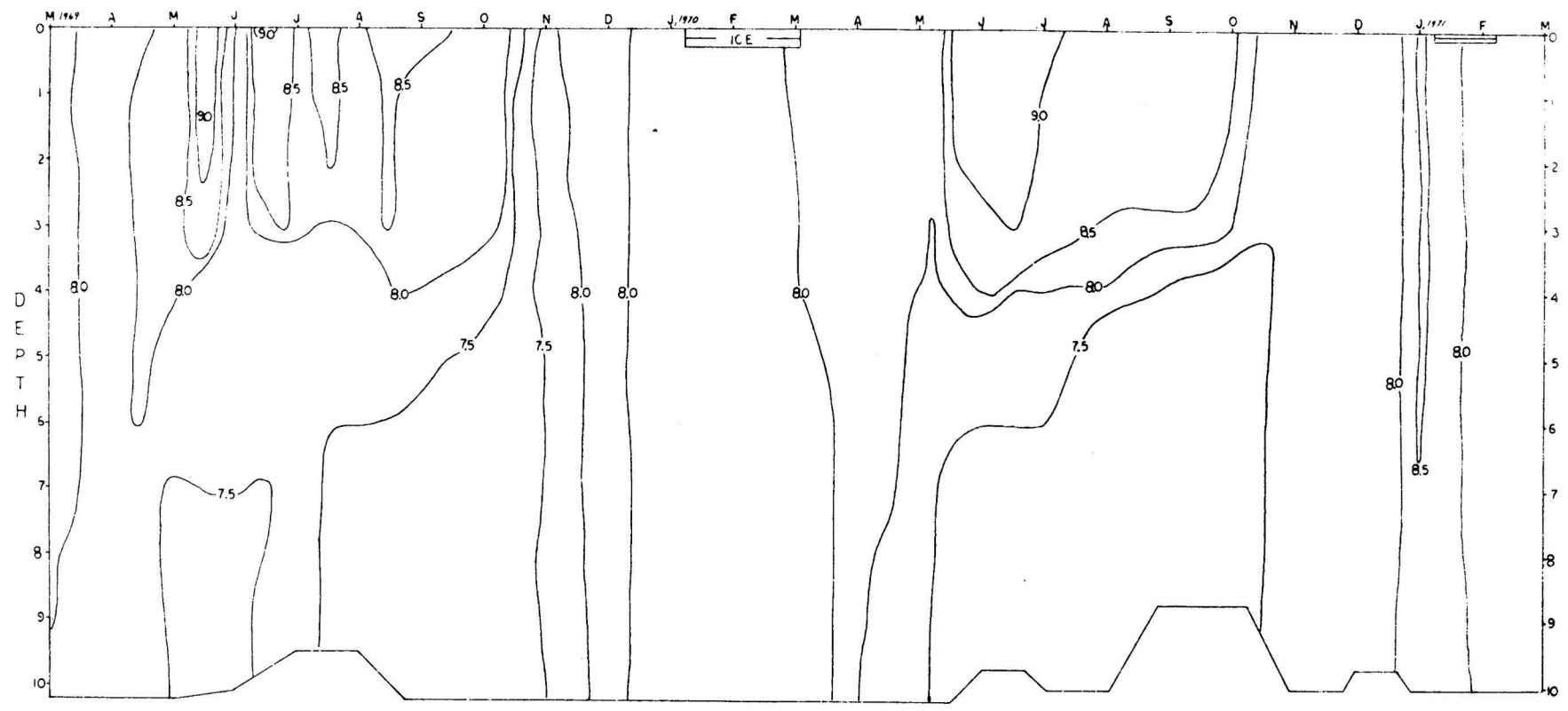


Figure 3. Variations in oxygen (mg/l) concentrations.

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 occurring 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 ± 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 precipitous 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) data 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^{2-} 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 CaCO₃/ l)

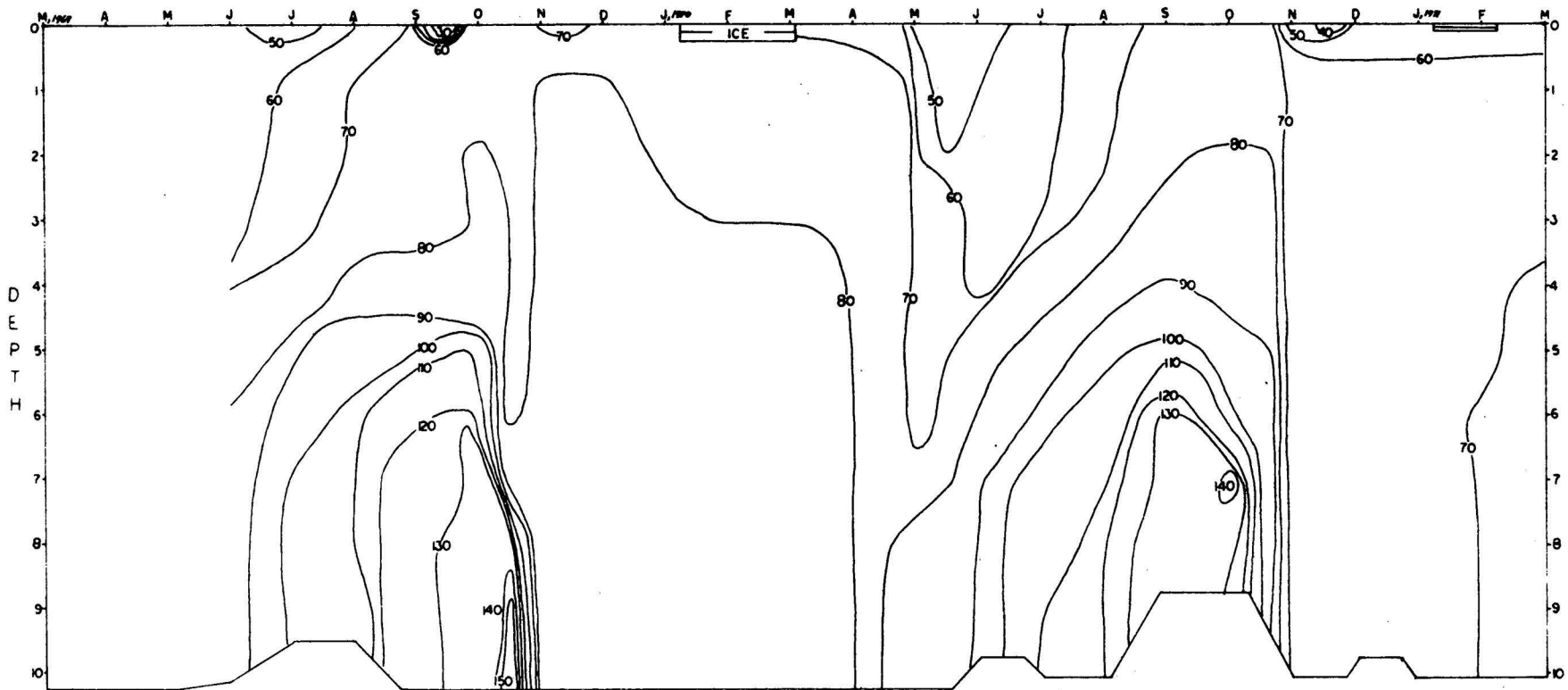
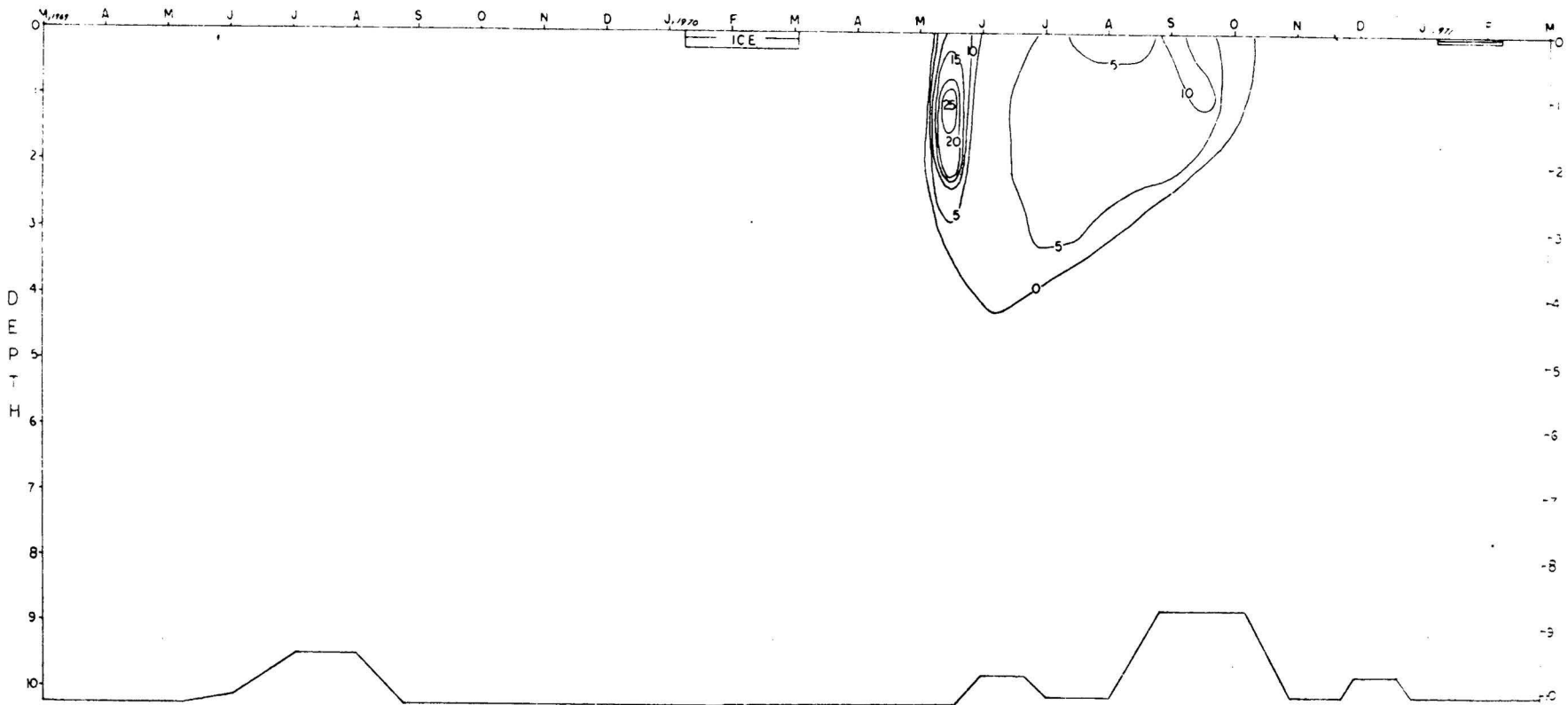


Figure 6. Distribution of Phenolphthalein-Alkalinity (mg CaCO₃/l).



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 ± 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 significant 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

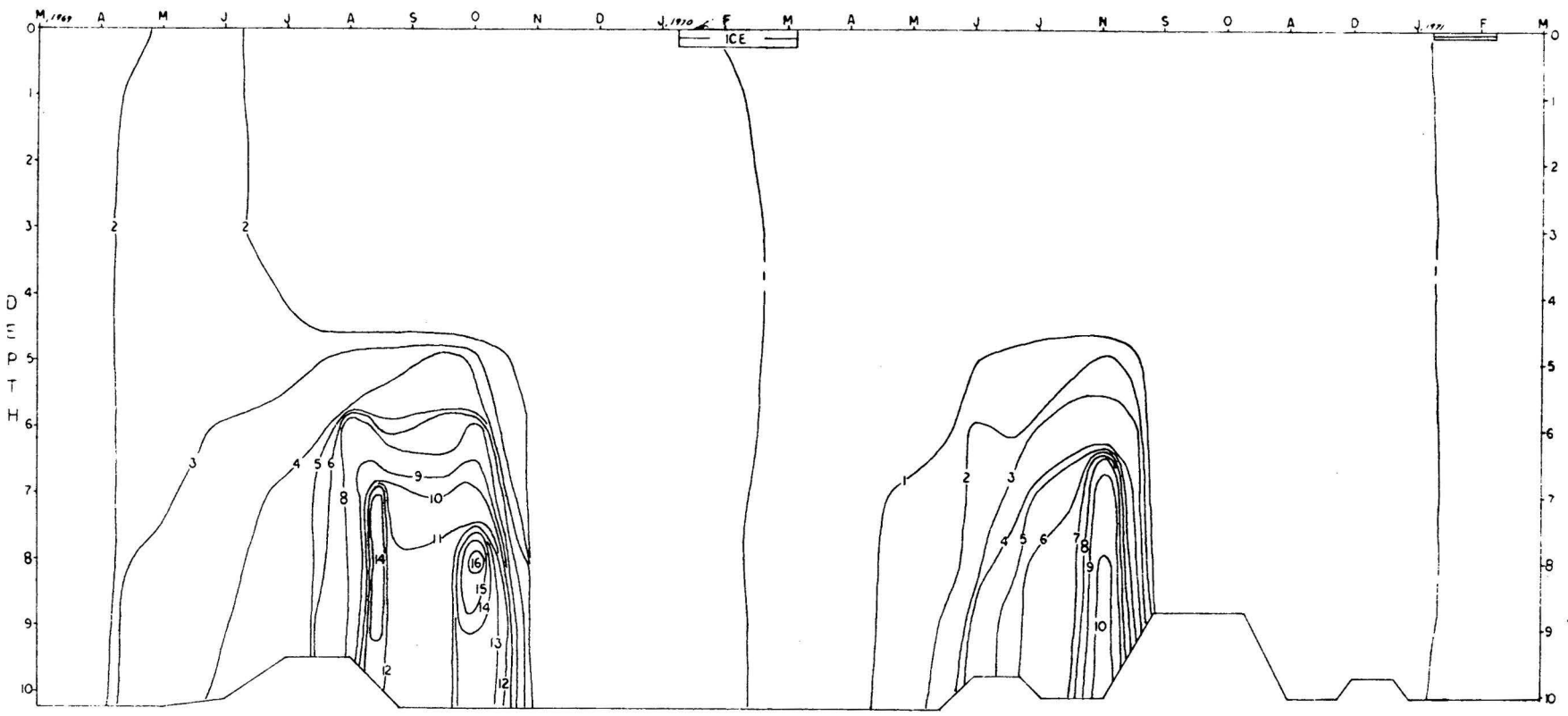


Figure 7. Variations in Ammonium-Nitrogen (mg/l) distribution.

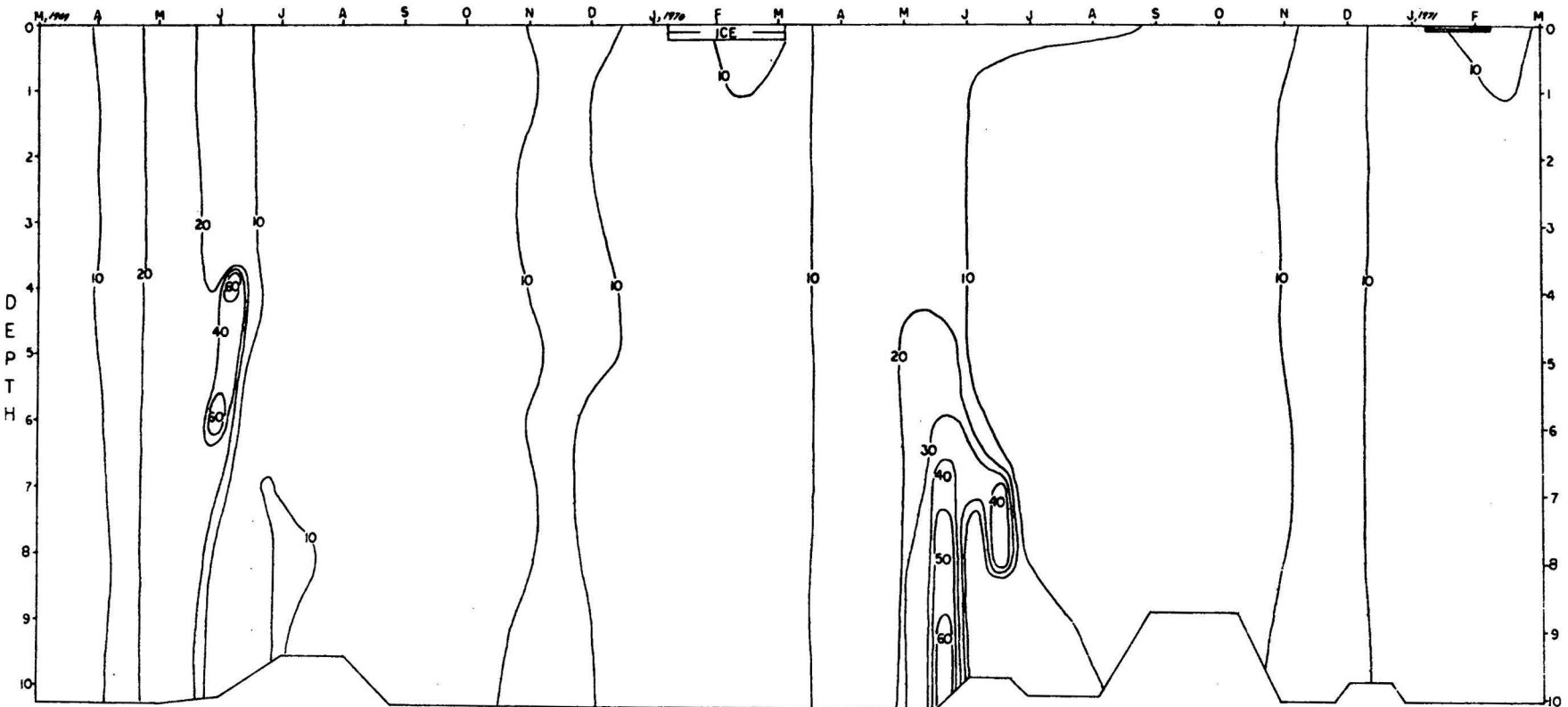
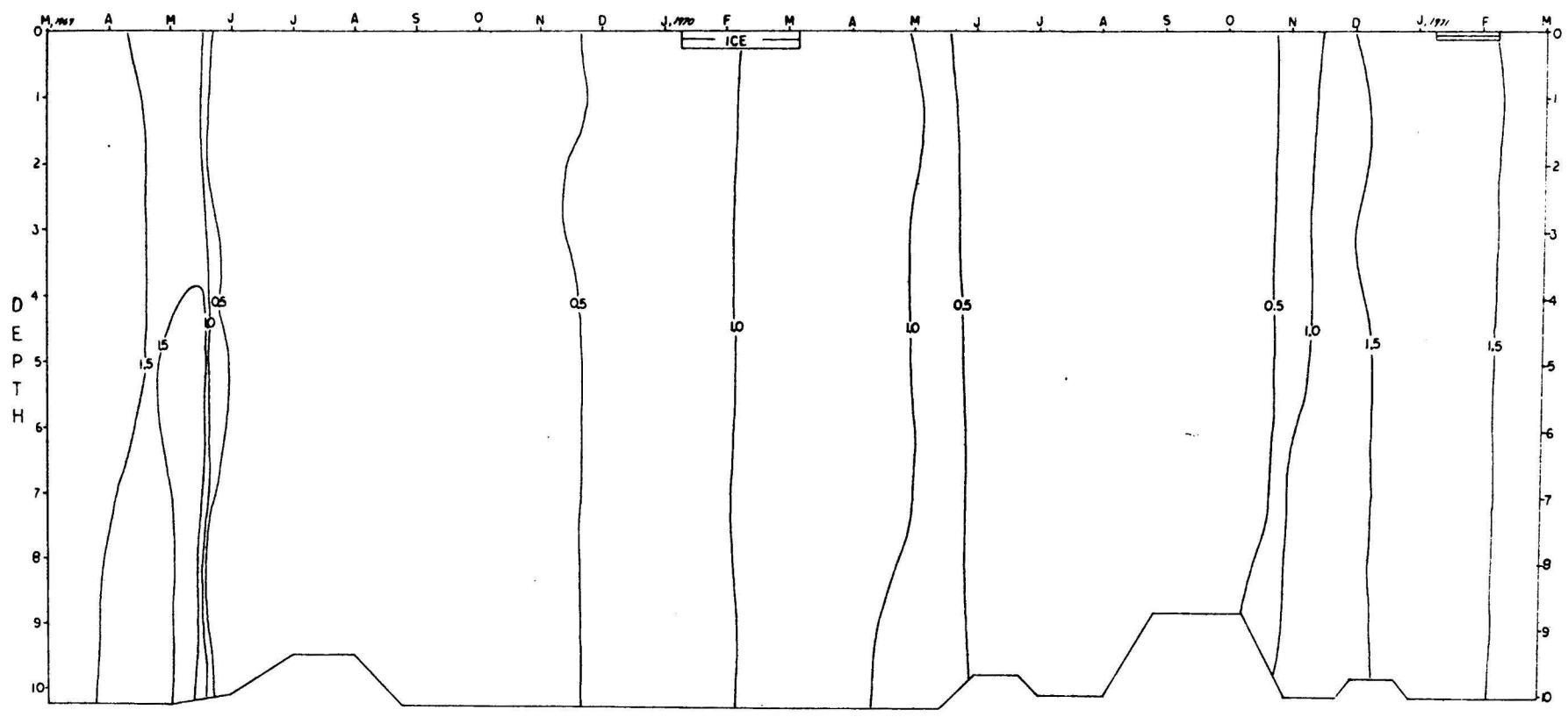


Figure 8. Nitrite-Nitrogen ($\mu\text{g}/\text{l}$) distributional pattern.

Figure 9. Distribution of Nitrate-Nitrogen (mg/l).



concentration observable. The nitrate-nitrogen profiles are nearly vertical throughout most of the year. The maximum concentration of 1.77 mg NO₃-N/l was associated with the debris rain from the unusually large Aphanizomenon bloom. A concentration of 1.30 - 1.60 mg NO₃-N is typical immediately after ice-out and the winter diatom die-off. The nitrate concentration is reduced approximately 0.25 mg/l during the development of the intense spring blue-green algal burst. This dying population however, contributes to increased levels in the hypolimnion. Following the blue-green burst there is a dramatic decrease in nitrate, down to 0.11 mg/l. The nitrate remains at these low levels until destratification. Beginning with destratification there is an immediate doubling of the nitrate concentration. The nitrate concentration increases rapidly until the winter regimen is established. During the winter regimen there is little net increase of nitrate, only minor fluctuation. There may be a minor increase in nitrate level under the ice but usually the observed concentrations are nearly the same prior to, during and immediately after ice formation. The nitrate annual cycle is unique, in that it lacks expected stratification. Specific areas of concentration are more probably related to bacterial action as noted in the nitrites. A comparison of nitrate-nitrogen and phytoplankton distributions suggest that green algae are the principal organisms responsible for the uptake of this nitrogen source. There appears to be little relationship between nitrate-nitrogen utilization and blue-green algae.

The annual orthophosphate distribution (fig. 10) is quite different from that of other chemical constituents. Trace levels are detected in March and under the ice cover. Typically there is a net increase during

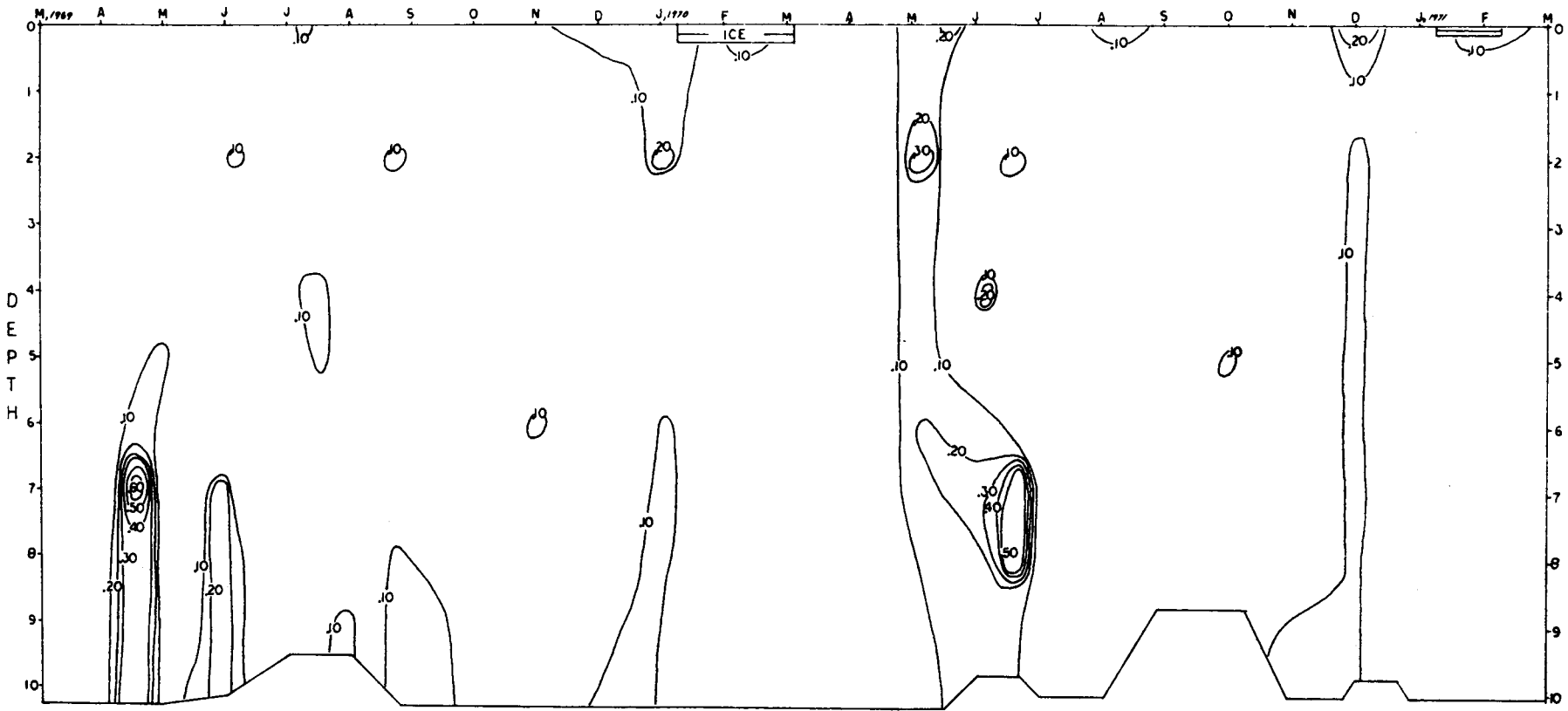
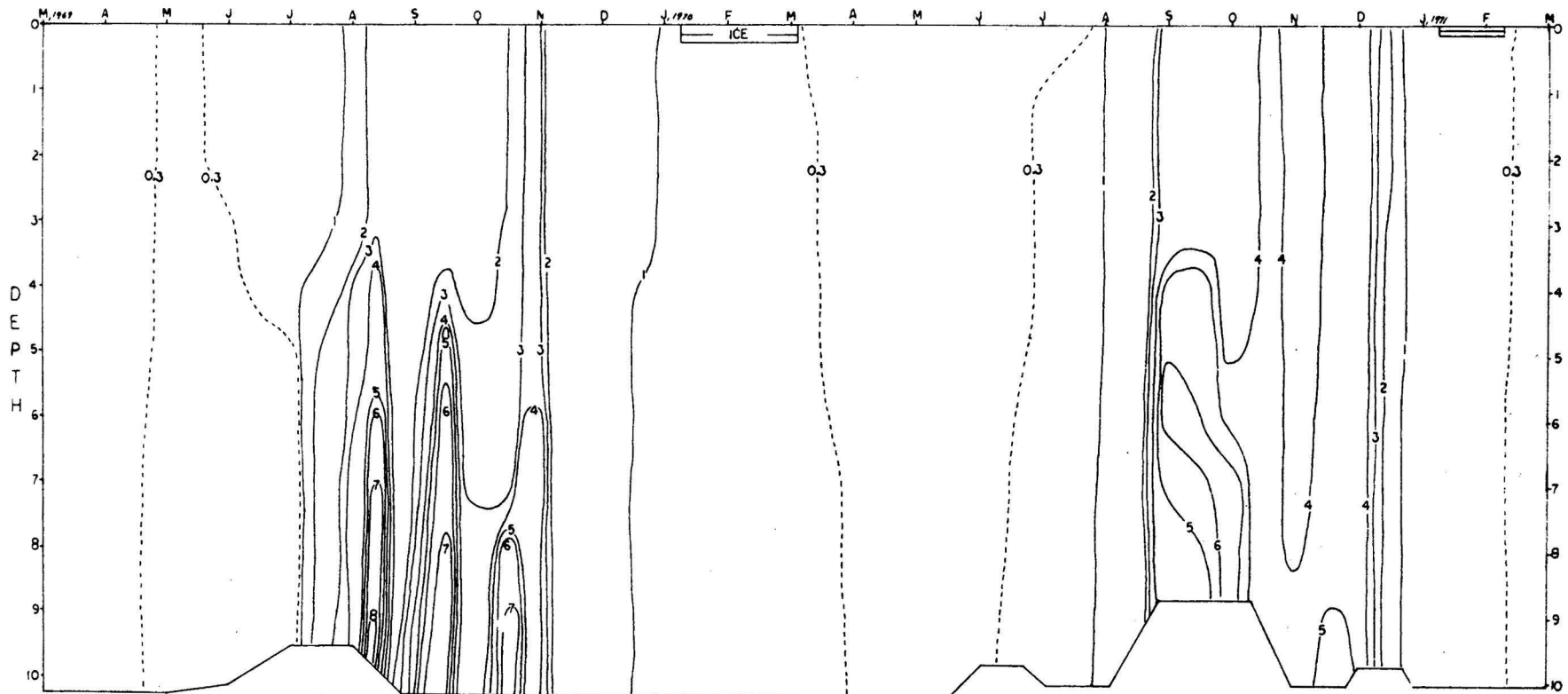


Figure 10. Changes in Ortho-Phosphate concentration (mg/l).

April and May with maximum surface concentration in June of approximately 0.05 - 0.06 mg/l. Maxima ten times greater, 0.56 - 0.68 mg/l, are recorded from the anaerobic bottom waters. These maxima are associated with the debris rain from the vernal blue-green algal bloom. The maxima appear to support large bacterial populations. During the summer there is a gradual decline to a minimum of about 0.0 - 0.02 mg/l. Isolated islands of higher concentrations can be found during this period. These islands accompany certain algal-bacteria associations. With destratification a sharp rise in ortho-phosphate can be noted, ie. up to 0.15 mg/l. This autumnal maximum gradually disappears with the development of the winter diatom population. Ortho-phosphate decreases to trace levels under the cover of ice. At the ice-water interface concentrations as great as 0.14 mg/l have been observed. The high concentrations are due to lysis of diatoms in contact with the ice. The contact probably results in freezing and rupturing of the cells.

The distribution of silicon (fig. 11) appears to be intimately associated with its utilization by diatoms and, also, thermal phenomena. The minimum concentrations of silicon, below detectable amounts, are noted after the winter diatom regime in March and April. The dying population releases some silicon and the level again rises. A population of silicon metabolizing chrysophycean algae develops which reduces the silicon concentration to trace levels. Figure 11 indicates, with a dotted line, the 0.3 mg/l isopleth at which silicon may be considered as limiting. This level is similar to that observed by Jørgensen (1957) in his study of Lakes Furesø and Lyngby Sø. Silicon levels remain quite low during most of the summer in the epilimnion and metalimnion. However, in the hypolimnion silicon accumulates up to 8.30 mg/l. The

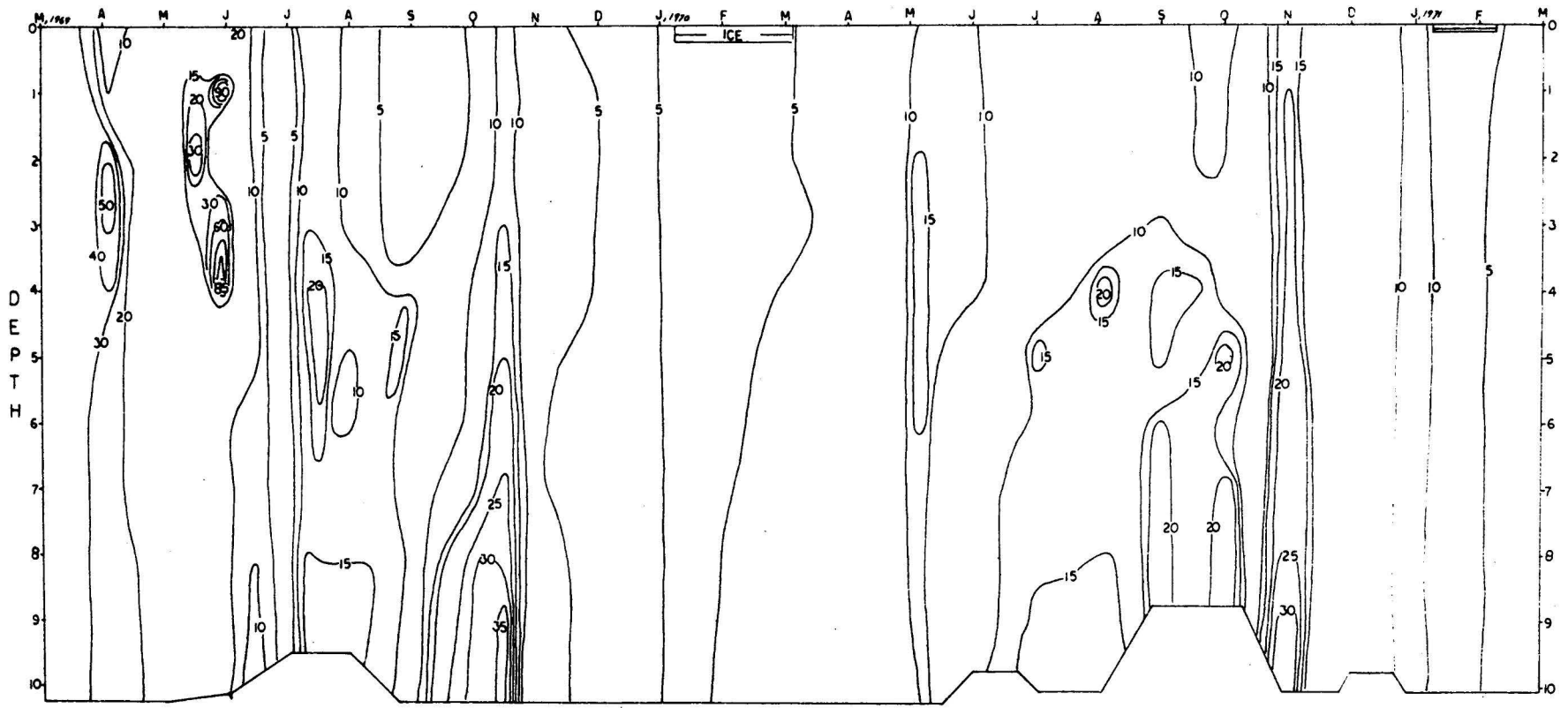
Figure 11. Silica (mg/l) distribution.



enriched hypolimnetic strata are thoroughly mixed with the upper layers during autumnal destratification resulting in 8.8 - 4.7 mg Si/l evenly distributed throughout the water column in October or November. This silicon is rapidly utilized by the developing winter diatom population. There is a precipitous decline to about 0.4 mg Si/l prior to icing. With the advent of freezing over the silicon levels recover temporarily before gradually reducing under the ice cover. The recovery is associated with the die-off of certain diatom species in the early winter. The silicon cycle has a single mode which occurs in conjunction with destratification. The peak is rapidly reduced with the winter diatom bloom to trace levels. The minimum slowly increases during the spring and summer to a peak in the hypolimnion. This later concentration is distributed throughout the water column at turnover. The concentration ranges from trace or undetectable levels to 8.3 mg Si/l.

Biomass measurements (fig. 112) aid in assessing the quantity and distribution of phytoplanktons. A review of biomass profiles between years 1969-1970 and 1970-1971 shows the impact of variations in weather on a year to year basis. The effect of violent storms or sustained windy conditions may cause a mixing of the upper few meters of the water column and result in a dispersed population. Typically this type of weather usually has intense cloud cover associated with it. The calm weather of March, 1969, provided conditions for a bulk fall-out of the winter diatom population, whereas the more turbulent conditions of March, 1970, produced a more even rain of diatom debris. With onset of stratification in 1969 the diatom association began to settle and temporarily accumulated in the region of the developing thermocline before it precipitously fell to the lake sediments. The variation in

Figure 12. Incidence of Biomass (mg/l).



the biomass profiles of the Aphanizomenon bloom in May, 1969, and May, 1970, reflects difference in weather patterns. Late April and early May of 1969 were marked by warm, cloudless days interspersed with a few mild spring showers. In contrast April and May of 1970 were noted for intense, sullen weather which included extended periods of heavy cloud cover and strong winds. The biomass of the blue-green algal bloom in 1969 remained compacted and near the surface with components falling out or floating to the surface when it dissipated. In 1970 the population was evenly dispersed in the upper layers with only minor concentration in mid-water. These events are reflected in the maxima and its vertical distribution profiles. In 1969, the bloom developed a maximum concentration of 33 mg/l at 2 meters, and decreased to 20 mg/l at both 1 and 3 meters, while only 6 mg/l occurred at the surface. The 1970 more homogenous bloom contained 10 mg/l at the surface, 13 mg/l at 1 meter and 17 - 18 mg/l from 2 to 6 meters. Portions of this Aphanizomenon-association float to the surface, cf. late May to early June, 1969, but the major fraction settles to the metalimnion where it disperses. Concomitant with summer stratification several isolated associations are evident. The epilimnetic waters contain a relatively low level stable biomass of 5 ± 2 mg/l. However distinct populations are noted in the metalimnion and hypolimnion. The metalimnetic zone contains a succession of populations. This succession is probably related to the utilization of large quantities of organic matter injected into the metalimnion by the decomposing Aphanizomenon-association. The metalimnetic associations usually reach maxima of about 20 mg/l against a background of 10 mg/l. These associations are short lived and probably reflect rapid changes in the composition of the organic debris resting at the metalimnion. In the hypolimnetic zone a

gradually increasing biomass develops during the summer which then declines until September. This hypolimnetic biomass attains a maximum of 16 - 17 mg/l but much of this increase is due to the accumulation of debris. Microscopic and pigment examinations indicate a paucity of living photosynthetic organisms. A second hypolimnetic maximum of greater magnitude is reached in October with maximum concentrations as great as 38 mg/l. This increase in biomass is the result of the development of a Merismopedia-association. At the onset of destratification the Merismopedia-association extends into the metalimnetic zone and a portion may be transported to the surface. Destratification typically occurs in late October or early November. Certain components from the admixture of epi-, meta- and hypolimnetic floras grow rapidly to produce the temporary autumnal phytoplankton peak -- the Oscillatoria-association. This Oscillatoria-association may attain concentrations as great as 15 mg/l in the surface layers. With complete destratification this association quickly dissipates with a parallel decrease in biomass. The winter regime supports a low biomass, 6 - 10 mg/l, with diatoms as the chief component. The diatom-association remains at a minimum until the lake is ice free. With increasing spring temperature this association reaches its maximum. The biomass data suggests four distinct regimes: a slowly developing winter regime reaching a maximum in March; a spring bloom in May and a stable, stratified summer regime terminated by a burst of blue-green algae in the fall before returning to the winter condition.

The incidence and concentration of the various biochromes provide a means of identifying seasonal distributions of phytoplankton regimes and association structure. These biochromes have quantitative as well as qualitative value. Chlorophyll-a is common to all photosynthetic organisms while chlorophylls-b and -c are limited to certain taxa (Bo-

gorad, 1962). Chlorophyll-b is present in the Chlorophyta as well as the Euglenophyta. Certain of the Chrysophyceae and Bacillariophyceae contain chlorophyll-c. This latter biochrome has also been reported for the Cryptophyceae by Haxo and Forks (1959), Jeffrey (1969) and others. Analysis of these pigments and their distributional pattern provides a technique for describing the contribution of specific phytoplankton taxa in the aquatic ecosystem. The technique supplies information for describing community structure of the standing crop, the recognition of major regimes and successional events within the phytoplankton complement. The succession of regimes is recognizable and frequently dynamic events within regimes are recognizable. Primary production can be assessed when this technique is used in conjunction with the oxygen data. Particular attention should be given to chlorophyll-a, since it is the chromo-enzyme responsible for oxygen production.

The analysis of chlorophyll-a distribution profiles (fig. 13) suggests four separate regimes with interconnecting transition periods. These regimes are identified by the season in which they occur, ie. winter, spring, summer, and fall. However, during the discussion of the phytoplankton these regimes will be identified by certain dominant taxa. The transition will also be characterized by specific algal types. The use of algal identifiers provides a better means of comparing similarities and differences between various lakes. The winter regime is characterized by a nearly uniform vertical distribution with a slight increase in concentration near the surface. With calm, clear bright days this regime achieves a concentration of 110 ug chlorophyll-a/l. This maximum was found in January of 1970 just prior to the lake icing over, but a parallel high concentration did not occur in 1971. A sharp

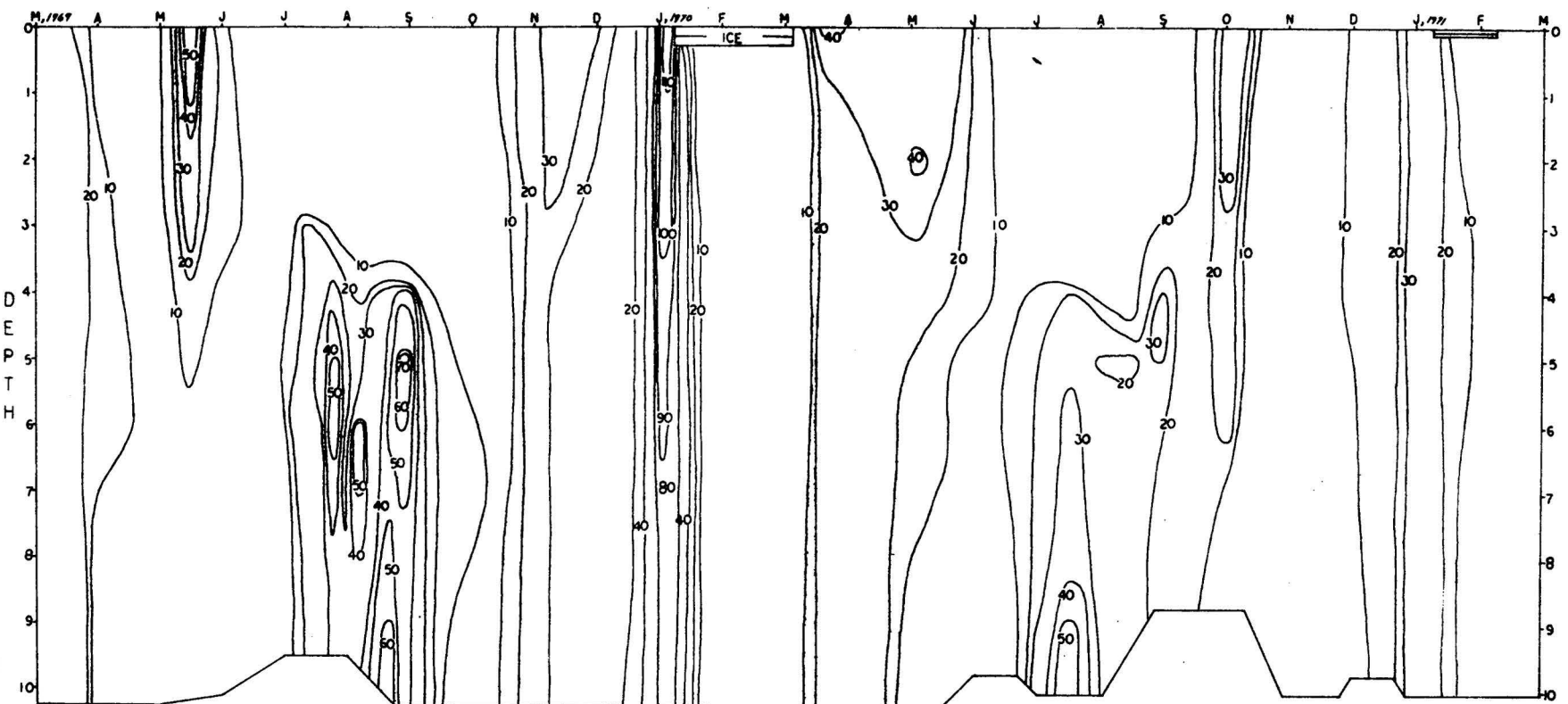


Figure 13. Variations in Chlorophyll-a ($\mu\text{g/l}$) concentration.

increase in chlorophyll-a concentration was noted in December, 1970, and January, 1971, with a maximum of only 43 ug/l. This low peak was undoubtedly due to the reduced insolation caused by long term inclement weather. The winter regime may contain some of the highest chlorophyll-a values recorded during the annual cycle. Even though the temperature remains quite stable during this period light levels decrease dramatically. Thus these high peaks occur during the period of minimum temperature and least insolation. With the advent of icing-over and the accumulation of snow, light may become limiting. Chlorophyll-a levels drop precipitously to 3 or 4 ug/l. The 1969-70 winter had the greatest accumulation of ice and snow. The ice attained a maximum thickness of 20 cm plus an added 30 cm layer of snow. These combined layers effectively attenuated the light and reduced photosynthesis. This reduction in photosynthesis is reflected in the reduced chlorophyll and oxygen concentration at depth, cf. fig. 2. The ice cover was much thinner in 1970-71, approximately 8 cm, without significant snow accumulation. Although chlorophyll-a values were reduced the light levels were adequate to maintain the photosynthesis-respiration balance. In March the winter regime very rapidly degenerates and much of the population rains to the sediments.

The transition between winter and spring regimes is marked by reduced chlorophyll-a levels. This transition flora is evenly distributed throughout the water column, concentrations of 5 - 10 ug chlorophyll-a/l are typical of this period.

In the spring there is a rapid burst of phytoplankton growth in the upper few meters. This second regime is short lived with chlorophyll-a levels approximately one-half that of the winter regime,

42 - 53 ug/l. The duration and concentration of this regime is dependent upon the weather. The water is nearly isothermal, with some slight warming at the surface, thus the lake is very susceptible to wind action. The effects of the wind is evident in the differences between 1969 and 1970 spring regimes. In May 1969 a very compact cell or chlorophyll-a rapidly developed, whereas in April and May 1970 a broad well mixed band developed. In both instances the spring regime dissipated quickly with the onset of stratification. The terminus occurs at about the 10 ug chlorophyll-a/l isopleth.

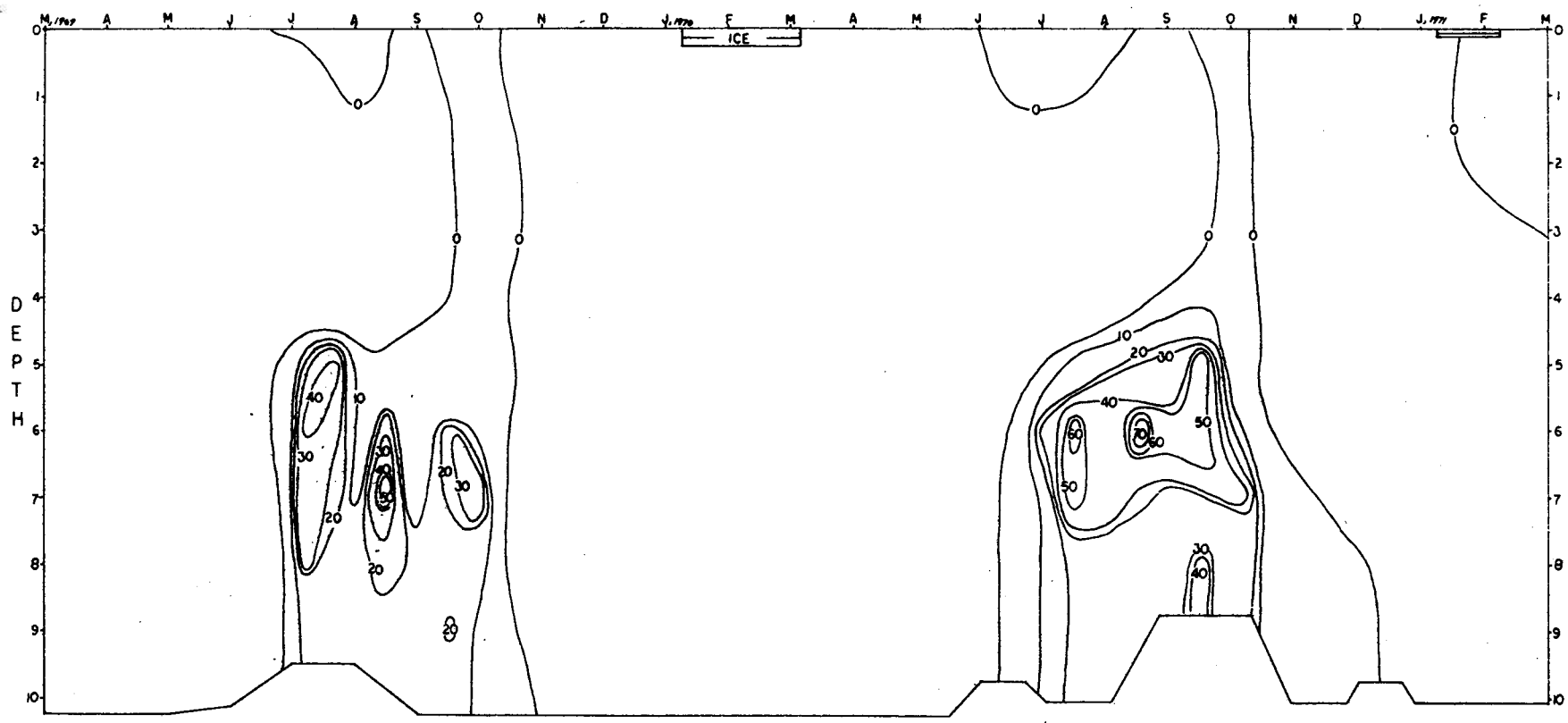
The summer distribution is complex since it develops when the lake is physio-chemically stratified. Three distinct vertical regions, with parallel transition zones, can be recognized. The chlorophyll-a concentration in the epilimnion is greatly reduced, with little variation. It contains a mean chlorophyll-a concentration of 7 ug/l. In the metalimnion and hypolimnion several separate, distinct concentrations develop with each of these concentrations representing a unique population. Three concentrations are detectable in the metalimnion as the season progresses. In the summer of 1969 the first reached a maximum chlorophyll-a concentration of 53 ug/l between 5 and 6 meters. The second, approximately one meter lower and at mid-summer, contains a similar quantity of chlorophyll-a. The last, occurring just prior to destratification, contains chlorophyll-a in concentrations greater than 75 ug/l. In the summer of 1970 the separate populations are less distinct, however these zones are still present but the development of the metalimnetic zones is markedly reduced when compared to those of 1969. The reduction in chlorophyll-a level is probably due to the reduced quantity of spring regime debris. As will be described later,

these metalimnetic concentrations are the results of pigmented, heterotrophic algae. These organisms require substantial amounts of organic substrate for their growth and development. In the hypolimnion a separate community slowly develops reaching a maximum of 55 - 60 ug/l just prior to destratification. This community develops near the water substratum interface, gradually expands upward until it is carried toward the surface and is dissipated during autumnal destratification.

The autumnal regime is short lived and typically occurs immediately after destratification. The population producing the fall peak has its origin in the summer hypolimnion and metalimnion. The autumnal maximum occurs in the upper layers during the months of October and/or November. Maxima of 31 to 36 ug/l occur at the surface and concentrations greater than 30 ug/l may be found as deep as two meters with the remainder of the water volume being well mixed. This autumnal concentration quickly decreases prior to the return of the winter regime.

Chlorophyll-b is limited to green algal and euglenoid phytoplanktons, therefore this biochrome can be used to identify populations of these organisms. The chlorophyll-b levels reflected in the profiles shown in figure 14 indicate not only presence or absence of specific phytoplanktons but locate their position and abundance. This biochrome is essentially absent during the winter regime. However in the later stages of winter and before the development of the spring regime a transition flora can be recognizable. Chlorophyll-b levels of 5 ug/l are recorded during the transition and continue through the spring regime. It should be noted that low levels of chlorophyll-b indicate that neither green algae nor euglenoids are the principal phytoplanktons involved in the spring bloom. Even though chlorophyll-a increases dramatically in May no

Figure 14. Distribution of Chlorophyll11-b ($\mu\text{g}/\text{l}$).



significant parallel increase in chlorophyll-b is observed. The summer regime contains vertical regions similar to those of chlorophyll-a. An even distribution of 1 - 3 ug/l is characteristic of the upper layer of the epilimnion with only trace levels in the remainder. Three distinct zones are identifiable in the metalimnion which can be superimposed upon similar chlorophyll-a zones. The maxima in the three successive metalimnetic zones are 43, 51 and 38 ug/l, respectively in 1969. Slightly higher concentrations were noted in 1970, ie. 60, 70 and 52 ug/l. As will be discussed later in further detail, these annual variations are caused by shifts in dominants within the associations. Chlorophyll-b was detectable at lower quantities in the hypolimnion with a single region occurring in September prior to destratification. Concurrent with destratification there is an even distribution throughout the water column. This pattern represents remnants of the redistributed terminal metalimnion concentration and a transitional flora component. The autumnal regime may contain traces of chlorophyll-b but these are transitory. This biochrome is undetectable from the first of November through January. An analysis of the annual distribution of chlorophyll-b suggests that the green algae and/or euglenoids only make a significant contribution during the summer and are in low numbers or are absent the remainder of the year.

Chlorophyll-c is limited to the cryptomonads, chrysoomonads and diatoms in the freshwater environment. The annual distribution of this biochrome is illustrated in figure 15. Chlorophyll-c may be found in great abundance during the winter regime with its diatom-association. Two different winter profiles were observed during the research period with the most typical present in the years 1969-70 and 1970-71. In

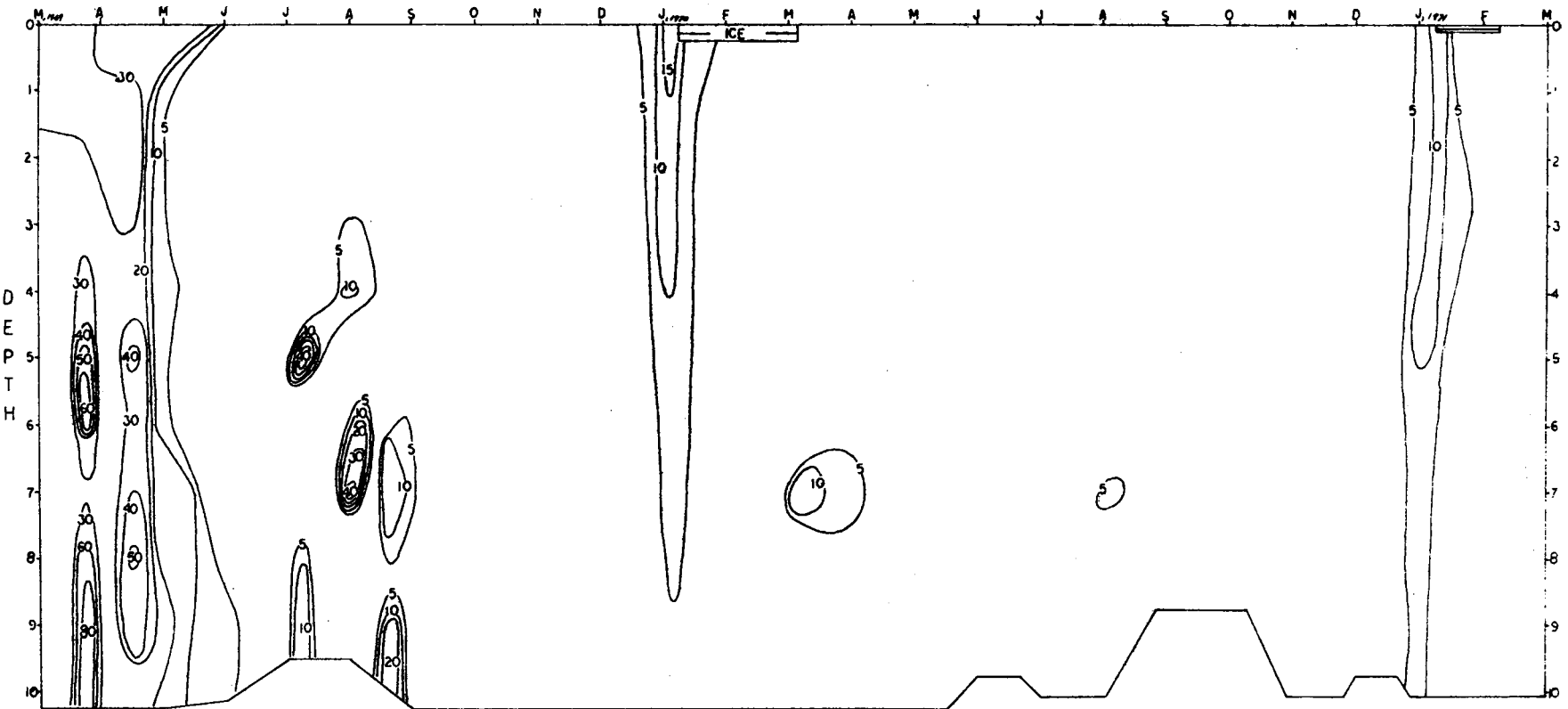


Figure 15. Chlorophyll 11-c ($\mu\text{g/l}$) distributional patterns.

these winter regimes a maximum of 13 ug chlorophyll-c/l was observed prior to the lake icing over. With ice and snow cover light was attenuated, also the cover reduced turbulence. Light is necessary for chlorophyll synthesis and maintenance; and without turbulence many of the organisms sank to greater depth with even lower light intensity. These two effects resulted in a net loss of chlorophyll-c. By the time ice and snow disappears in February or March chlorophyll-c has dropped to the 2.5 ± 0.5 ug/l level. The winter preceeding the experimental period was mild and the lake lacked ice cover. The milder weather with greater insolation resulted in a tremendous diatom population. This out-of-the ordinary population resulted in gradually increasing concentrations until it reached a maximum of 67 ug/l in March, 1969. The precipitous decline of the winter community can be traced by the accumulation of the biochrome in the deeper layers. Traces of the pigment are present throughout the water column until late May, but were undetectable until after thermal stratification. The summer regime usually lacks chlorophyll-c in the epilimnion, however it is present in the metalimnion and hypolimnion. In the summer of 1969 the metalimnion contained three isolated concentrations which succeeded one another and occupied different positions. The first and second maxima attained concentrations up to 40 ug/l, while the third contained only 10 ug/l. Microscopic examination of the organisms within these concentrations indicate the presence of a cryptomonad component with diatoms lacking. Three chlorophyll-a and -b concentrations were also previously noted during the summer of 1970 however only one chlorophyll-c concentration was detected and only one area containing cryptomonads was found in the plankton analysis. This area corresponded to the observed chlorophyll-c

peak of 4.5 ug/l at 7 m in August. In 1969 the hypolimnion contained two transitory concentrations. The earliest represents a partial regrowth of the large winter diatom flora and the second, a distinct concentration which dissipates with fall destratification. With autumnal destratification chlorophyll-c is reduced to trace or undetectable levels. Low levels of 1 - 3 ug chlorophyll-c/l are collected from the upper 4 meters during the autumn-winter transition. The annual chlorophyll-c distribution was characterized by a bimodal distribution, one mode representing the winter regime and the second occurring in several units in the metalimnion during the summer. Each of these modes are produced by different phytoplanktons.

The phytoplankton complex contains greater than one hundred fifty species during the annual cycle. An inventory of the taxa present in the plankton is given in Table 1. Certain of these taxa are major contributors to specific regimes and transitions. Table 2 presents a compilation of the spatial and vertical distribution of dominant contributors. The vertical water column is divided into three depth zones based upon the summer stratification pattern. These depth zones are equivalent to the epilimnion, surface to 3 meters; metalimnion, 4 to 6 meters; and hypolimnion, 7 meters to the bottom. This table only notes the presence or absence of the alga but not its quantity.

The phytoplankton complex may be divided into four major regimes with interconnecting transition floras. The winter regime is dominated by the diatoms Cyclotella, Melosira, Asterionella, Synedra and Fragillaria. The maximum concentration of Cyclotella is approximately 10 million cells/l while Synedra, and Asterionella maxima are only one-tenth that amount. Fragillaria may reach twice the Asterionella

Table 1. Inventory of Phytoplanktons from Lake Fayetteville

Chlorophyceae	staurastrum chaetoceros
Volvocales	S. furcigerum
Chlamydomonas spp.	S. spp.
Carteria spp.	Staurodesmus dickii
Dysmorphococcus variabilis	S. spp.
Peteromonas lenticularis	
Gonium sociale	Euglenophyceae
G. pectorale	Euglenales
Pandorina morum	Anisonema truncatum
Eudorina elegans	Astasia curvata
Volvox spp.	A. klebsii
Tetrasporales	Cyclidiopsis sp.
Asterococcus limneticus	Euglena ehrenbergii
Gloeocystis vesiculosum	E. klebsii
Paulschulzia pseudovolvox	E. oxyuris
Sphaerocystis schroeteri	E. pisciformis
Radiococcus nimbatu	E. schmitzii
Chlorococcales	E. torta
Actinastrum hantschii	E. tripteris
Ankistrodesmus falcutus	Eutreptia viridis
Botryococcus braunii	Lepocinclis ovum
Chodatella sp.	L. radiata
Chlorella sp.	Petalomenas sp.
Closteriopsis longissima	Phacus brevicaudata
Coelastrum microporum	P. longicaudata
C. scabra	P. pyrnum
C. sphaericum	P. suecica
Dactylococcopsis raphidioides	Sphenomonas quadrangularis
Dictyosphaeridium pulchellum	Strombomonas deflandrei
Kirchneriella lunaris	Trachelomonas bernardinensis
Micractinium pusillum	T. granulosa var. oblonga
Nephrocytium agardhianum	T. hispidis
Oocystis solitaria	T. hystrix
O. spp.	T. raciborskii
Pediastrum duplex	T. raciborskii var. rossiea
P. simplex	T. rugosa
Planktosphaera gelatinosa	T. syndnensis
Quadriqula chodati	T. volvocina
Scenedesums bifaga	
S. quadracauda	Pyrrhophyceae
S. spp.	Gymnodiniales
Tetraedron constrictum	Gymnodinium lacustre
T. minimum	Peridinales
T. multicum	Ceratium hirundinella
Tetrallantos lagerheimii	Peridinium cinctum
Tetrastrum staurogeniforme	P. cunningtonii
Conjugatophyceae	Cryptomonadophyceae
Zygnematales	Cryptomonadales
Closterium spp.	Chilomonas paramaecium
Cosmarium spp.	Cryptochrysis sp.
Desmidium baileyi	Cryptomonas caudata

C. erosa
C. marsonii
C. ovata
C. tetraphyrenoidosa

Chrysophyceae

Chrysomonadales

Chrysochromulia parvula
Chrysococcus diaphonus
C. minutus
C. rufescens
Dinobryon divergens
D. sertularia
Kephyrion cupuliforme
K. rubi-claustri
K. schmid
Kephyriopsis ovum
K. cincta
Mallomonas acaroides
M. candata
M. coronata
M. helvetica
M. pseudocoronata
M. tousurata
M. sp.
Pseudokephyrion pilidum
P. schilleri
P. spirale
p. undulitissimum

Stenokalyx inconstans

S. laticallis
Synura petersenii
Uroglenopsis sp.

Bacillariophyceae

Centrales

Coscinodiscus lacustris
Cyclotella chaetoceras
C. meneghiniana
C. stelligera
Melosira ambigua
M. granulata
M. islandica
M. italica
Rhizosolenia eriengis
Stephanodiscus niagare

Pennales

Asterionella formosa
Cymbella spp.
Fragillaria crotonensis
Gomphonema spp.
Navicula spp.
Surirella sp.
Synedra acus

Cyanophyceae

Chroococcales

Aphanocapsa sp.
Coleoaphaerium keutzingianum
C. naeglianum
Chroococcus turgidus
Cyanodictyon sp.
Dactylococcopsis smithii
Gomphosphaera aponina
Merismopedia trolleri
(incl. *M. marsonii*)
M. sp.
Microcystis aeruginosa
M. pulvera
M. spp.
Rhabdoderma lineare

Oscillatoriales

Anabaena circinalis
A. flos-aquae
Aphanizomenon flos-aquae
Lyngbya birgeii
Oscillatoria agardhii
O. augustania
O. tenera
O. spp.
Spirulina okensis

Table 2. Seasonal Distribution of selected Phytoplanktors

Taxon / Date	1969												1970												1971											
	H	A	M	J	J	A	O	D	J	F	M	A	M	J	J	A	O	N	O	J	F	M														
Asterionella formosa	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Cyclotella spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Fragillaria crotonensis	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Stephanodiscus niagare	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Melosira spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Synedra acus	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Ceratium hirundinella	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Peridinium spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Ocellularia tenora	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Coleosphaerium spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Aphanisomenon flos-aquae	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Gloeocystis vesiculosus	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Betryococcus braunii	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Ankistrodesmus spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Planctosphaera gelatinosa	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Sphaerocystis echinasteri	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Pediastrum spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Staurastrum spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Cryptomonas spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Scenedesmus spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Glosterium spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Coelastrum spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Tetraedron spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Bacillaria elegans	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Chlamydomonas spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Carteria spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Ocnium spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Stauridesmus spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Trachalmonas spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Euglena spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Leptocaulis spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Phacus spp.	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Sphenomonas quadrangularis	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Chlamydomonas paramecium	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Spirulina densa	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Ocellularia angustata	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Rhabdoderus linearis	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Ocellularia agardhii	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Marimopectis trolleri	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															
Anabaena circinalis	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■															

■ Present in 0 - 3 meters
 ■ Present in 4 - 6 meters
 ■ Present in 7 - 10 meters

concentration, 2 million cells/l and Melosira approximately one-third. Maximum concentration of the diatom flora is attained immediately prior to ice cover formation and at the terminus of the winter regime. Ice with snow cover interferes with the expending diatom population by reducing insolation and turbulence. Lacking adequate light, growth is reduced or halted. Without turbulence to provide the necessary buoyancy the diatoms sink out of the water column. The precipitation from the surface layers places the diatoms in a less desirable habitat with even lower light levels and reduces turbulence. For comparative purposes this winter regime would be best identified as a "diatom association." During the last phase of this association, a transition flora develops containing Planktosphaera, Scenedesmus, Staurastrum, Oscillatoria tenera, Coelosphaerium and certain golden-brown algae. The browns are represented by the Chrysophytes Mallomonas, Dinobryon, Synura and Uroglena as well as the dinoflagellates Ceratium and Peridinium. The winter-spring (diatom-Aphanizomenon) transition can be identified by the presence of motile Chrysophyceae. Therefore the vernal transition is named the chrysomonad-transition. Aphanizomenon and Anabaena grow very rapidly in May to form the spring regime. At its peak Aphanizomenon may contribute 7 million and Anabaena 1.6 million trichomes/l. These two genera constitute $98 \pm 1\%$ of the spring blue-green algal bloom. Because of its dominance Aphanizomenon is used as the identifier of this association. By early June much of the remnants of the Aphanizomenon-association has settled into the metalimnion and hypolimnion. The green algae are observed during the summer. This epilimnetic flora is composed of the typical planktonic chlorococcalean and tetrasporalean genera. Pediastrum, Scenedesmus, Oocystis and Coelastrum are important members

of this flora as are Sphaeracystis and Gloeocystis. These organisms occur at concentrations of one- to ten-thousand colonies per liter. In June the metalimnetic zone contains numerous euglenoids, particularly Trachelomonas (80,000 cells/l), however greater numbers of colorless euglenoids and cryptomonads eg. Sphenomonas and Chilomonas, are present. These and other species appear after the debris from the Aphanizomenon-association collects in the metalimnion. Cryptomonas spp. also increase in number during this period up to a maximum of 200,000 cells/l in 1969 while only one-tenth this number appeared in 1970. The second association develops in July and is typified by a marked increase in Cryptomonas marsonii and Mallomonas pseudocoronata; Scenedesmus coenobia are also common. Scenedesmus attains quantities of 44,000 coenobia/l, E. marsonii and M. pseudocoronata at 52,000 and 72,000 cells/l respectively in 1969. These organisms were present in about one-fifth this quantity in 1970. The lower concentrations of the 1970 metalimnetic floras are related to the reduced amount of debris available from the Aphanizomenon bloom. The third association develops at the end of the summer regime. Its composition is characterized by well developed Euglena variabilis (14,000 cells/l) plus Cryptomonas marsonii and C. ovata (57,000 and 43,000 cells /l, respectively) populations. The hypolimnetic flora developed slowly after vernal stratification until it is dispersed by autumnal destratification. Prior to destratification the population raises above the water-substrate interface to invade the lower region of the metalimnion. This lowermost flora contains Merismopedia trolleri, Oscillatoria agardhii, Rhabdoderma, the colorless euglenoids Sphenomonas and Cyclidiopsis, plus the green algae Pediastrum simplex and Tetraedron minimum. Merismopedia attains a concentration of 25.5 million cells/l and the filamentous blue-green algae Oscillatoria and Rabdoderma are present in quantities of

900,000 and 11,700,000 trichomes/l. The green algae occur in much lower quantities of 9.5 to 15 thousand organisms/l. With destratification the summer flora is dispersed throughout the water, bringing an end to the complex summer regime. The summer-autumn transition is represented by survival and expansion of selected members of the summer flora, eg. Pediastrum increases to 220,000 coenobia/l and Sphaerocystis to 200,000 colonies/l. The summer-autumn transition is dominated by green algae, thus is titled the chlorophycean-transition. The autumnal regime contains remnants of the transition flora plus some members of the summer flora re-introduced into the upper waters. Anabaena, Aphanizomenon and other Cyanophyceae dominate this regime. Aphanizomenon, however, attains a lower maximum than in the spring, 50-75 thousand vs. 7 million trichomes/l. Coleosphaerium and Anabaena reach peaks of ca. 50,000 colonies or trichomes/l. These blue-green algae comprise about 80% of the autumnal phytoplankton population. The cyanophycean-association terminates dramatically by the lysing of most of the blue-greens and the die-off of the remaining phytoplankton. Very low levels of phytoplankton mark the transition between the autumnal cyanophycean-association and the winter diatom-association. By late November the total number of phytoplanktons is only about 40,000 organisms/l. The transition is the period of precipitous decline of the cyanophyte population and a gradual increase in the diatoms. The phytoplankton sequence is repeated with four regimes of winter-diatoms, a vernal Aphanizomenon-association, a complex, stratified summer regime, and an autumnal cyanophycean-association. These regimes are interspersed with transitional flora composed of chrysophytes, dinoflagellates or tetrasporalean and chlorococcalean green algae.

The assessment of lake trophic status has led to certain methods of classification. Early investigators recognized that relative dominance of selected phytoplankton might be used to identify the trophic status. Lemmerman's (1904) and Wesenberg-Lund's (1905) results were used by Teiling (1916) to apply to terms Caledonian and Baltic, respectively to lakes poor and rich in nutrients. Naumamm (1917, 1919) applied the nomenclature, eutrophic and oligotrophic to nutrient rich and deficient lakes. Thurnmark (1945) suggested that the number of species of the Chlorococcales vs. Desmidiaceae was a reliable indicator of trophic status in Swedish lakes. Nygaard (1949) expanded Thurnmark's concept of developing five different quotients which were applied to Danish lakes and pounds. The quotients of both Thurnmark and Nygaard were applied to Lake Fayetteville data. The quotients were determined for the standard throw-net, 5 meter to surface and 10 meter to surface vertical haul and, also, with the data from the inverted microscope technique. With each of these methods the caution discussed by Brook (1965) were employed.

Nygaard's (1949) compound quotient was applied to the data from the enumeration method for the preparation of figure 16. The enumeration data was employed since it presented the most complete inventory of the plankton. The integrated 5- and 10-meter-to-surface frequently did not contain a complete inventory of the species, thus were of less value. Replicate tows or hauls may result in a wide range of values. It should be noted that the values for the surface at one meter interval are comparable to those of Thurnmark, Nygaard and Brook. The typical throw-net technique employed by the three researchers would seldom sink below 1 or 2 meters thus limiting their sample to a very small portion of the

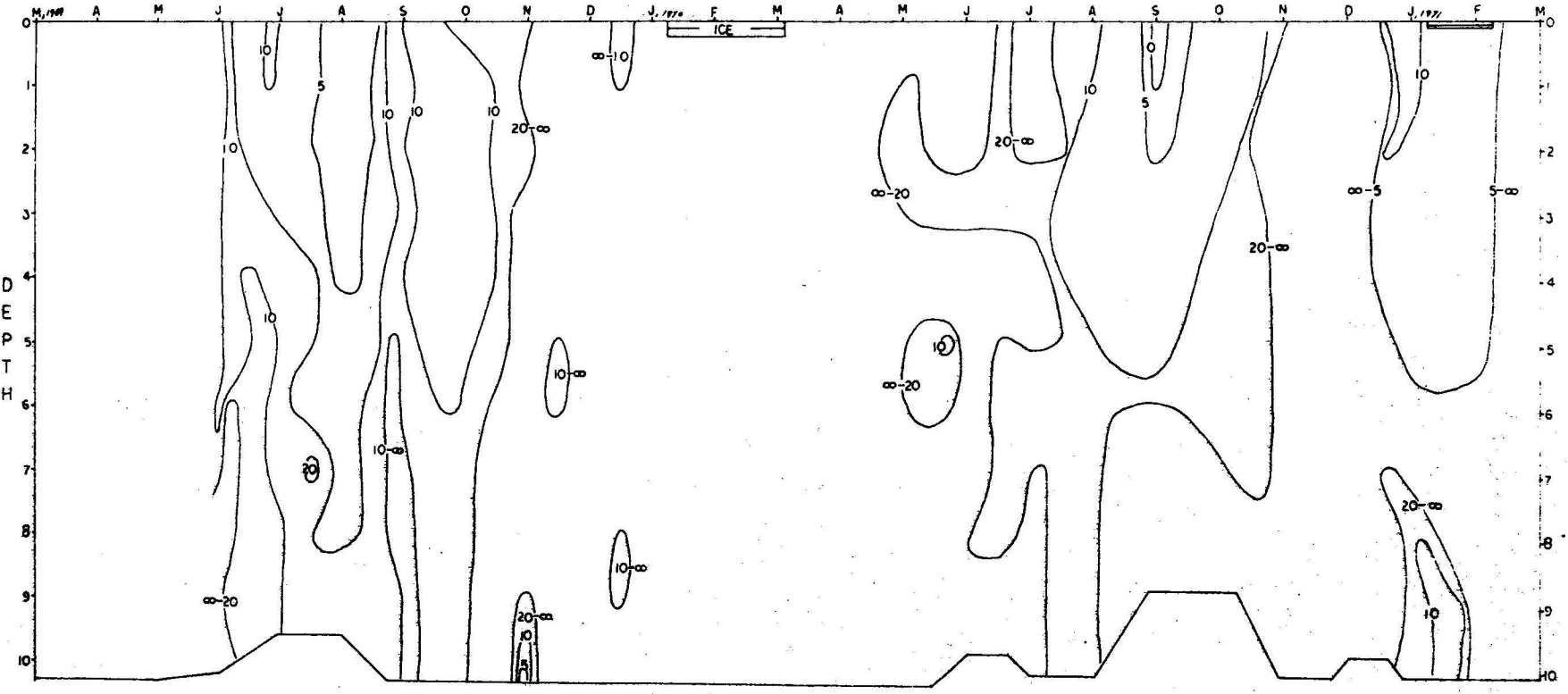


Figure 16. Vertical and seasonal arrangement of Nygaard's Compound Phytolankton Quotient

lake. Also each of these researchers assumes the continual presence of the indicator species, however, this assumption cannot be supported by any of the sampling techniques employed in this study. Surface values from Lake Fayetteville varied from zero in September, 1970, through infinity for most of the remainder of the year. Summer surface values varied from 4.3 to 18 within one week. When compared with Nygaard (1955), studies of Lake Fayetteville vary from chloniotrophic to strongly eutrophic. Similar ranges are expressed at the lower depth. Table 2 demonstrates the major source of error in the application of the quotients. Only two of the forty organisms are present on a perennial basis. The remainder are absent or sink to greater depth where they would not be collected by the throw-net or vertical haul methods. They may also be in such low numbers that they would not be observed with the enumeration technique. The profiles shown in figure 16 do not express a pattern which is applicable to known phytoplankton associations. In retrospect, the various quotients do not reflect a correct view of the trophic status of the lake and, also, cannot be applied to identify annual successional phases. At present it appears that specific algae may suggest point-in-time events but do not represent the trophic or pollution status of the lake.

DISCUSSION

Certain patterns and relationships emerge from the results of this research. The distribution of these "natural" communities provide a basis from which changes in water quality can be judged. The algae respond rapidly to slight changes in water quality, i.e. the algae are continually monitoring water quality. An understanding of the algal component of the aquatic ecosystem provides an integrated approach for

detecting and suggesting means of causing changes in water quality. The interrelations of the organisms and various parameters are to be expanded and refined with the aid of computer analysis. However, anticipating the support of the mathematical treatment, certain correlations are present and discussed, as well as, a comparison with other lakes and reservoirs.

The euphytoplankton community is subdivided into principal, succeeding regimes. These successive regimes follow one another in a predictable pattern. Fortunately the aquatic biologist has the opportunity to observe the patterns of succession several times since they occur on an annual basis. The annual pattern observed in Lake Fayetteville is unique, principally because of the lake's geographic position. This geographic position places this lake in an ideal climatic location, and is clearly reflected in the thermal cycle. In the winter Lake Fayetteville reaches the minimum temperatures observed in northern North American and European lakes while in the summer the thermal patterns are similar to subtropical and tropical lakes. These extremes, from 2.8° with 20 cm ice plus snow cover to 37°, provide a wide range of temperature. The rapid change provides temperature stresses which produce clearly delineated survival and growth configurations.

Temperature profiles (fig. 2) and phytoplankton regimes (table 2) suggest certain interrelationships, however these relationships are usually not simple but multivariate. This interrelationship includes not only temperature tolerance but also the transport of various chemical and biological components. The transport is modified by wind action, thermal stability and density gradients. In the winter diatoms dominate almost to the exclusion of all other algae, with the exception of a few

Chrysophyceae and dinoflagellates. These later algae, with the addition of certain green algae, increase in number as the diatoms disappear. The diatom regime incorporates silicon in the production of the silicious diatom frustule resulting in a net reduction of this ion. Silicon may be a limiting factor in sustaining the regime but also the ammonium-nitrogen concentration is depressed. Ammonium is the principle nitrogen source for the diatom since neither nitrate nor nitrite concentrations change significantly. Phosphate is actively taken up by the diatoms and only trace amounts are detectable by the terminus of the association. Peak concentration may occur immediately prior to and during icing. It should be noted that the phosphate concentration rises dramatically with the decline of the diatom bloom. These peaks appear to be the results of cell lysis. The biomass, chlorophylls-a and -c clearly define the development, maintenance and decline of the association. These latter three analyses are extremely useful in following the dynamics of phytoplankton populations.

The Chrysophycean-association, which succeeds the diatom-association, is composed of armored chrysophytes, dinoflagellates and certain green algae. These plankton increase in number as the diatoms disappear. The silicious armored members of this association further depress the silicon concentration but have little effect on the other chemical parameters sampled. This population has a high growth and photosynthetic rate. The photosynthetic rate is high enough to modify the pH upward through the utilization of the bicarbonate ion. This association, as well as the winter diatom association, is vertically dispersed along the equally vertical thermal profile.

At the onset of stratification an Aphanizomenon-association develops

in the upper 5 meters. This population is large enough to produce the typical pea soup or green paint appearance. During this bloom the lake may be misinterpreted as polluted. This is in deference to its appearance two weeks prior to and after the bloom peak. During the bloom, oxygen concentration temporarily increases to 247% saturation. With the rapid growth and photosynthetic capacity of this population carbon dioxide and bicarbonate levels drop with a concomitant increase of pH to 9.2. Nitrate level decreases rapidly from 1.08 mg/l immediately before to 0.5 mg/l after the bloom. The other nitrogen sources appear not to be significantly altered. The profiles of phosphate suggest that it is not limiting. The levels of phosphate occurring in Lake Fayetteville are similar to other lakes. Our data suggests that nitrate and carbon-source are probably the more important and may become limiting. Considering the size of the Aphanizomenon bloom, ie. 7 - 9 million trichomes/l with a biomass of 33 - 65 mg/l, the phosphates are remarkably only slightly changed. With the lysing of the bloom, however, there are increases of phosphates near the bottom and in the metalimnion. Microscopic examination confirms the presence of disrupted trichomes in these concentration regions. The fate of this association can be traced via biomass concentrations. A portion of the dying Aphanizomenon sinks into the developing metalimnion and another fraction floats to the surface. Chlorophyll data is useful for determining the physiological state of the organisms. Comparison between the biomass (fig. 12) and chlorophyll-a (fig. 13) discloses the usefulness of the biochrome method. The islands of biomass lack a corresponding island of chlorophyll-a therefore the biomass island is dead and incapable of photosynthesis and contributing to further primary production. A note of

(caution: it is important that chlorophyll degradation products, eg. phaeophytin, etc., not be included in chlorophyll determination.

Phaeophytin was isolated from the islands of Aphanizomenon floating to the surface and sinking into the metalimnion suggesting the origin of the biomass but indicating that it is non-functional. Chlorophylls -b and -c showed little change in this association since blue-green algae contain only chlorophyll-a and constituted 97 - 99% of the population. Oxygen (fig. 3) decreases with depth since circulation is reduced and the Aphanizomenon attenuates the light. Oxygen decreases immediately after the bloom as bacteria begin metabolizing the dying population. The debris rain supports an algal population in the metalimnion and during late summer a hypolimnetic population. The oxygenated zone extends to greater depth as summer progresses. This is due to the growth of Euglena, Trachelomonas, Cryptomonas and other algae in the metalimnion. These and their colorless equivalents are capable of metabolizing the organic debris from the spring bloom and the bacteria. The hypolimnion is devoid of oxygen; however, certain blue-green algae and bacteria are capable of growing under these anaerobic conditions. These include: Merismopedia trolleri, Oscillatoria agardhii, Spirulina, and others.

During the summer several associations develop both vertically and horizontally. Vertical distribution follows thermal stratification with epi-, meta- and hypolimnetic associations. The epilimnetic flora consists almost exclusively of green algae. These organisms occur in low numbers but are photosynthetically active. Their activity is reflected in the high pH values (fig. 4), the reduced bicarbonate levels (fig. 5) and increase "P" alkalinity levels (fig. 6). The organisms in this strata

are capable of withstanding temperature above 35⁰ 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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