THE DISTRIBUTION OF PHYTOPLANKTON AND PRIMARY PRODUCTIVITY NEAR THE WESTERN SHORE OF LAKE ERIE

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ABSTRACT

THE DISTRIBUTION OF PHYTOPLANKTON AND PRIMARY PRODUCTIVITY

NEAR THE WESTERN SHORE OF LAKE ERIE

By

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The populations of phytoplankton in near shore areas of western Lake Erie were studied from 1 May 1970 to 7 November 1970. Data were gathered on the distribution of phytoplanktonic numbers, volumes, composition, structure, and productivities in near shore waters of western Lake Erie, a man-made embayment, and a polluted river. Samples for population estimates were collected at monthly intervals. Primary productivity was estimated usually twice per month using the L-D bottle oxygen method.

Nearly 200 species of phytoplankton were observed during the study, the majority of which were common to all areas investigated. Negligible vertical population differentiation was found within stations during the investigation. Greatest numbers were observed in the spring, but greatest phytoplanktonic volumes were observed in late summer. Spring populations, dominated by diatoms, were displaced during the summer by increasing percentages of green and blue-green algae. The rate and composition of the succession varied among the sampling stations.

Greatest species diversities commonly occurred at the inshore areas. Most frequently the lowest equitability was found in the river. Least phytoplanktonic volumes, blue-green algal volumes, mean individual volume, and primary productivities were generally observed in the river. Greatest phytoplanktonic numbers, volumes, and productivities, as well as volumes of diatoms and green algae were most frequently observed in

the man-made embayment. The lake was generally observed to be intermediate in most categories but usually had the least community respiration.

Water temperatures appeared to be a major factor regulating class composition in the spring and late fall. Light appeared to influence phytoplanktonic productivity through photoperiod variation and limited light penetration. Productivity in the embayment closely followed photoperiod. Wind induced turbulence helped to increase the turbidity in the area, reducing light penetration so that little productivity occurred below 1 m. The high turbulence in the lake also appeared to effect a reduction of productivity by causing a disorientation of the plant cells. Neither phosphorus nor carbon concentrations seemed to limit productivity during the study, however phosphate concentrations did pulse with the blue-green algae bloom in the lake. Nitrogen concentrations appeared to be related to seasonal successional patterns in the dominant classes, especially the blue-green algae. Grazing pressure by the zooplankton may have suppressed phytoplanktonic abundances while effecting an increase in the mean individual size of the populations.

The level of primary productivity indicated that the area is in a highly eutrophic state as a result of man induced nutrient enrichment. The area was observed to be nearly exclusively heterotrophic. Most of the sestonic community respiration probably is non-phytoplanktonic in nature. Analysis of the data suggests that increased nutrient enrichment leads to decreased mean individual sizes of the phytoplankton and increased species diversities; these relationships contrast with results obtained in earlier ecological studies.

THE DISTRIBUTION OF PHYTOPLANKTON AND PRIMARY PRODUCTIVITY NEAR THE WESTERN SHORE OF LAKE ERIE

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DEDICATION

This thesis is dedicated to the ideal of world peace through world unity.

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INTRODUCTION

The purpose of this paper is to examine and compare the phytoplankton populations and associated primary productivity of near shore areas in western Lake Erie to two shoreline areas in order to determine distributional variations in population parameters. This investigation was conducted as part of a comprehensive ecological study undertaken to provide base-line information on which the heated water discharges from a new fossil fuel steam electric plant could be evaluated. Information on the distribution of environmental parameters that can potentially influence phytoplankton distributions have been obtained through that study.

Lake Erie has historically been the receptacle of urban and industrial effluents. Vorce (1882) recognized the potentially adverse effects of waste disposal to Lake Erie nearly a century ago. Subsequently, continual use of the lake as a waste depository has created many habitat and chemical alterations that have, in turn, brought about biotic changes in the lake (Carr, 1962; Davis, 1964). Currently, Lake Erie is considered highly eutrophic. This is in many respects particularily true of the shallow western basin which receives the largest concentrations of effluents via the Detroit and Maumee rivers (Powers and Robertson, 1966). Some fear has been expressed that the high concentrations of waste in Lake Erie under certain periodic meteorological conditions will result in an unprecedented mortality to resident aquatic organisms (Carr, *et al.*, 1965).

Under extended periods of calm, hot weather, stratification of the lake can result in severe anaerobiosis from decomposition of discharged waste organic material and settling plankton.

Phytoplankton are responsible for nearly all of the primary productivity in the western basin because of limited light penetration and suitable substrate for benthic plants (Chandler, 1944). It is believed that limited competition for nutrients and massive daily additions to the dissolved nutrient load yields phytoplankton populations capable of supporting very large animal communities (Gottschall and Jennings, 1933). Continual nutrient enrichment has resulted in consistent increases in annual phytoplankton crops (Arnold, 1969) with the classical annual bimodal biomass patterns becoming less noticeable (Michalski, 1968; Davis, 1969), a result of the increasing eutrophic conditions.

The regulators of phytoplanktonic productivity that stand out most commonly as limiting factors are levels of various nutrients, toxicants, light, temperature, and grazing by secondary producers. Most often limiting in freshwaters are nutrient concentrations. Among the macronutrients, low phosphorus, nitrogen and carbon levels are frequently associated with limited productvity (Deevey, 1972). Less frequently, various micronutrients also have been observed in quantities sufficiently low to limit algal productivity (Goldman, 1972). Light and temperature tend to define the limits of seasonal productivity, particularly in the winter (Verduin, 1956). Consequently, under most natural conditions, when no other limiting condition exists, maximum seasonal productivity would be expected when temperature and light were maximum, i.e., during the summer. Within the confines of these limiting factors, the composition and accumulation of phytoplankton can be further regulated by grazing pressure, primarily from the zooplankton (Brooks, 1969).

DESCRIPTION OF STUDY AREA

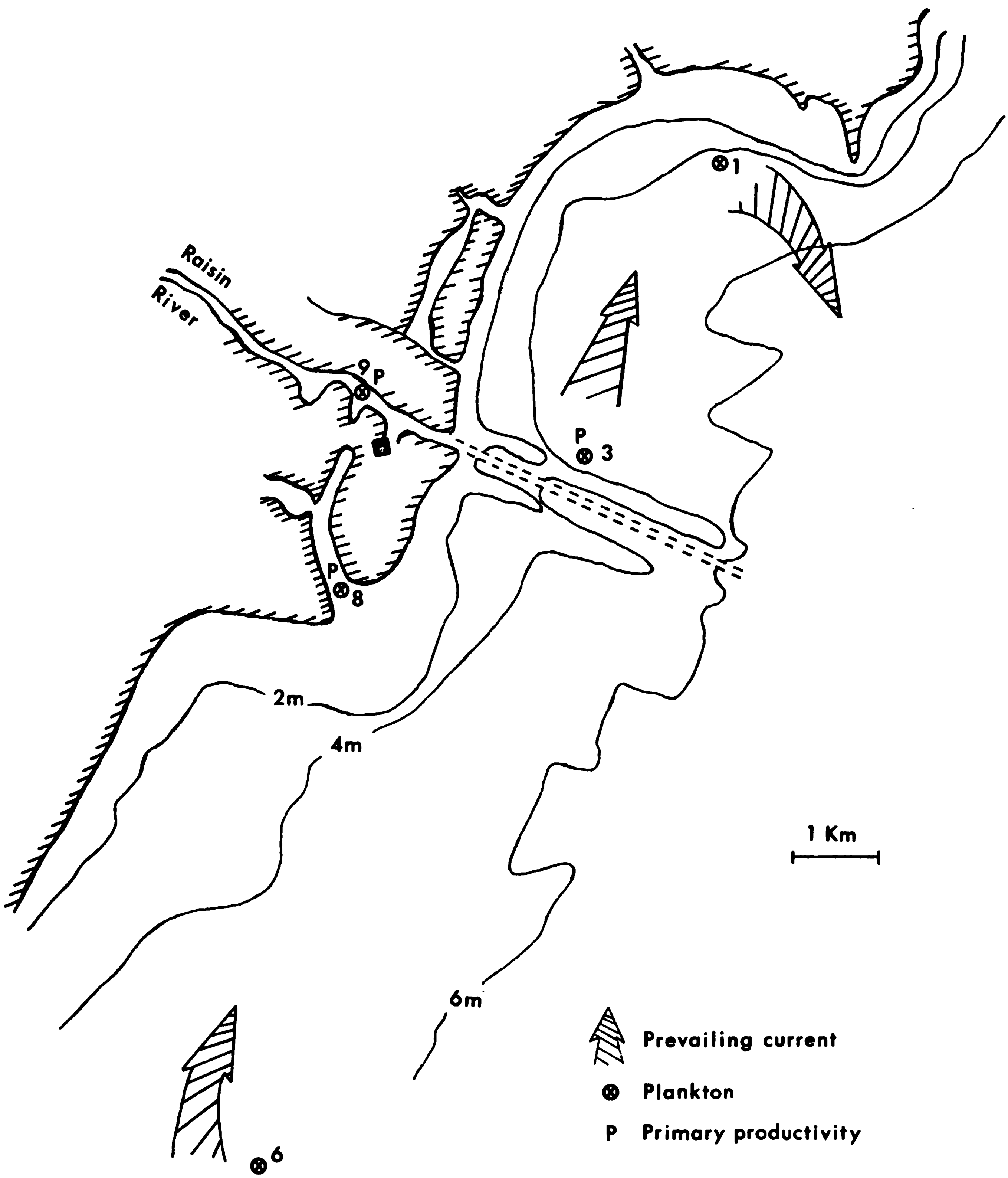
The western basin of Lake Erie has an average depth of 7.3 m, with a surface area of 3,276 km^2 (Carr, et al., 1965). The Detroit River discharges into the western basin at about 5000 m^3/sec and accounts for 95% of the inflow to the lake (Casper, 1965). This inflow delivers approximately 97,500 metric tons of nitrogen and 42,600 metric tons of phosphorus to the lake each year (conversions from Harlow, 1966). Water from the Detroit River flows southward into the western basin and contributes with wind variation to the formation of discontinuous clockwise eddy currents in the Toledo-Detroit area (Hartly, et al., 1966). As a result, northeastward currents prevail along the Michigan shore. The western basin has a flow-through time of about two months and the entire lake about three years (Verduin, 1969).

Stations selected for study of the near-shore phytoplankton of Lake Erie centered on the mouth of the River Raisin at Monroe, Michigan (Figure 1). Three lake stations were positioned approximately parallel to the prevailing north-easterly current (Figure 2): one about 5 km north of the mouth of the river and 1.5 km from shore (station 1); one about 1.0 km east of the river mouth (station 3); and the last south of the mouth about 10.5 km and 3 km from the shore (station 6). Bottom sediments of the north lake station range from course gravel to silt and clay, station 3 is predominantly sand, and the south lake station is primarily silt and clay.

Two inshore stations were selected for comparison with the lake (Figure 2). A discharge canal (station 8), 2.5 km long by 150 m wide,

Figure 1. Map of the study area in relation to western Lake Erie.

Figure 2. Map of the study area including positions of the sampling stations.


Raisin
River
9 P
P
3
1
P
8
2m
4m
6m
6
1 Km
Prevailing current
Plankton
P Primary productivity

was constructed during 1969-1970 to carry cooling water effluent from the steam electric plant. During this study, no water flowed through the discharge canal. It was essentially an embayment of Lake Erie, in which water freely exchanged with the lake during storms and seiches. A minute flow ($< 1\ m^3$/sec) from Plum Creek, a tributary also contributed to the discharge canal. Bottom composition of the 6-7 m deep dredged canal was silt, clay and plant debris (mainly of marsh origin).

The second inshore station (station 9) was located in the highly polluted River Raisin. The river receives primarily treated municipal wastewater and papermill wastes from Monroe, Michigan. A putty-like sediment combined with paper fiber and traces of oil make up the river bottom. Depths of 6-7 m are maintained in the river by annual dredging. Mean river discharge, measured by the U.S. Geological Survey during 1970, was 17 m^3/sec, but varied from a high mean monthly discharge in the spring (41.9 m^3/sec) to the low mean monthly discharge in the summer (3.3 m^3/sec).

Chemical and physical conditions of the study area during the study period are presented in detail by Nalepa (1972) and Cole (1972). A brief summarization of pertinent observations follows. Water temperatures varied uniformly among the three lake stations which differed only slightly from the inshore stations in the spring. During early May temperatures in the lake were 12.8 to 15 C, 17 C in the discharge canal and about 14 C for the river. Maximum temperatures for all five stations were reached in August (about 25 C). Thereafter, the temperatures dropped steadily. Ice formed along the shore in December and by the middle of January an ice pack had formed in Brest Bay.

Seasonal fluctuations in oxygen were similar for all stations with the exception of the river which was always lower. Maximum oxygen concentrations occurred in early May, ranging from 9 mg/liter in the lake to 5.5 mg/liter in the river. Concentrations decreased to the minima recorded on 11 October 1970 with 4 mg/liter found in the lake to 0.5 mg/liter in the river. In late October the oxygen concentrations began to rise sharply in a delayed response to seasonal cooling.

Highest nitrate-nitrogen concentrations (> 5.0 mg/liter) were observed for all parts of the study area in the spring and lowest concentrations ($\sim$ 0.02 mg/liter) in August and September. Concentrations then gradually increased into winter. River concentrations were significantly higher ($p < 0.05$) than the rest of the area about half of the time during the spring and consistantly higher ($p < 0.05$) during the entire summer.

Total phosphorus concentrations fluctuated sporadically during the study. Most stations had lowest concentrations during the spring and early summer. A notable pulse occurred at most stations in August. Consistantly higher concentrations ($p < 0.05$) were found throughout the study in the river, with intermediate concentrations observed in the lake and discharge canal.

Similar seasonal changes in sestonic organic carbon (> 0.45 μ) occurred at all stations during the study. Highest concentrations occurred in May. The concentrations decreased then fluctuated until late August when another peak developed. Concentrations averaged consistantly lower in the lake, with the inshore areas averaging 3-12 mg/liter higher.

Suspended solids (seston), consisting mainly of detritus, resuspended bottom material, and plankton, represents the total particulate material (> 0.45 μ) in the water. The Maumee and Detroit rivers deliver large quantities of suspended material to Lake Erie, the bulk of which remains in the western basin (Pinsak, 1967). This material essentially remains in suspension, through wind generated turbulence, and contributes to the low light penetration observed by Verduin (1969) to be less than 5% at 1 m.

During 1970, the seston had three definite peaks at the lake stations: 15 May, 63 mg/liter; 4 August, 36 mg/liter; and 15 September, 33 mg/liter. Little variation was encountered between the lake stations but inshore values were generally about twice those of the lake. Much of the detritus in the water during the early months of the study had as its source the irregular dredging activities in the discharge canal and during the later summer months the dredging of the River Raisin shipping channel. At no time during this study did the secchi disc reading at any station exceed 1 m.

Zooplankton distributions were found to be generally uniform among the lake stations which differed from the inshore stations (Nalepa, 1972). Highest biomass occurred at the lake stations while highest densities occurred in the discharge canal. The river had the lowest density and biomass. Although the density and biomass differed widely among the lake and inshore areas the species composition was essentially the same.

Parkhurst (1971) investigated the fish populations concurrently with this study and found an uneven distribution throughout the study area. The greatest density and biomass of fish occurred in the discharge canal. For most of the study, the river was devoid of fish.

Various weather parameters on the days for which primary productivity estimates were made are given in Table 1. Observations were made at the Toledo (Ohio) Express Airport (U.S. Dept. of Commerce, 1970). Climatic conditions on sampling days were generally representative of the typical seasonal conditions experienced.

Table 1. Meteorological conditions on days primary productivity estimates were made including each month's means (M.M.) (U.S. Dept. of Commerce, 1970).

Date 1970	% Possible Sunshine	% Sky Cover (Sunrise to Sunset)	Average Wind (Km/hr)	Wind Direction	Mean Air Temperature
5/1	0	100	27.4	SW	18.9
5/15	52	60	15.3	SW	20.0
5/27	53	70	17.7	W	13.9
M.M.	52	63	16.3	W	16.2
6/10	28	80	10.1	S	23.3
6/23	100	10	8.9	S	18.9
M.M.	66	58	13.8	W	19.6
7/7	92	50	13.0	SW	21.1
7/21	98	20	11.1	NW	16.1
M.M.	63	68	12.9	NW	21.8
8/4	95	50	9.5	NW	16.1
8/24	86	30	8.0	W	18.9
M.M.	73	46	11.1	E	20.8
9/1	91	30	6.4	NE	14.4
9/29	59	70	10.9	SW	7.8
M.M.	53	69	12.6	W	17.8
10/27	25	80	15.9	E	15.6
M.M.	49	63	14.2	W	12.2

MATERIALS AND METHODS

Field Procedures

Samples for phytoplankton population analysis were collected at four week intervals from 1 May 1970 to 7 November 1970. Additional population data were collected on 23 January 1971 and 18 February 1971. Primary productivity estimates were made during the ice free season of this period at three of the stations (3, 8, 9) at approximately bi-weekly intervals when possible.

Duplicate samples from each of two depths, 0.5 and 2.5 m, were collected from each station for population analysis. The lake stations were marked with buoys and the duplicate samples taken about 150 m east and west of each buoy. Inshore stations were identified from on-shore reference points and the duplicate samples were taken about 65 m apart. Samples were collected with a clear, Plexiglas, 8.1 liter Van Dorn water bottle. From each sample 500 ml were preserved with 1.5% solution of formalin (Weber, 1968). The remaining 7.6 liters were analyzed for zooplankton (Nalepa, 1972) and water chemistry (Cole, 1972).

Samples for estimation of primary productivity were collected with a 4.1 liter PVC Van Dorn water bottle. Samples were taken from the surface, 0.5, 1.5, and 2.5 m. The water from each level was delivered by gravity flow from the water bottle to two 300 ml DO light bottles and two dark bottles, formed by double wrapping 300 ml DO bottles with black plastic tape. The dark bottles were painted white to prevent their excess heating from solar radiation. Foil caps, secured by a rubber band, were placed on the stoppers of the dark bottles after filling. When the four bottles from a specific depth were filled, they were attached to a suspension rod and hung from an incubation float at the depth from which the sample was drawn. On most occasions the tropholytic zone of the three stations occurred at 2.5 meters at all three stations.

In situ incubation of the samples was conducted for approximately a four hour interval over the noon period, inorder to obtain estimates from the periods of maximum photosynthetic activity (Morgan and Strass, 1969; Vollenweider, 1969).

Gross primary productivity estimates were made by the change in oxygen method (Strickland, 1960). Oxygen concentrations were determined prior to and upon completion of the incubation. Analysis of oxygen on 15 May, 27 May, 10 June, and 27 October were completed using the Winkler dissolved oxygen test. On the remaining dates a Yellowsprings Model 51A oxygen meter with self-stirring probe was used. The meter was periodically standardized against Winkler determinations.

Dawn to dusk primary productivity estimates were made on 1 July 1970. The estimates were made over four time intervals in the lake (station 3) and discharge canal (station 8).

Laboratory Procedures

Population samples were returned to the laboratory for enumeration by the membrane filter method described by McNabb (1960) and recently adopted by Standard Methods (A.P.H.A., 1971). Briefly, a 5 to 40 ml aliquot of the 0.5 liter phytoplankton population sample, depending on population concentration, was filtered through a 2-inch filter (type HA, 0.45μ). The filter was placed on a 2x3 inch microscope slide, coated with emersion oil for clearing the filter, and stored horizontally in the dark until enumerated. The filters were examined with a dark phase microscope at 200X and 430X. The frequency-occurence of each species was calculated from observations made in 30 fields from each filter. Conversion from the number of occurrences of a species observed in the 30 fields to its density per milliliter was based on the formula given by McNabb (personal communication), modified to fit this study's data:

$$\text{no./ml} = \frac{d \times 10^9}{(\text{microscope quadrant area in } \mu^2) \times (\text{ml filtered})}$$

where d, based on frequency occurrence, is found in a table in McNabb's (1960) paper.

Identification on the filters was impossible for most species of unicellular centric diatoms, many species of pennate diatoms, species of the diatom genus *Melosira*, and the genera *Aphanizomenon* and *Oscillatoria*. Proportional counts were made of appropriate mounts. These results were applied to the total counts of the undistinguishable taxa from the filters to determine their respective abundances. Material for proportional diatom counts was prepared according to Weber (1970), except that combustion of the organic material was accomplished in a muffle furnace at about 540° C for 30 minutes. Mounts of diatoms were made with hyrax (Hanna, 1930). The genera of *Aphanizomenon* and *Oscillatoria* were identified from separate wet mounts of the material and the proportions determined were applied to the total counts of the two genera on the appropriate filter. At no time was there noticeable numbers of dead plant cells in fresh samples as observed by Verduin (1951), therefore, no effort was made to eliminate dead material in the counts.

Species identifications were made through use of keys by Tiffany (1934, 1937), Taft (1942, 1945, 1964), Taft and Kishler (1968), Prescott (1962, 1970), Weber (1966), Hustedt (1930), Patrick and Reimer (1966), and Hohn and Hellerman (1963). Revisions in classification are according to Palmer (1962). Aid in the general identification of phytoplankton, especially diatoms, was given by Mr. B. H. McFarland and Dr. C. I. Weber of the Analytical Quality Control Laboratory, EPA, Cincinnati, Ohio. More specific taxonomic problems were referred to Dr. C. D. McNabb, Michigan State University.

Biomass determinations were completed by making random measurements (generally > 10) of each species, throughout the sampling period, with a Whipple micrometer (Welch, 1948). The annual means of these measurements for each species were calculated and applied to geometrical solids that most closely resemble the species' shape to determine their average annual volume for the cell, colony, or filament. With those species where insufficient measurements were made, values for computing volumes were obtained from the literature.

Experimental Analysis

Two-way analysis of variance was applied to the population data gathered on each date to assess vertical (depth) and horizontal (station) differences. The parameters analyzed included total numbers, total biomass, numerical diversity, numerical equitability, volumetric diversity, volumetric equitability, mean individual species volume, Cyanophyceae (Blue-green algae) volume, Chlorophyceae (green algae) volume, and Bacillariophyceae (diatom) volume. Tukey's multiple comparison test (Mendenhall, 1968) was used to identify significantly different ($p < 0.05$) values when the analysis of variance indicated that differences existed.

All statistical calculations were based on the per milliliter values calculated from the original frequency occurrence obtained during microscopical analysis.

Diversity was calculated by the Shannon formula,

$$\bar{d} = - \sum_{i=1}^{S} \frac{N_i}{N} \log_2 \frac{N_i}{N},$$

and equitability, or uniformity of species composition, by

$$E = \frac{2^{\bar{d}}}{S},$$

$\underline{N}$ being the total number of individuals observed, $\underline{N_i}$ being the number of individuals in the $\underline{i}$th species and $\underline{S}$ being the total number of species (MacArthur, 1965).

Since no difference was found in the vertical distribution at the stations, a phenomenon observed by others for Lake Erie (Chandler, 1940; Verduin, 1951; Hintz, 1955), the data obtained in the four replicates at each station are presented as means for the station. From means for total numbers and total biomass, conversions to total phytoplanktonic carbon content were made using appropriate formulae from Strathmann (1967).

The primary productivity data were interpolated to estimate the productivity and respiratory rates for the 1 and 2 m intervals. Duplicate data for the same levels at the station were averaged to determine metabolic activity of the column under a square meter. Oxygen concentrations were converted to carbon concentrations using the carbon to oxygen ratio, 0.312, as suggested by Westlake (1969).

RESULTS

Phytoplankton Abundance

Spatial variation

Total numbers and volume: Virtually no differences in numbers or volumes were detected between depths during the study but differences among stations occurred frequently (Appendix, Tables A1 and A2). Differences among stations on any particular date were as much as an order of magnitude, but relative abundances among stations often changed from one sampling date to the next. However, some consistant trends are recognized.

The river (station 9) consistently had the smallest volume of phytoplankton, being significantly lower ($p < 0.05$) than the stations with the greatest abundance on 87.5% of the dates. Numbers of the phytoplankton in the river, however, did not consistently rank lower or higher than other stations. In the discharge canal (station 8) both numbers and volumes of phytoplankton were significantly greater than stations with the least abundance of many (62%) of the dates sampled. These observations are reflected in the annual averages presented in Table 2. Volumes were greatest in the discharge canal, intermediate in the lake, and least in the river. Numbers were also greatest in the discharge canal, while highly variable among the lake stations. The average of all lake stations was similar to average river numbers of phytoplankton.

The relative ranking of volumes and numbers at the stations indicate that the river had the smallest mean individual phytoplankton

Table 2. Means by sampling station of numbers, volumes, mean individual volumes, and class volumes for all dates sampled during the study.

Station	Mean Numbers (no./ml)	Mean Volumes (x 10^4 μ^3/ml)	Mean Individual Volumes (μ^3)	Mean Blue-green Volume (x 10^4 μ^3/ml)	Mean Green Volume (x 10^4 μ^3/ml)	Mean Diatom Volume (x 10^4 μ/ml)
1	2002	1582	9,583	784	97	342
3	1332	1525	10,187	1170	116	238
6	1075	1450	10,338	1125	59	221
8	2638	1744	7,809	1014	162	552
9	1583	685	5,355	416	54	200

volumes. The average size of the river's phytoplankton was consistently lower than at the remaining stations (Appendix, Table A3). None of the remaining stations had consistently greater mean individual volumes than other stations in this study.

Volumes by class: Class composition by volume varied among stations while vertical distribution remained uniform. The river consistently had a lower volume of blue-green algae than the other stations (Appendix, Table A4). This was reflected in low annual means for the river as well (Table 2). There was a tendency for blue-greens to be more abundant most frequently in the discharge canal but not much more frequently than in the lake.

Both green algae (Appendix, Table A5) and diatoms (Appendix, Table A6) were more abundant by volume in the discharge canal when there were identified ($p < 0.05$) differences in abundances among the stations. Significant differences occurred on about half of the dates sampled. The tendency for greater abundances in the discharge canal is reflected in the annual mean volumes (Table 2). The relative volumes in the lake and river varied from date to date. No consistent differences were observed between the two areas, although annual means were slightly lower in the river than in the lake (Table 2).

Phytoplankton in classes other than the three major classes discussed above played a minor role in the near and inshore waters of Lake Erie in 1970. Euglenophyceae, primarily *Euglena* sp., made up 1% of the volume of the south lake station and 10% in the discharge canal during May. *Ceratium hirundinella*, a dinophycean, accounted for 4 to 6% of the phytoplanktonic volume in the lake during late July. This species made an appearance (3% by volume) in the discharge canal almost two months later and was never important in the river (< 1%).

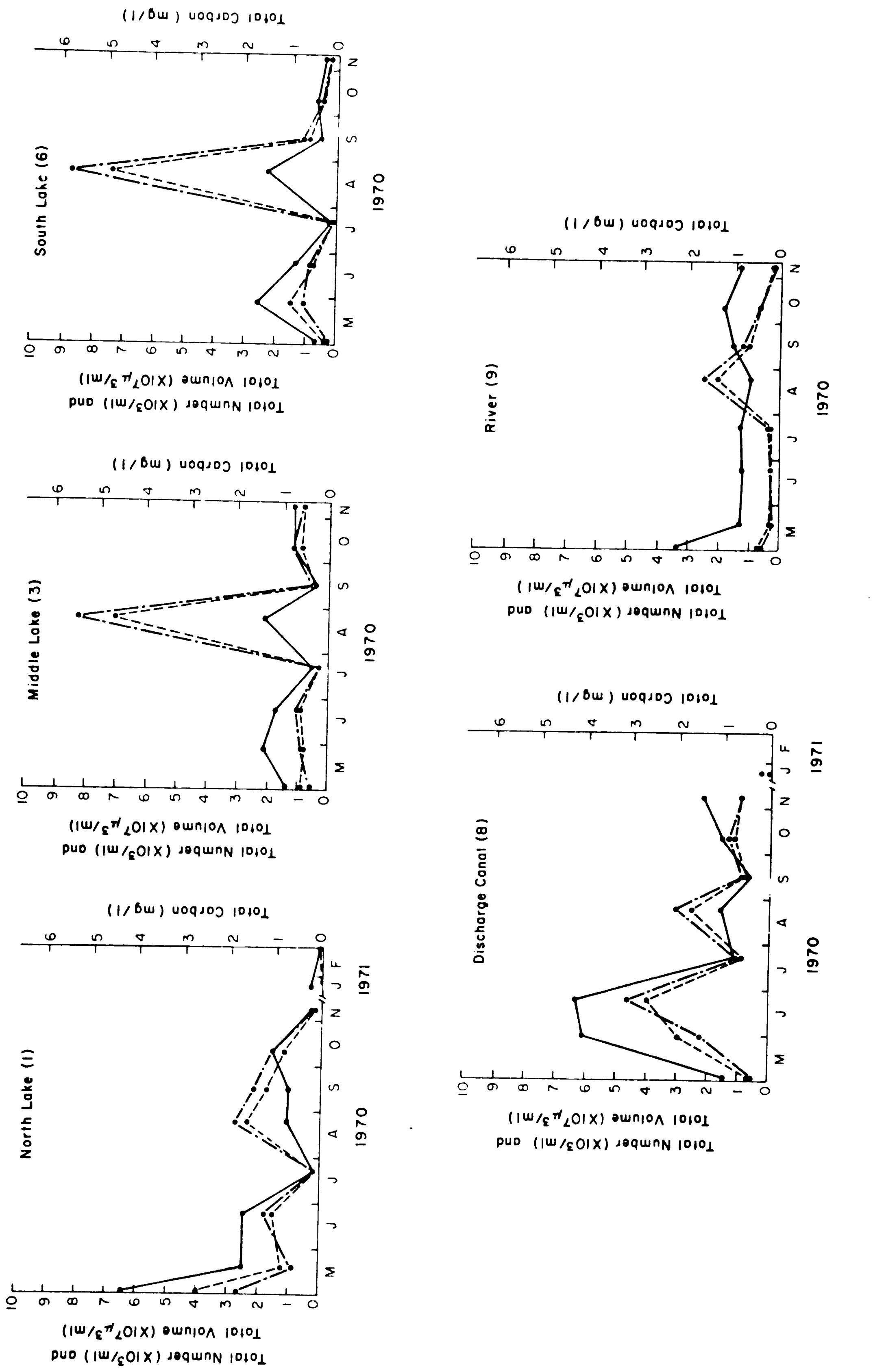
Seasonal variation

Total numbers, volumes, and carbon: Seasonal changes in phytoplankton numbers, volumes, and carbon content were fairly uniform throughout the study area (Figure 3). Remnants of a spring phytoplankton bloom were detected at the north lake and river stations when sampling began on 1 May 1970. The maximum density of phytoplankton found in the lake (2530/ml) was recorded at that time. The maximum density (6333/ml) found at any station during the study occurred in late June in the discharge canal. A summer minimum occurred in late July in the lake and discharge canal. After that period the abundances increased at all stations to bloom proportions (mid-August). At this time the maximum phytoplanktonic volumes were recorded for the lake (7.38×10^7 μ^3/ml) and the river (2.08×10^7 μ^3/ml). After the bloom, phytoplankton volumes, numbers, and carbon sharply declined to low fall concentrations.

Winter phytoplankton concentrations were much lower than concentrations found for the other seasons. Near the north lake station on 23 January 1971, shortly after safe ice formed, a mean volume of 1.40×10^6 μ^3/ml was observed with a mean count of 438/ml. When sampled three weeks later on 18 February 1971 the volume in the lake had decreased to a mean of 1.85×10^5 μ^3/ml with an average number of 147.5/ml. The discharge canal had similar concentrations at this time: a mean volume of 2.11×10^5 μ^3/ml and a mean number of 327/ml.

Carbon concentrations changed generally like the volumes and numbers (Figure 3). However, planktonic carbon concentrations were proportionally lower in the spring and fall than numbers and volumes and proportionally higher during summer. Explanation for these variations are revealed when seasonal changes of the major classes are considered.

Figure 3. Mean numbers, volumes, and carbon contents of phytoplankton by stations. _____ numbers; ----- volumes; -.-.- carbon.



North Lake (1)
Middle Lake (3)
South Lake (6)
Discharge Canal (8)
River (9)
Total Number (X10³/ml) and
Total Volume (X10⁷μ³/ml)
Total Carbon (mg/l)
M J J A S O N J F
1970
1971

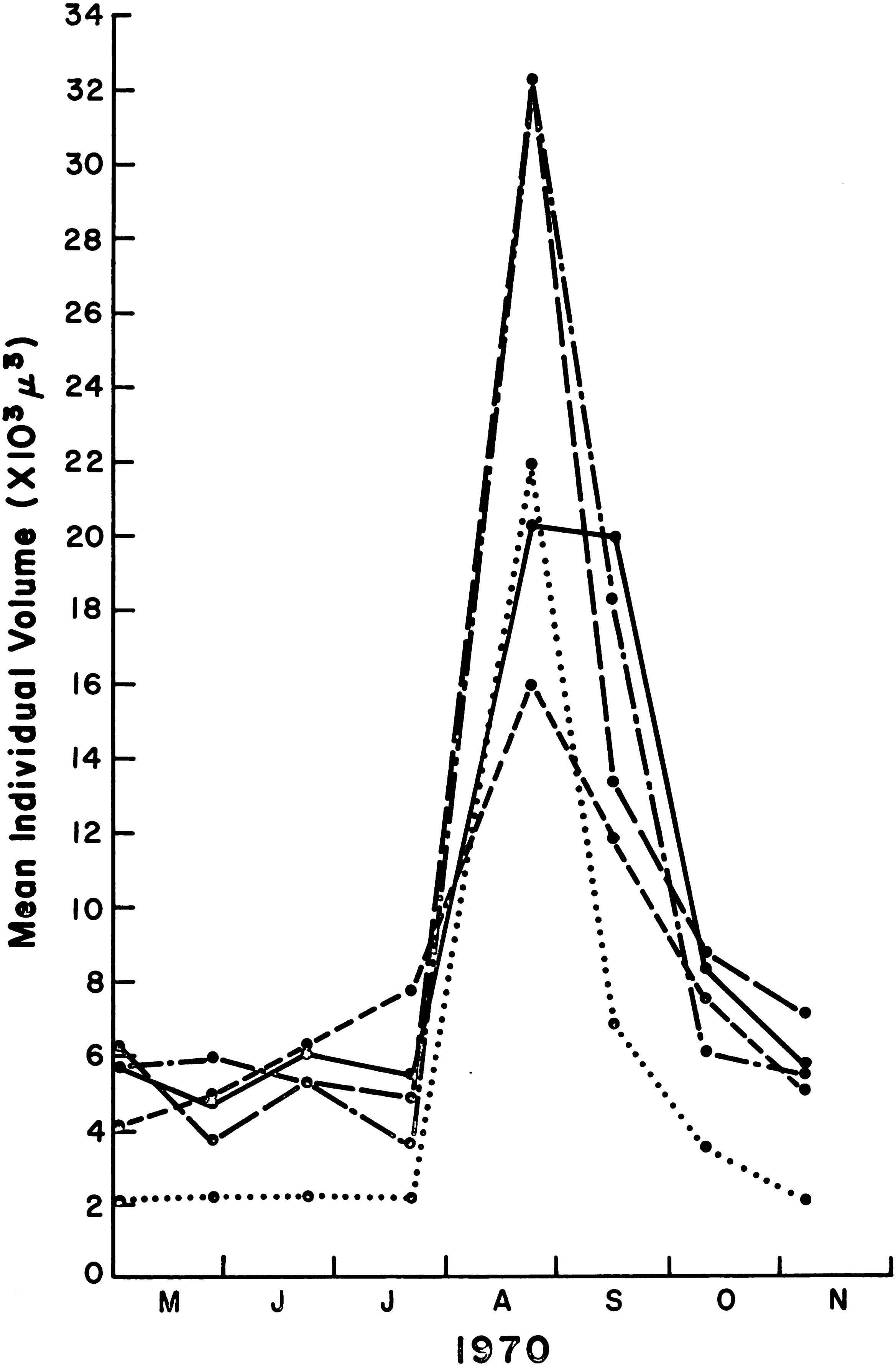
Fluctuation in the ratio of carbon content to numbers or volumes are the result of fluctuations in the abundance of diatoms in relation to the other classes. Diatoms have a lower carbon content than do other species classes (Strathmann, 1967).

Seasonal dynamics of the dominant algal classes, which differ in average volumes per species, also can help to explain seasonal shifts in mean individual phytoplankton volume (Figure 4). Similar seasonal dynamics of the mean individual volumes existed at all stations. They remained rather constant from spring to mid-summer, then increased sharply in late July. After peaking in August, corresponding with the blue-green bloom, the mean individual volume declined through the fall.

Class dynamics: Successional patterns in class volume composition were generally the same at all stations (Figure 5). Diatoms, the spring dominants, were replaced first with increasing percentages of green algae then with larger percentages of blue-green algae until the blue-greens comprised over 90% of the phytoplanktonic standing crop in mid to late summer. During the fall the proportions of blue-green algae decreased while diatoms increased. The summer replacement of diatoms and green algae by blue-green algae was most rapid in the discharge canal. The summer's green algal concentrations were most persistent in the river. Of the inshore stations, the discharge canal was most similar to the north and south lake stations while the river had the greatest similarity to the mid-lake station.

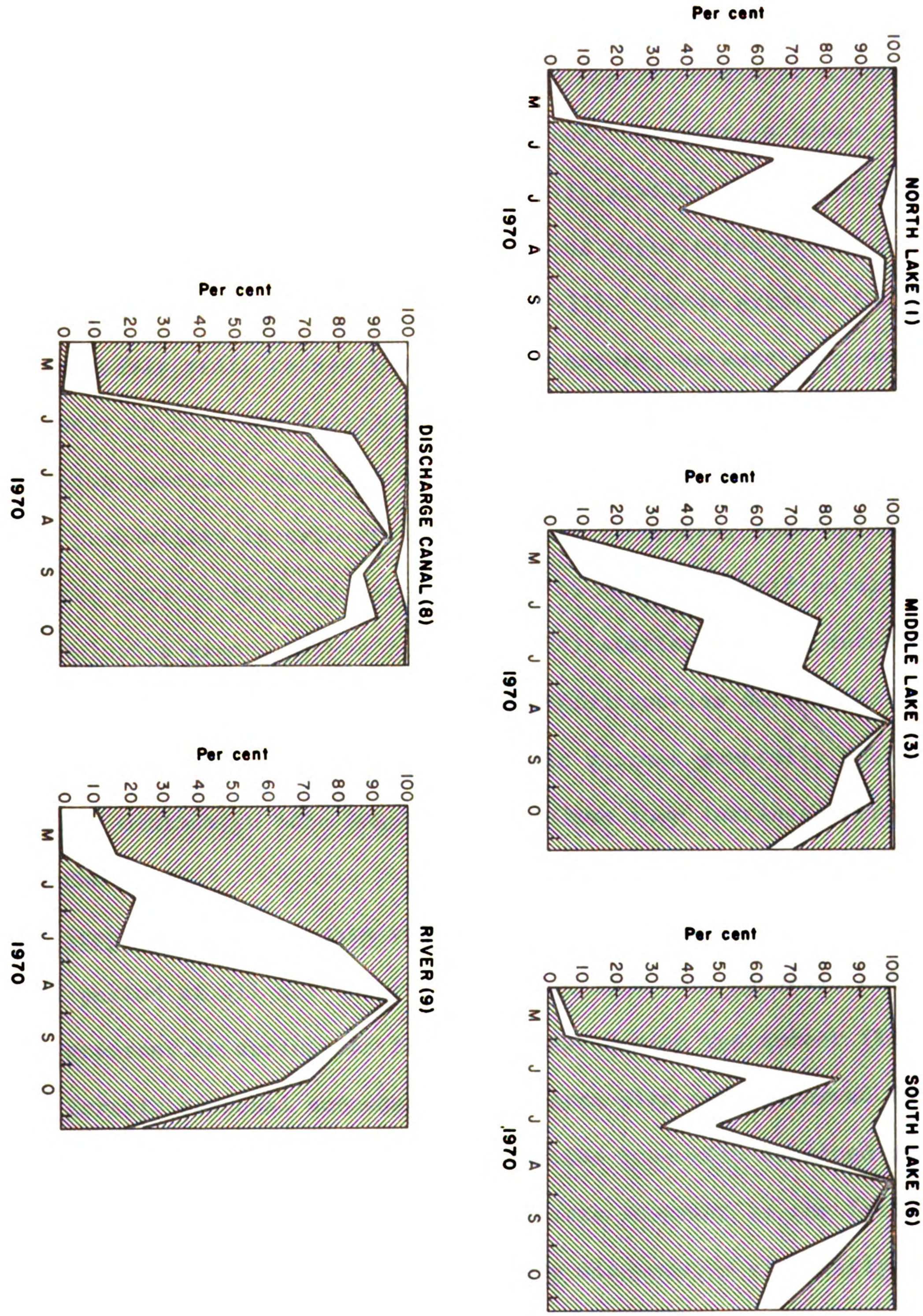
Species dynamics: Twelve major phytoplankton species were observed during this study: five diatom species (*Melosira granulata*, *Stephanodiscus astreae*, *S. binderanus*, *S. niagarae*, and *Coscinodiscus radiatus*),

Figure 4. Mean volume of phytoplankton organisms by station. _____ north lake; - - - middle lake; -.-.- south lake; ----- discharge canal; ..... river.



Mean Individual Volume (X10³ μ³)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
M
J
J
A
S
O
N
1970

Figure 5. Mean seasonal variation in volumetric composition of phytoplankton classes at the sampling stations during the study. Lower hatched area - blue-green algae; lower clear area - green algae; upper hatched area - diatoms; upper clear area - others.


NORTH LAKE (1)
MIDDLE LAKE (3)
SOUTH LAKE (6)
DISCHARGE CANAL (8)
RIVER (9)
Per cent
0 10 20 30 40 50 60 70 80 90 100
M J J A S O
1970

five blue-green species (Anacystis cyanea, A. elachistra var. conferta, Anacystis sp., Aphanizomenon flos-aquae, and Oscillatoria sp.), and two green species (Coelastrum sphaericum and Pediastrum duplex). These species all exhibited one of two basic volumetric dynamics patterns, irrespective of taxonomic class or stations: One pattern where the species' fluctuation between stations were generally similar with no obvious deviations and the other where the stations experienced dramatic unpredictable deviations with time (Figures 6-11). These erratic fluctuations were probably real, rather than sampling errors, because they occurred regularly in half the dominant species but were negligible in the remaining species. Sampling errors would, presumably, appear with about equal probability in each of the species. Therefore, some species appeared more constant in their ability to maintain their populations.

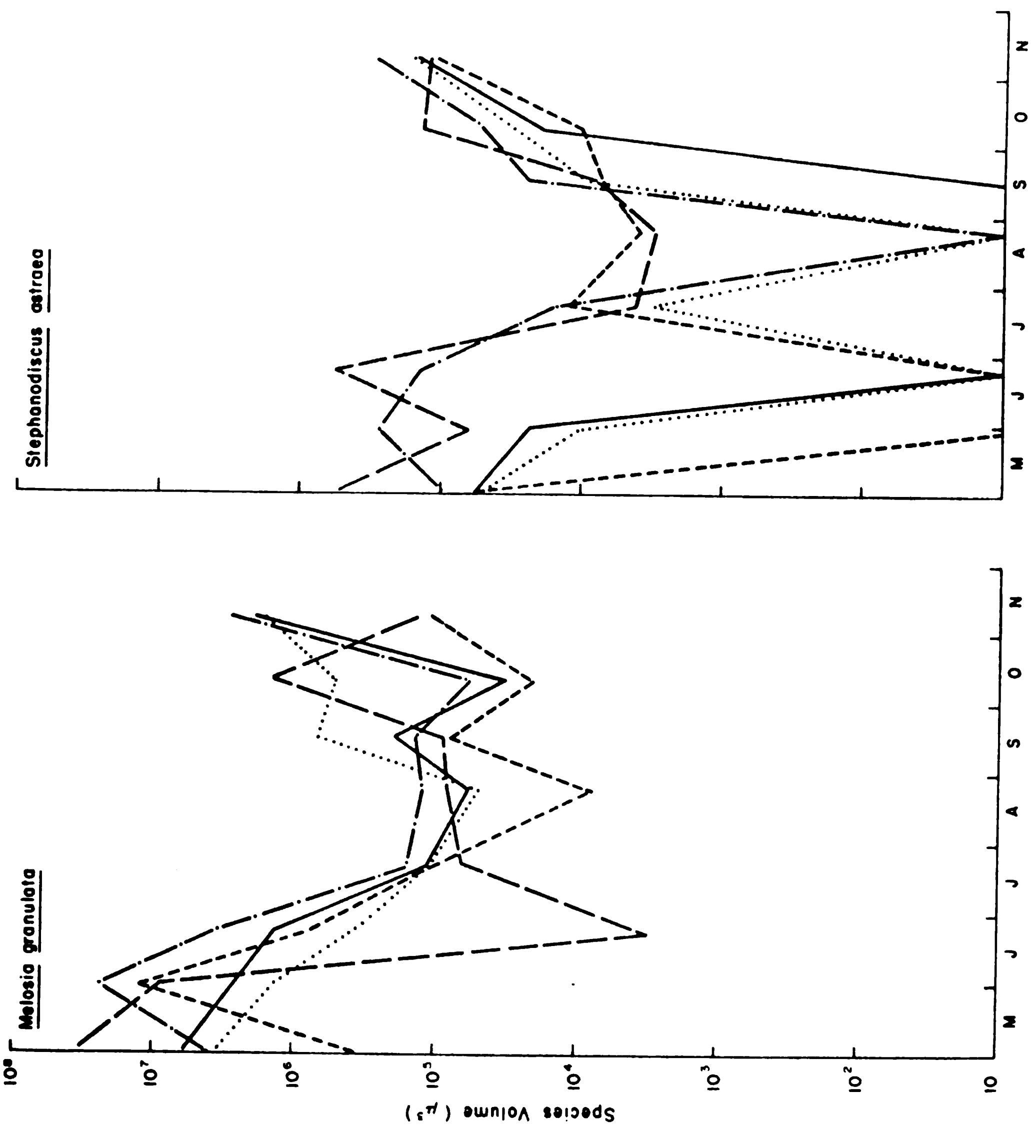
Melosira granulata was present at all stations on all dates during the study and was the dominant phytoplankton species during the spring (Figure 6). From spring dominance, their volumes generally decreased to a summer minimum in late August. The volume then increased erratically into the fall.

Stephanodiscus astraea volumes varied strongly throughout the study period at all but the north lake station. In general, volumes were greatest in spring and fall and least during the summer (Figure 6).

Erratic seasonal successional patterns also were observed for S. binderanus (Figure 7). High spring volumes generally declined during the spring and summer with slight increases observed in the fall.

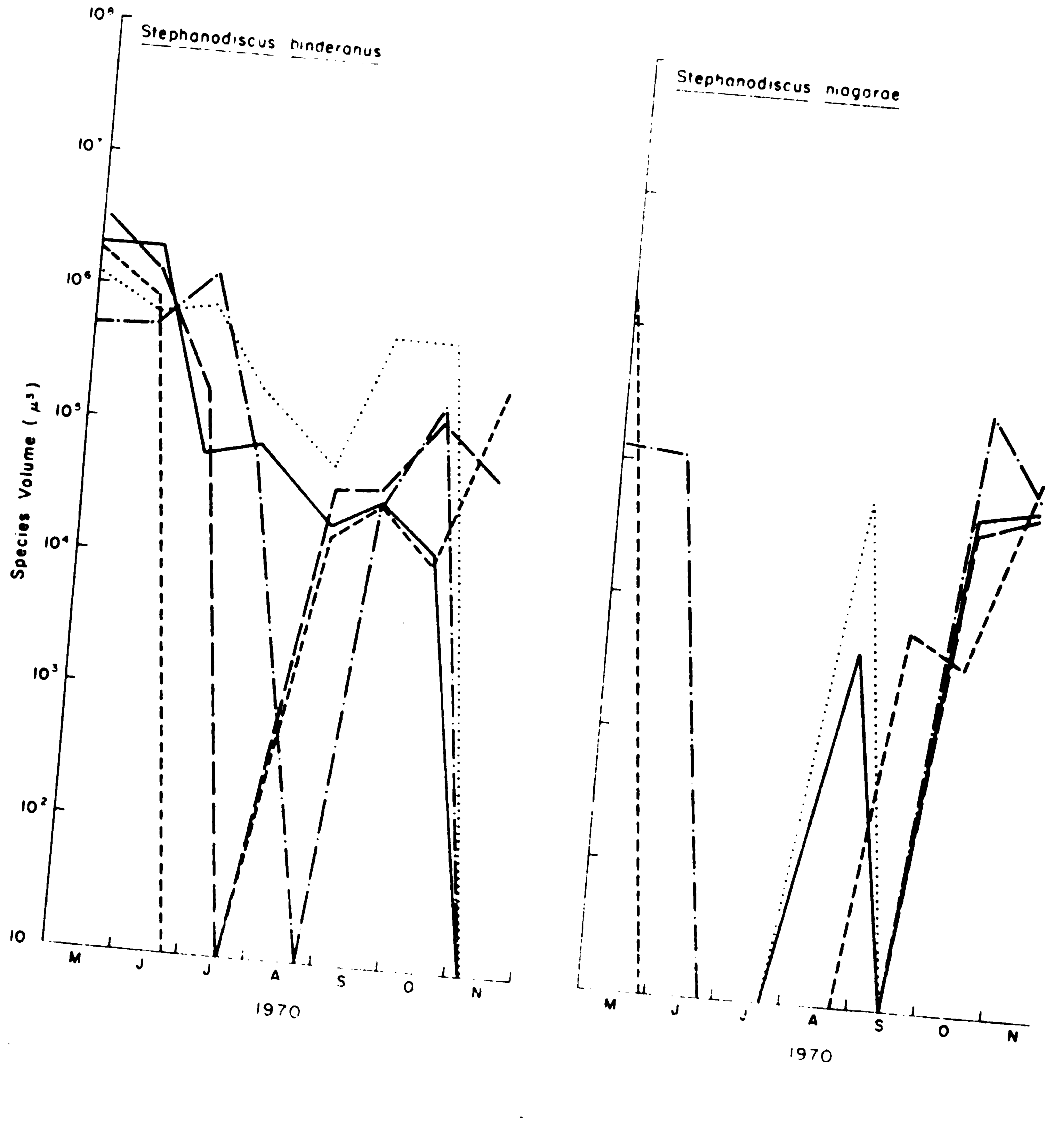
Large spring volumes of S. niagarae disappeared completely from the lake by the end of May (Figure 7) and from the discharge canal by late June. A small pulse occurred at the river and mid-lake stations

Figure 6. Seasonal dynamics by volume of Melosia granulata and Stephanodiscus astraea at the sampling stations. - - - north lake; ____ mid-lake; ---- south lake; -.-.- discharge canal; .... river.



Melosia granulata
Stephanodiscus astraea
Species Volume (μ^3)
10
10^2
10^3
10^4
10^5
10^6
10^7
10^8
M J J A S O N
1970

Figure 7. Seasonal dynamics by volume of _Stephanodiscus binderanus_ and _S. niagarae_ at the sampling stations. - - - north lake; ____ mid-lake; ---- south lake; -.-.- discharge canal; .... river.



Stephanodiscus binderanus
Stephanodiscus niagarae
Species Volume (μ³)
10⁸
10⁷
10⁶
10⁵
10⁴
10³
10²
10
M
J
J
A
S
O
N
1970
M
J
A
S
O
N
1970

in conjunction with the summer blue-green bloom. The abundance of *S. niagarae* generally increased during the late summer and fall in the lake and discharge canal, but was absent from the river after the mid-summer pulse.

Of the major species observed, the diatom *Coscinodiscus radiatus* displayed the least spatial and temporal variability (Figure 8). Spring volumes gradually increased to the maximum observed volumes in late summer and fall.

Anacystis cyanea was absent from the spring samples but increased rapidly during the summer and established phytoplanktonic dominance of the summer blue-green bloom (Figure 8). Their populations then declined moderately during the fall. Although temporal variation in the volume of this species was great, the changes were spatially uniform.

A. elachistra var. *conferta* was abundant at one or more stations during the whole study but contributed to the total abundance at all stations most consistently during the summer blue-green bloom (Figure 9). Their abundance sharply declined in the lake during the fall while it remained relatively but unpredictably high at the inshore sites.

Anacystis incerta attained greatest abundance in June before the other abundant blue-green algae. But they also contributed greatly to the mid-August bloom (Figure 9). The population volumes also changed erratically with little uniformity among stations.

Both species of abundant filamentous blue-green algae, *Aphanizomenon flos-aquae* and *Oscillatoria* sp., exhibited similar seasonal dynamics (Figure 10). Maximum abundance was observed in late summer and early fall at all stations except the discharge canal where the seasonal maximum was reached in late June.

Figure 8. Seasonal dynamics by volume of *Coscinodiscus radiatus* and *Anacystis cyanea* at the sampling stations. - - - north lake; ____ mid-lake; ---- south lake; -.-.- discharge canal; .... river.

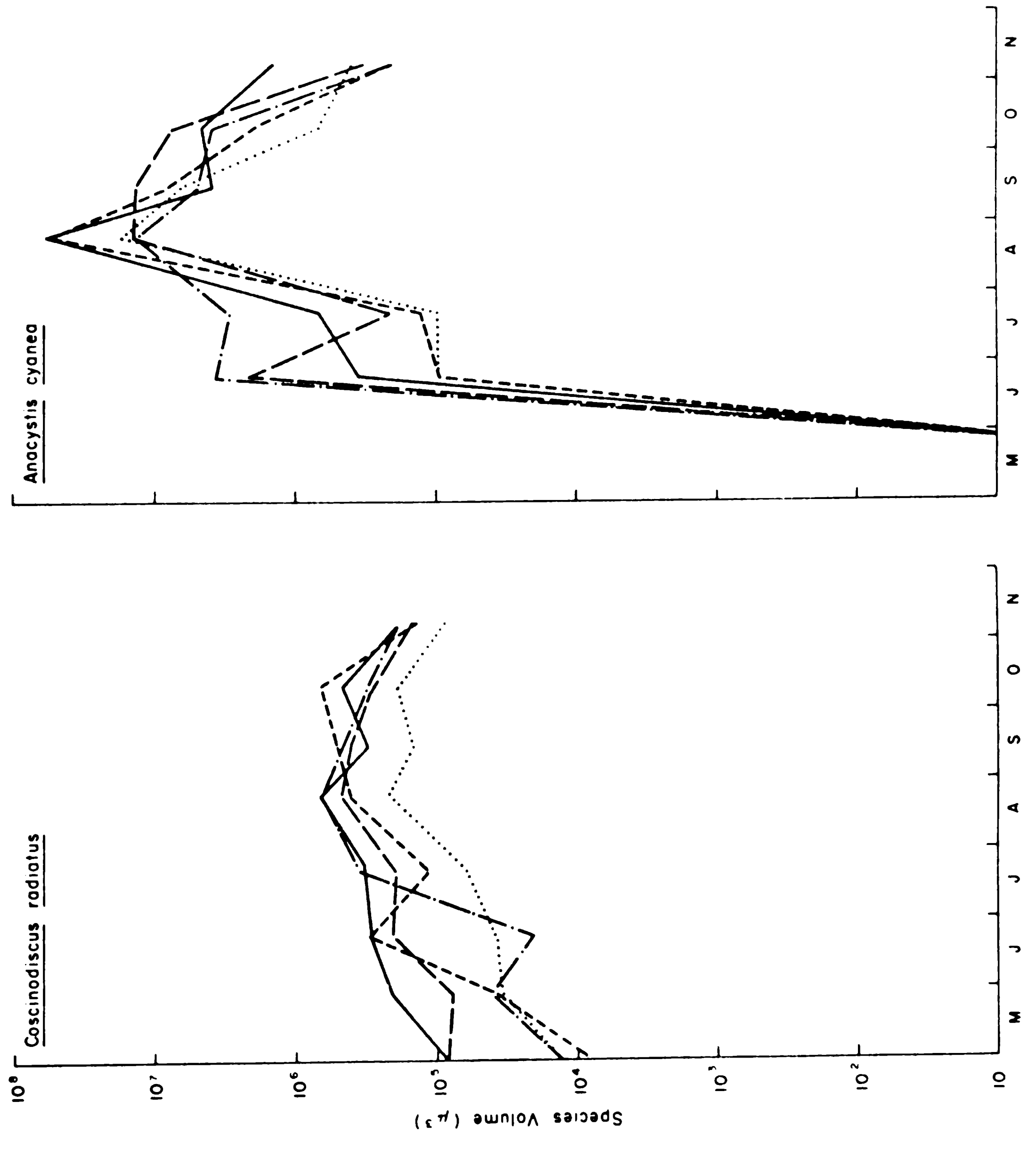
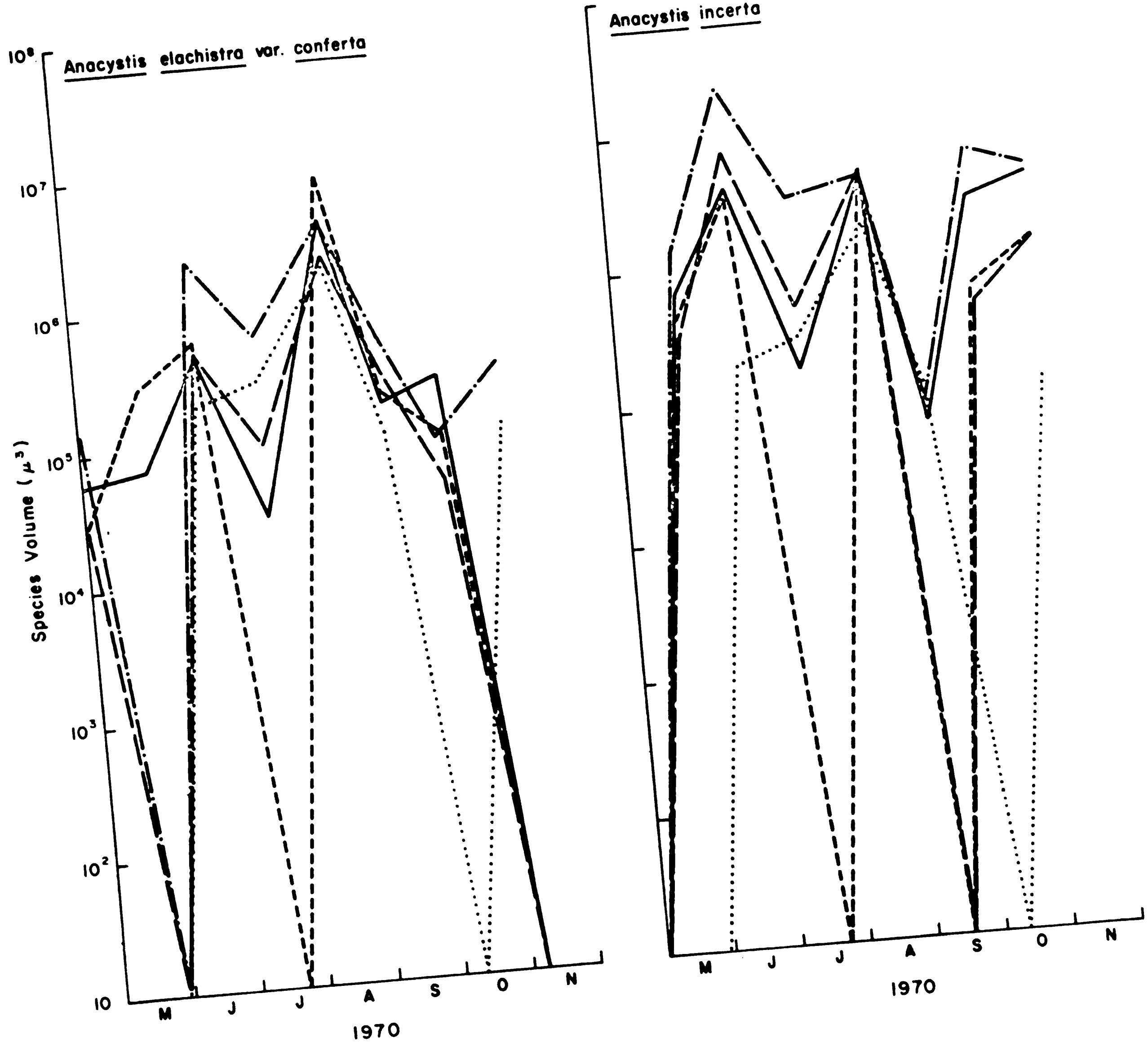
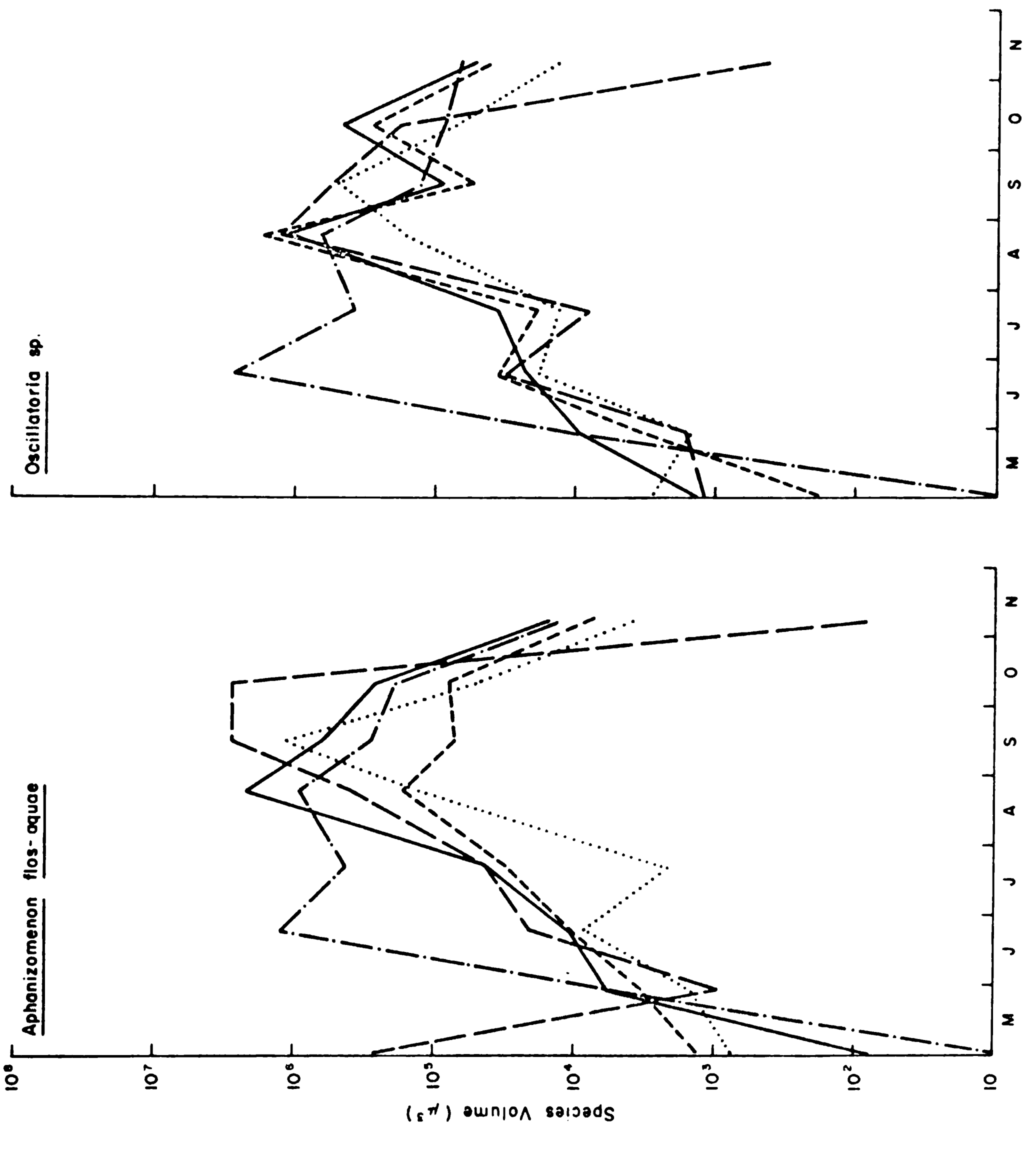

Coscinodiscus radiatus
Anacystis cyanea
Species Volume (μ^3)
10^8
10^7
10^6
10^5
10^4
10^3
10^2
10
M J J A S O N
1970
M J J A S O N
1970

Figure 9. Seasonal dynamics by volume of *Anacystis elachistra* var. *conferta* and *A. incerta* at the sampling stations. - - - - north lake; _____ mid-lake; ---- south lake; -.-.- discharge canal; ..... river.



Anacystis elachistra var. conferta
Species Volume (μ^3)
10^8
10^7
10^6
10^5
10^4
10^3
10^2
10
M
J
J
A
S
O
N
1970
Anacystis incerta
M
J
J
A
S
O
N
1970

Figure 10. Seasonal dynamics by volume of *Aphanizomenon flos-aquae* and *Oscillatoria* sp. at the sampling stations. - - - - north lake; ____ mid-lake; ---- south lake; -.-.- discharge canal; ..... river.


Aphanizomenon flos-aquae
Oscillatoria sp.
Species Volume (μ^3)
10^8
10^7
10^6
10^5
10^4
10^3
10^2
10
M
J
J
A
S
O
N
1970
M
J
J
A
S
O
N
1970

The two major green phytoplankton species found were quite different in their seasonal distribution (Figure 11). Pediastrum duplex increased from low spring volumes to maximum in late June, then uniformily decreased little during the rest of the study period. Spring and early summer volumes of Coelastrum sphaericum completely disappeared during the August blue-green bloom, but reappeared to nearly their pre-bloom abundance afterwards.

Of the minor species, three deserve special mention. Cyclotella meneghiniana commonly occurred in the river where it comprised up to 5.8% of the phytoplankton volume. While it was frequently found at other stations, its role was much less important.

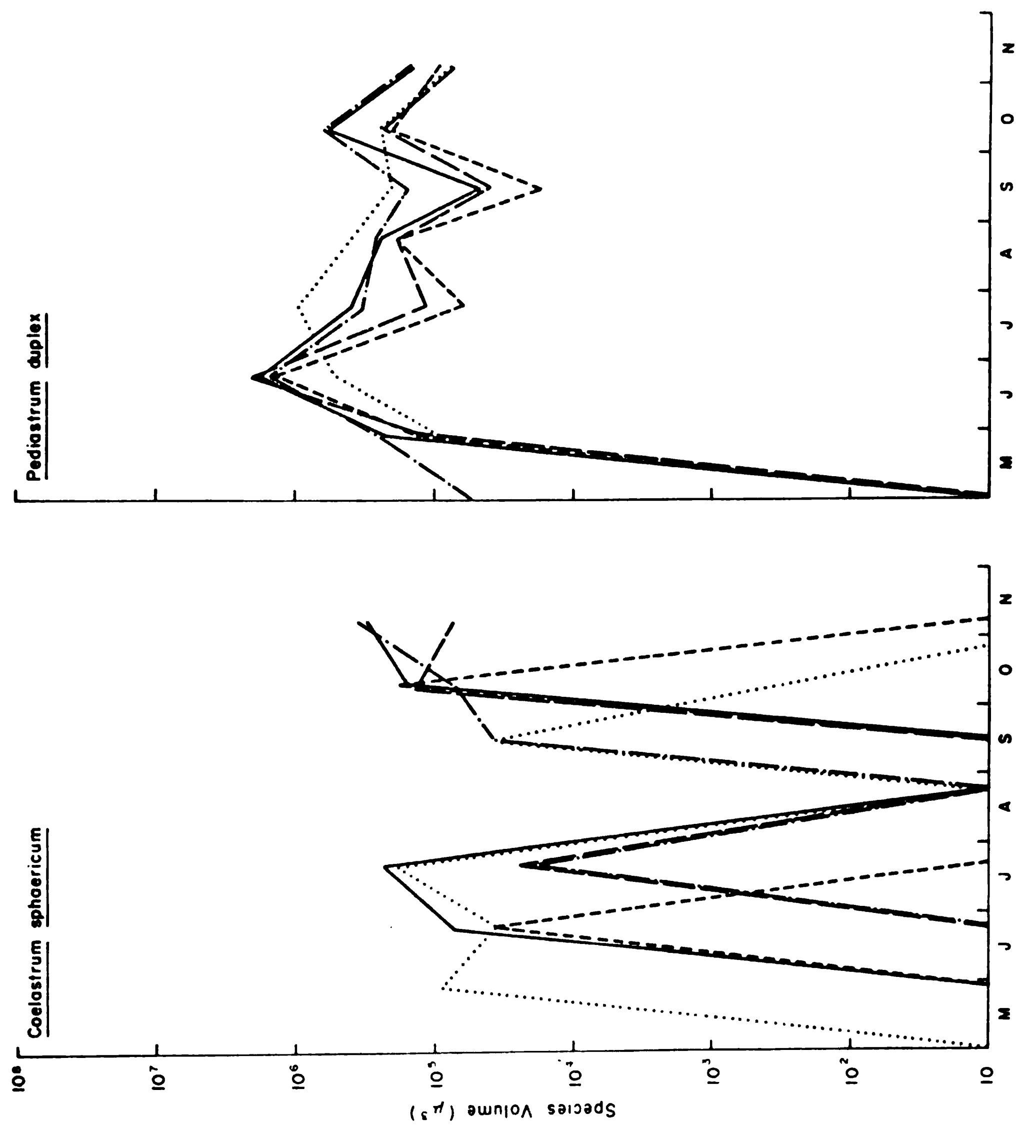
Botryococcus sudeticus occurred commonly in the spring samples when it accounted for up to 17% of the phytoplanktonic volume of the lake. Its abundance then decreased to a rare and unimportant occurrence.

Euglena sp. occurred frequently throughout the study area during this investigation, but with one exception, it accounted for less than 1% of the total phytoplankton volume. It comprised about 10% of the volume in the discharge canal during the spring.

Phytoplankton Diversity and Equitability

Nearly 200 different species of phytoplankton were observed during this study. Of these species 94 were diatoms, 23 were blue-green algae, 79 were green algae, and the remaining few were from the Euglenophyceae, Dinophyceae, and Chrysophyceae (Table 3). Not all species were found at all stations, but there was nearly (> 95%) complete overlap between the species found at the lake stations and the species observed at the inshore stations over the study period. A slightly greater number of species was found in the discharge canal

Figure 11. Seasonal dynamics by volume of Coelastrum sphaericus and Pediastrum duplex at the sampling stations. - - - - north lake; ____ mid-lake; ---- south lake; -.-.- discharge canal; .... river.



Coelastrum sphaericum
Pediastrum duplex
Species Volume (μ^3)
10^8
10^7
10^6
10^5
10^4
10^3
10^2
10
M J J A S O N
1970
M J J A S O N
1970

Table 3. Species found during study listed by class with corresponding mean annual species volumes (μ^3).

CLASS *Species*	MEAN VOLUME
CYANOPHYCEAE	
A. quaduplicatum (Menegh.) Bréb.	42
Anabaena ukn 1	2,640
Anabaena ukn 2	631
Anacystis cyanea (Kütz.) Dr. & Daily	81,991
A. elachista W. & G. S. West var. *conferta* W. & G. S. West	37,692
A. grevillei (Berk.) Kütz.	201,552
A. incerta (Lemm.) Dr. & Daily	106,447
A. limnetica (Lemm.) Dr. & Daily	967
A. minuta (Ag.) Menegh.	535
A. pulchra Gardn.	8,181
A. thermalis (Menegh.) Dr. & Daily	165
Aphanizomenon flos-aquae (L.) Ralfs	4,936
Coccochloris ukn 1	15,339
C. nidulans (Richt.) Dr. & Daily	1,527
C. peniocystis (Kütz.) Dr. & Daily	151
C. rupestris (Lyngb.) Spreng.	418
G. lacustris Chodat	268
G. naegelianum (Ung.) Lemm.	3,882
Marssoniella elegans A. Braun	25
Oscillatoria sp.	4,139
Spirulina laxissima G. S. West	126
unknown blue green colony	836
unknown blue green unicellular	78
CHLOROPHYCEAE	
Actinastrum gracilimum G. M. Smith	1,405
A. hantzschii Lagerheim	131
A. hantzschii Lagerheim var. *fluviatile* Schroeder	248
Ankistrodesmus convolutus Corda	14
A. falcatus (Corda) Ralfs	38
Botryococcus braunii Küetzing	3,882
B. sudeticus Lemmermann	14,137
Chlorella ellipsoidea Gerneck	421
C. vulgaris Beyerinck	579
Closterium sp.	194
Coelastrum microporum Naegel	4,808
C. reticulatum (Dang.) Senn	18,092

Table 3 (con't.)

CLASS *Species*	MEAN VOLUME
CHLOROPHYCEAE (con't.)	
C. sphaericum Naegeli	31,059
Coelastrum sp.	28,736
Cosmarium bipunctatum Boergesen	20,897
Cosmarium sp.	1,151
Crucigenia alternans G. M. Smith	219
C. apiculata (Lemm.) Schmidle var. *eriensis* Tiffany & Ahlstrom	1,764
C. fenestrata Schmidle	302
C. irregularis Wille	114
C. lauterbornei Schmidle	1,005
C. quadrata Morren	103
C. tetrapedia (Kirch.) W. & G. S. West	198
Dactylococcopsis smithii R. & F. Chodat	491
Dictyosphaerium ehrenbergianum Naegeli	171
D. planctonicum Tiffany & Ahlstrom	3,195
Gloeocystis vesiculosa Naegeli	905
Golenkinia radiata (Chod.) Wille	408
Kirchneriella contorta (Schmidle) Bohlin	229
K. lunaris (Kirch.) Moebius	54
K. obesa (W. West) Schmidle	94
K. subsolitaria G. S. West	8
Kirchneriella sp.	96
Lagerheima quadriseta (Lemm.) G. M. Smith	46
Micractinium eriense Tiffany & Ahlstrom	1,928
M. pusillium Fresenius	7,238
Micractinium sp.	2,185
Mougeotia sp.	6,222
Oocystis borgei Snow	225
Oocystis sp.	199
Pandorina morum (Muell.) Bory	619
Pediastrum biradiatum Meyen	31,161
P. boryanum (Turp.) Meneghini	5,089
P. duplex Meyen	14,675
P. simplex (Meyen) Lemmermann	14,907
P. tetras (Ehr.) Ralfs	1,854
Planktosphaeria gelatinosa G. M. Smith	1,317
Pleodorina sp.	15,708
Polyedriopsis quadrispina G. M. Smith	227
Quadrigula closterioides (Bohlin) Printz	156
Q. lacustris (Choda) G. M. Smith	26

Table 3 (con't.)

CLASS *Species*	MEAN VOLUME
CHLOROPHYCEAE (con't.)	
Scenedesmus abundans (Kirch.) Chodat	34
Scenedesmus acuminatus (Lagerh.) Chodat	248
S. bernardii G. M. Smith	75
S. bijuga (Turp.) Lagerheim	81
S. denticulatus Lagerheim	118
S. dimorphus (Turp.) Kuetzing	176
S. opoliensis P. Richter	91
S. quadricauda (Turp.) de Brébisson	106
S. quadricauda (Turp.) de Brébisson var. *alternans* G. M. Smith	21
Schroederia setigera (Schroeder) Lemmermann	61
Selenastrum bibraianum Reinsch	490
S. gracile Reinsch	202
S. minutum (Naeg.) Collins	31
S. westii G. M. Smith	49
Sphaerocystis schroeteri Chodat	2,036
Staurastrum sp.	10,761
Tetraedron arthrodesmiforme (G. S. West) Woloszynska	226
T. caudatum (Corda) Hansgirg	16
T. pentraedricum W. & G. S. West	14
T. trigonum (Naeg.) Hansgirg	48
T. trigonum (Naeg.) Hansgirg var. *gracile* (Reinsch) De Toni	26
Tetraspora sp.	57
Tetrastrum elegans Playfair	75
T. glabrum (Roll) Ahlstrom & Tiffany	155
T. heteracanthum (Nordst.) Chodat	75
T. staurogeniaeforme (Schroeder) Lemmermann	75
unknown green colony	920
unknown green unicellular	123
Westella botryoides (W. West) de Wildemann	690
W. linearis G. M. Smith	1,216
BACILLARIOPHYCEAE	
Achnanthes lanceolata Bréb.	403
A. minutissima Kützing	119
Amphora ovalis Kütz var. *pedunculus* Kützing	340
Asterionella formosa Hassall	523

Table 3 (con't.)

CLASS *Species*	MEAN VOLUME
BACILLARIOPHYCEAE (con't.)	
Centric ukn 1 (*Cyclotella glomerata* Bachmann?)	36
Centric ukn 2	108
Centric ukn 3	122
Cocconeis diminuta Pant.	25
C. disculus Schum.	220
C. placentula Ehrenberg	114
Coscinodiscus radiatus Ehrenberg	3,618
Cyclotella bodanica Eulenst.	832
C. kutzingiana Thwaites	445
C. meneghiniana Kütz.	850
C. ocellata Pant.	241
C. stelligera Grun.	71
Cymatopleura solea (Breb.) W. Smith	3,430
Cymbella affinis Kütz.	1,006
C. ventricosa Kütz.	121
Cymbella sp.	49
Diatoma tenue Ag.	978
D. vulgare Bory	9,542
Epithemia sorex Kütz.	3,225
E. turgida (Ehr.) Kütz.	4,953
Eunotia curvata (Kütz.) Lagerst.	1,133
E. pentinalis (Kütz.) Rabenhorst	1,125
Fragilaria brevistriata Grun.	664
F. capucina Desmaziéres	361
F. construens (Ehr.) Grunow	1,866
F. crotonensis Kitton	6,524
F. leptostauron (Ehr.) Hustedt	11,699
F. pinnata Ehrenberg	1,584
Fragilaria sp.	3,783
Gomphonema constrictum Ehrenberg	1,844
G. olivaceum (Lyngbye) Kütz.	657
G. parvulum Kütz.	353
G. sarcophagus	3,326
Gyrosigma spencerii (W. Smith) Cleve.	5,734
Hantzschia amphioxys (Ehr.) Grun.	2,011
Melosira ambigua (Grun.) O. Müller	1,317
M. distans (Ehr.) Kütz.	2,413
M. granulata (Ehr.) Ralfs	6,828
M. islandica O. Müller	3,802
Meridion circulare Agardh	2,127
Navicula bacillum Cleve.	3,461
N. contenta Grun.	1,084

Table 3 (con't.)

CLASS *Species*	MEAN VOLUME
BACILLARIOPHYCEAE (con't.)	
N. cryptocephala Kütz.	601
N. cuspidata Kütz.	10,912
N. exigua (Gregory) O. Müller	703
N. gastrum Ehr.	2,690
N. hungarica Grun.	300
N. mutica Kütz.	1,226
N. pupula Kütz.	950
N. salinarum Grunow	594
N. tripunctata (O. F. Müll.) Bory	2,376
N. viridula Kütz.	7,046
N. ukn 1	122
N. ukn 2	499
N. ukn 3	9,236
Neidium dubium (Ehr.) Cleve.	8,847
Nitzschia acicularia W. Smith	384
N. amphibia Grunow	245
N. angustata (W. Smith) Grunow	3,915
N. dissipata Grunow	1,004
N. filiformis (W. Smith) Hustedt	691
N. gracilis Hantzsch	628
N. holsatica Hustedt	112
N. linearis W. Smith	3,968
N. palea (Kütz.) W. Smith	495
N. sigma (Kütz.) W. Smith	1,307
N. sigmoidea (Ehr.) W. Smith	16,632
N. ukn 1	577
Opephora martyi Herib.	2,733
Pennate ukn 1	1,232
Pennate ukn 2	85
Pinnularia borealis Ehrenberg	1,730
P. viridis (Nitzsch.) Ehrenberg	6,172
Pinnularia sp.	301
Rhizosolenia eriensis H. L. Smith	9,842
Rhoicosphenia curvata (Kütz.) Grun.	119
Stephanodiscus alpinus Hustedt	2,215
S. astraea (Ehr.) Grun.	3,095
S. binderanus (Kütz.) C. Weber	10,616
S. niagarae Ehr.	16,409
S. tenuis Hustedt	429
S. ukn 1	381
Surirella angusta Kütz.	1,570
S. ovata Kütz.	1,102

Table 3 (con't.)

CLASS *Species*	MEAN VOLUME
BACILLARIOPHYCEAE (con't.)	
Synedra acus Kütz.	2,062
S. nana Meister	115
S. parasitica W. Smith	220
S. ulna (Nitzch.) Ehr.	4,109
Tabellaria fenestrata (Lyngbye) Kütz.	1,860
T. flocculosa (Roth) Kütz.	1,857
EUGLENOPHYCEAE	
Euglena sp.	2,171
Trachelomonas sp.	532
DINOPHYCEAE	
Ceratium hirundinella (O. F. Müell.) Dujardin	10,173
Peridinium sp.	6,234
CHRYSOPHYCEAE	
Dinobryon sp.	3,013

(147) than in the river (125) or at the three lake stations (from north to south: 121; 123; 116).

During the sampling period the most kinds of species consistently were found in the inshore areas, particularly the discharge canal. The number of species erratically increased from spring to fall throughout the study area (Table 4). All stations in the spring had nearly the same number of species. Over the summer the greatest number of species were found at the inshore stations. In the fall the lake stations had approximately the same number of species as the river while the discharge canal continued to have greater numbers.

Table 4. Number of species found on each date and the annual means by station.

Date	Stations				
	1	3	6	8	9
2 May 1970	43	47	46	49	36
28 May 1970	53	53	54	54	57
23 June 1970	54	58	48	72	64
21 July 1970	50	62	31	70	66
23 August 1970	64	50	53	58	63
15 September 1970	41	48	38	65	62
10 October 1970	66	60	62	82	67
7 November 1970	56	66	58	72	57
Annual Means	53.4	56.6	48.8	65.3	59.0

Mean species diversity calculated by station from numbers of phytoplankton differed significantly ($p < 0.05$) among stations on all of the dates sampled (Appendix, Table A7). As with the numbers of kinds of species that were observed (Table 4), the inshore stations tended to have greater diversities than those for the lake stations. Diversities in the discharge canal ranked greatest 87.5% of the time. The river ranked in the highest category on 75% of the dates. The lake stations varied inconsistantly among themselves.

Discernable differences ($p < 0.05$) in equitability (calculated with numbers of phytoplankton) were also detected among stations on each date (Appendix, Table A8). Only the river station demonstrated anything that approached a consistant rank among stations. On 62.5% of the observations, the river fell into the smallest equitability category. The remaining stations varied inconsistently. Apparently, the relatively high diversities found in the inshore areas originated from the greater number of species per unit volume rather than from greater equitability of species abundances.

Seasonal averages in diversity and equitability further emphasize the greater diversity of the inshore areas over the lake stations while the equitabilities among the five stations remained quite similar (Table 5).

Diversity and equitability estimates were also calculated on volumetric measurements. Although volumetric calculations of diversity and equitability differed from numerical calculations in absolute value, the relative values among stations were similar.

The seasonal dynamics of diversity and equitability by station over the period of investigation are summarized in Figure 12. These estimates of values for the north and middle lake stations were low in

Figure 12. Mean diversity and equitability of phytoplankton by station on each sampling date. Upper hatched boxes - diversity; lower clear boxes - equitability.

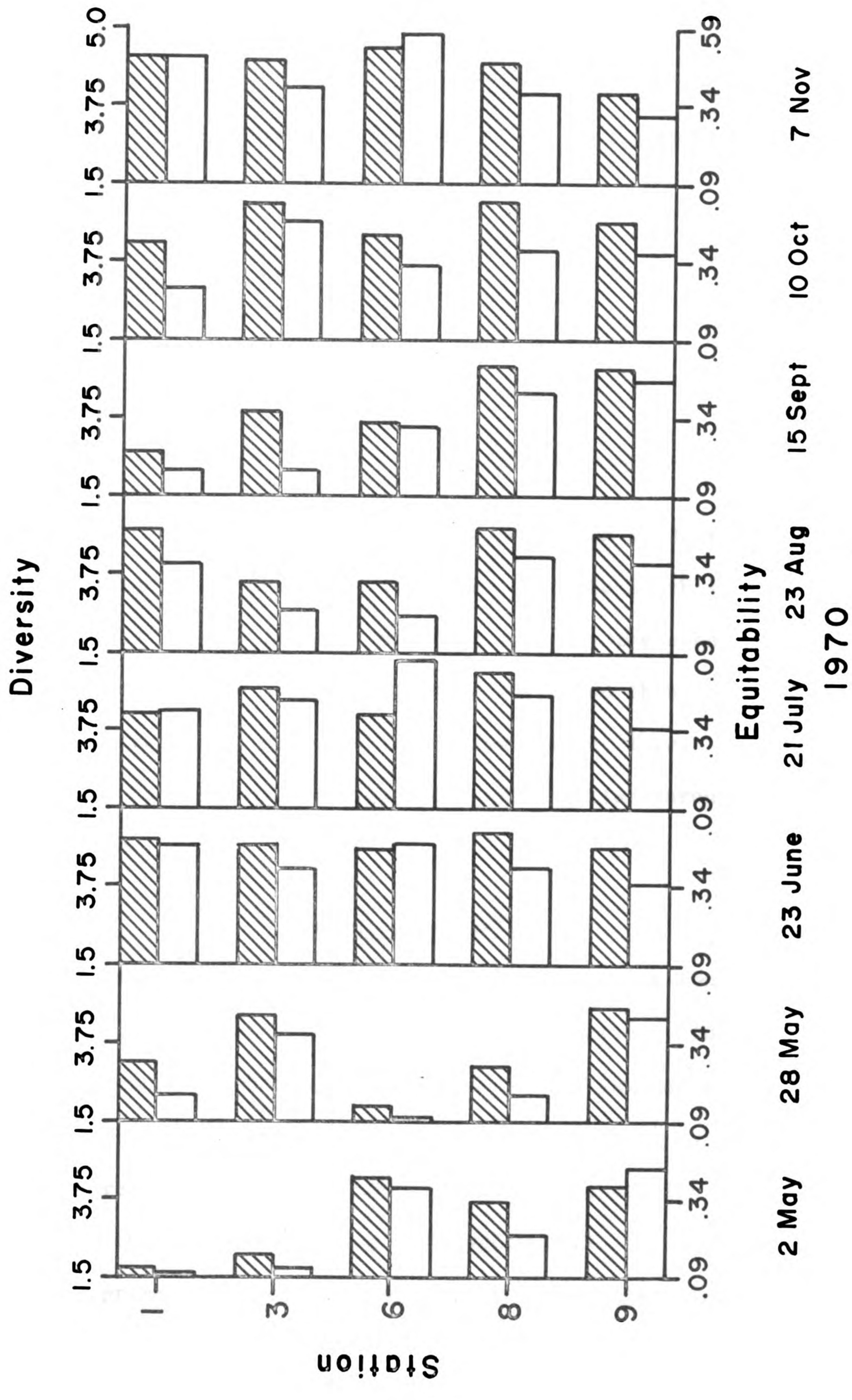

Diversity
1.5
3.75
5.0
Equitability
.09
.34
.59
2 May
28 May
23 June
21 July
23 Aug
15 Sept
10 Oct
7 Nov
1970
Station
1
3
6
8
9

Table 5. Mean diversities and equitabilities at the sampling stations during the study period.

Station	Numerical Diversity	Numerical Equitability
1	3.44	0.313
3	3.73	0.344
6	3.53	0.373
8	4.09	0.360
9	4.06	0.390

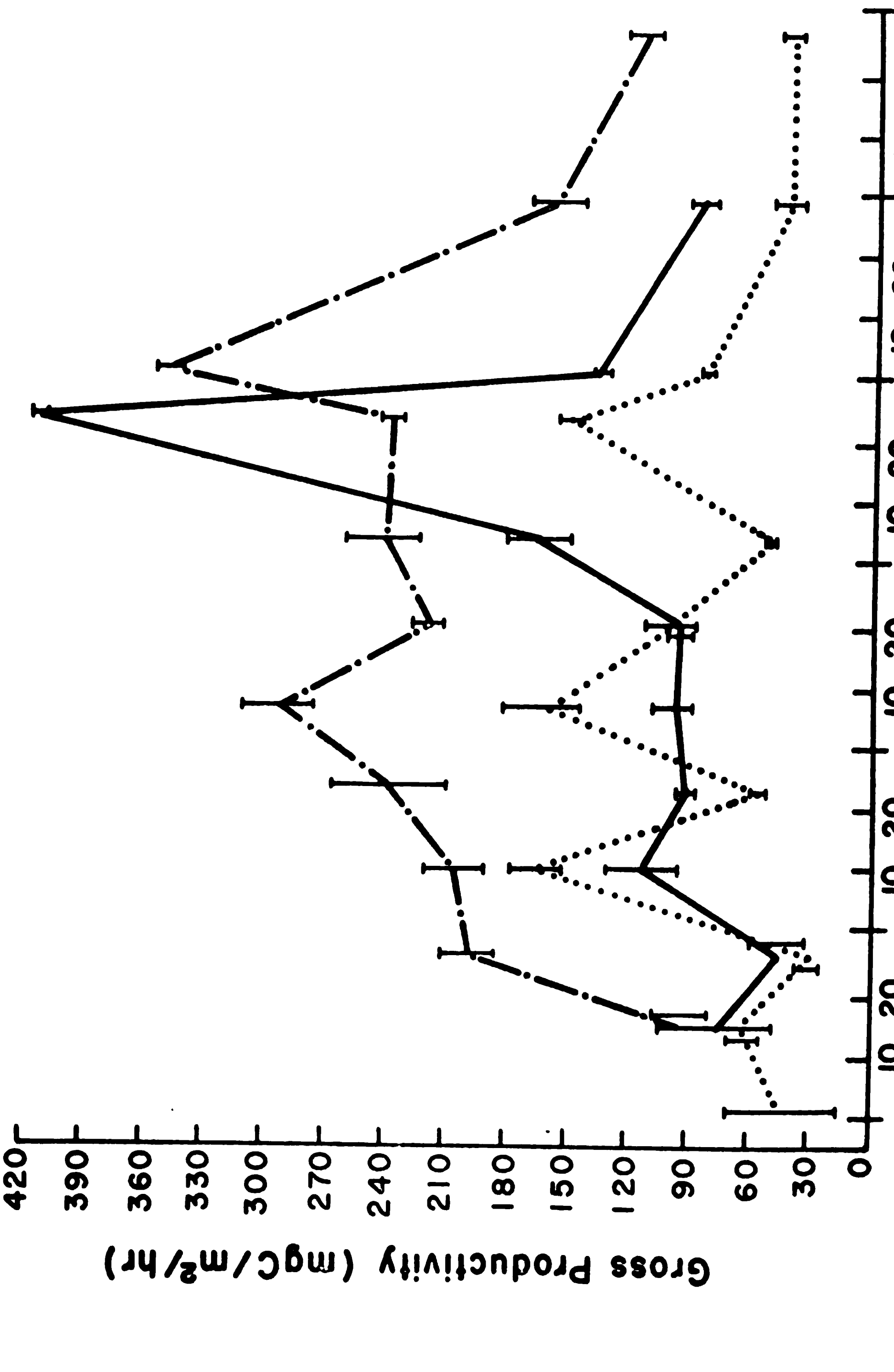
the spring, increased until the late summer when it decreased and then gradually increased in the fall. Values for the south lake station were somewhat higher in early May than found at the other lake stations; they dropped in late May, increased in June, and then followed the general pattern that occurred in the rest of the lake. Inshore stations had fairly constant diversities and equitabilities throughout the sampling period.

Community Metabolism

Mean midday gross primary productivity was most consistently greatest in the discharge canal (Figure 13). Productivity in the discharge canal was exceeded on only one occasion at the lake station. This occurred during the summer blue-green algae bloom when midday productivity in the lake reached 412.5 $mgC/m^2/hr$. Maximum productivity in the discharge canal was observed a week later (350 $mgC/m^2/hr$).

The primary productivity in the river never exceeded that of the canal, but it significantly (± 2SE) exceeded productivity in the lake

Figure 13. Mean gross primary productivity ($\bar{x} \pm 1$ SE) estimated during midday incubation periods. ____ lake; -.-.- discharge canal; .... river.


Gross Productivity (mgC/m²/hr)
0
30
60
90
120
150
180
210
240
270
300
330
360
390
420
10 20
May
10 20
June
10 20
July
10 20
Aug
10 20
Sept
10 20
Oct
1970

during the summer on one occasion. For most sampling dates mean river productivity was lower than lake productivity.

Primary productivity in the lake generally increased from spring to late summer when it peaked strongly during the August blue-green algae-bloom. After the bloom the lake productivity returned to the relatively stable pre-bloom summer level.

Profiles of average gross primary productivity for the three stations over the study period show that the highest rates of production occurred at the surface level in each case (Figure 14). Rates of decline from the surface to 0.5 m were similar at all three stations with lower rates of decline existing from 0.5 to 1.5 m. Little change was experienced where there was low to negligible productivity from 1.5 to 2.5 m at the stations. Hence, the majority of the primary productivity in the study area was observed to occur in the top 1.5 m of the water column.

Estimates of diurnal primary productivity were made on 1 July 1970 for the lake (station 3) and discharge canal (station 8). Maximum productivity was observed to occur during early afternoon (Figure 15). At this time the discharge canal was found to produce 3730 $mgC/m^2/day$ while the lake produced 1935 $mgC/m^2/day$.

Mean community respiration estimated during the productivity incubations are listed in Table 6. On two occasions oxygen increased in the dark bottles resulting in positive respiration values. These samples, 23 June 1970 in the discharge canal and 1 September 1970 in the lake, are omitted from the table.

Community respiration was nearly always lowest in the lake. The greatest community respiration measured in the lake (288 $mgC/m^2/hr$) corresponded with the blue-green algae bloom.

Figure 14. Profiles of average gross primary productivity over the study period. ____ lake; .... discharge canal; -.-.- river.

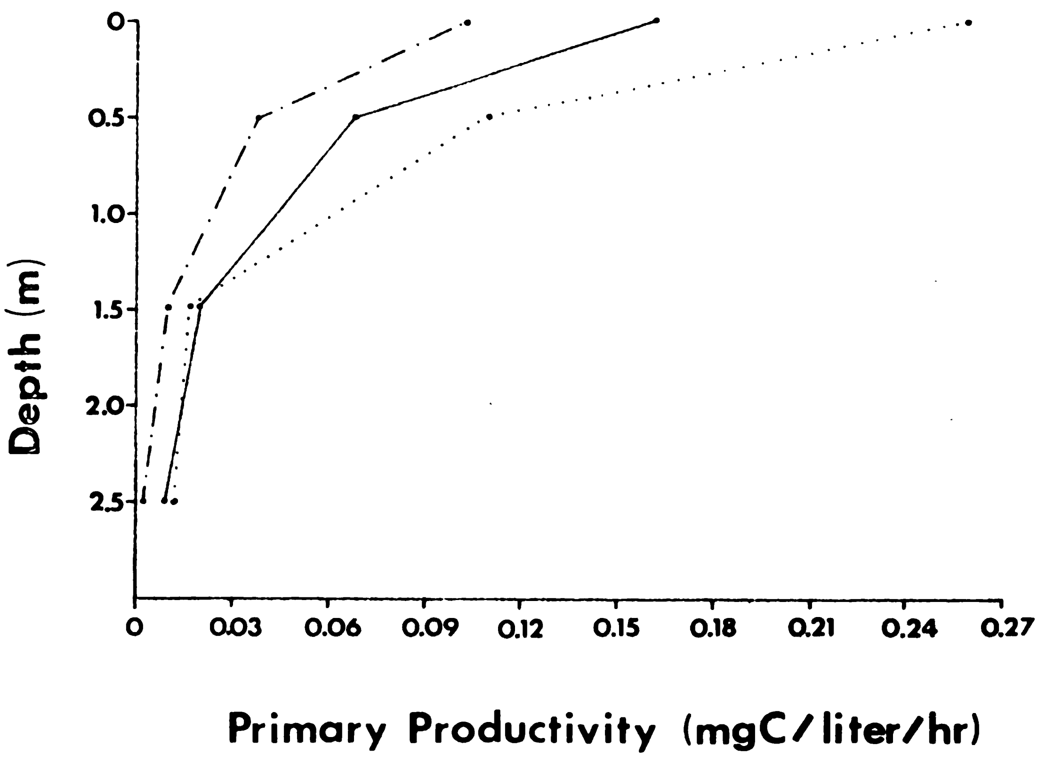
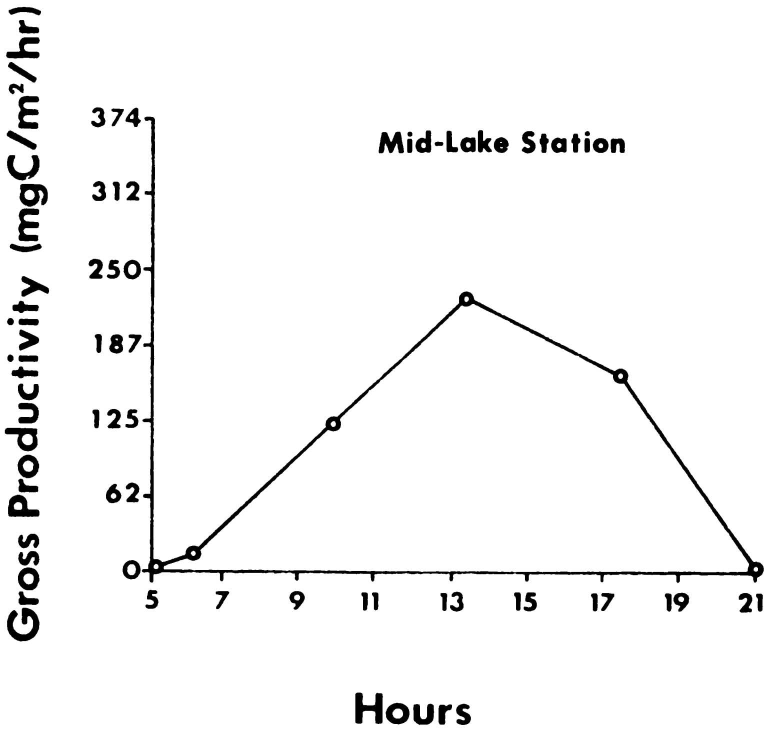

Depth (m)
0
0.5
1.0
1.5
2.0
2.5
0
0.03
0.06
0.09
0.12
0.15
0.18
0.21
0.24
0.27
Primary Productivity (mgC/liter/hr)

Figure 15. Diurnal primary productivity in the lake and discharge canal on 1 July 1970.


Gross Productivity (mgC/m²/hr)
374
312
250
187
125
62
0
Mid-Lake Station
5
7
9
11
13
15
17
19
21
Hours

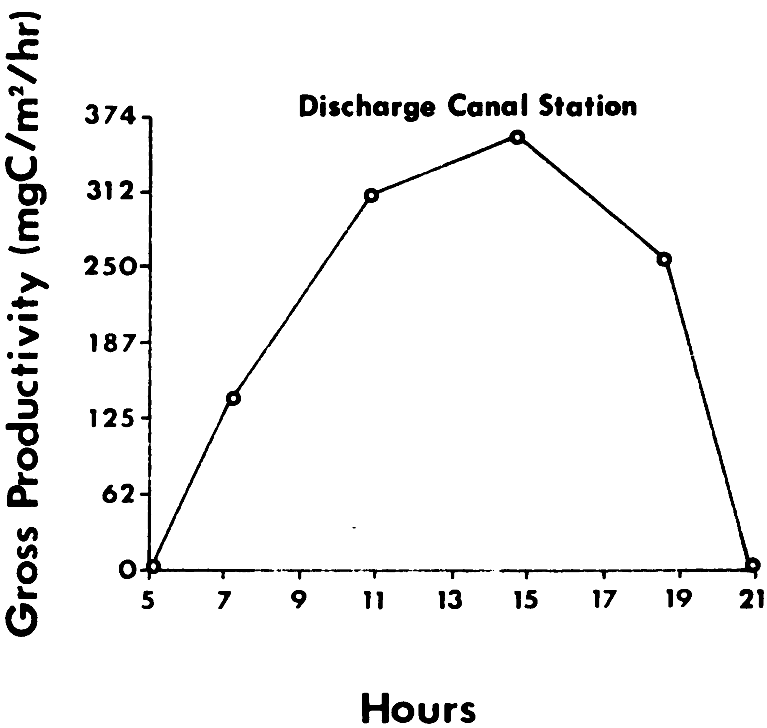

Gross Productivity (mgC/m²/hr)
374
312
250
187
125
62
0
Discharge Canal Station
5
7
9
11
13
15
17
19
21
Hours

Table 6. Mean community respiration ($mgC/m^2/hr$) estimated during productivity incubation at the sampling stations ($\bar{x} \pm 1$ SE).

DATE	LAKE	DISCHARGE CANAL	RIVER
5-1	-	-	307 ± 17
5-15	116 ± 27	116 ± 33	293 ± 12
5-27	75 ± 0	590 ± 28	674 ± 13
6-10	122 ± 34	477 ± 91	321 ± 16
6-23	75 ± 8	-	131 ± 15
7-7	47 ± 8	110 ± 6	214 ± 33
7-21	69 ± 4	260 ± 31	279 ± 21
8-4	107 ± 6	345 ± 55	190 ± 7
8-24	288 ± 59	218 ± 11	185 ± 21
9-1	-	360 ± 11	211 ± 1
9-29	23 ± 12	12 ± 6	88 ± 28
10-27	-	1259 ± 19	198 ± 0

Maximum respiration at both inshore areas (excluding the aberrant fall discharge canal value resulting from possible instrument error) was recorded on 27 May 1970. At that time communities in the discharge canal consumed 540 $mgC/m^2/hr$, while the river community consumed 674 $mgC/m^2/hr$. During the spring the river respiration exceeded the respiration in the discharge canal. Similar community respiration occurred at both inshore areas during the first part of the summer. Respiration in the discharge canal tended to exceed respiration in the river for the remainder of the study period.

DISCUSSION

Diurnal Productivities and Community Respiration

Midday estimates of primary productivity do not allow for the influence of the length of day on overall daily productivity. In order to compare primary productivity estimates with previous work, the daily productivity was estimated for each sampling date at the three stations sampled based on the diurnal estimates of 1 July 1970. Assuming that the shape of diurnal productivity curves and the time of peak production remained constant, daily productivities were calculated by constructing curves around the time of peak productivity observed on all sampling dates and the corresponding times of dawn and dusk. Calculations based on the areas under the curves were used to represent the diurnal productivities.

Mean daily and seasonal productivities by station are listed by season in Table 7. The daily values found are comparable to the lower limits of the range of primary productivity values summarized in Saunders' (1964) review of values for the western basin of Lake Erie. The values estimated were indicative of eutrophic conditions defined by Rodhe (1969) as resulting from man induced nutrient enrichment.

Total respiration on a daily basis was calculated by simply multiplying by 24 the mean hourly respiration observed during the productivity estimates at the stations. Similar day to night community respiration rates were found by Verduin (1957) in Lake Erie. The daily respiration values were used to calculate the ratios of mean daily

Table 7. Estimated mean seasonal gross primary productivity of the phytoplankton at the sampling stations.

	Lake	Canal	River
Spring			
$gC/m^2/day$	0.9 (4)[1]	2.0 (4)	0.8 (5)
$gC/m^2/season$	78.3	185.8	71.0
Summer			
$gC/m^2/day$	1.7 (6)	2.7 (6)	1.5 (5)
$gC/m^2/season$	159.2	250.7	141.2
Fall			
$gC/m^2/day$	0.7 (1)	2.2 (2)	0.7 (2)
$gC/m^2/season$	62.9	100.1	63.7
Total			
$gC/m^2/274$ days	300.4 (11)	536.5 (12)	275.9 (12)

[1]Designates number of sampling dates

phytoplanktonic gross primary productivity to community respiration (P/R) at the sampling stations. Examination of these ratios in Table 8 show that the study area, except on rare occasions, is heterotrophic. The river particularly consumed more than was produced. Most of the respiration is probably contributed by organisms other than the phytoplankton, primarily bacteria. This is most obvious in the river. For example, on 27 May 1970, when the highest respiration was observed in the river, the highest coliform bacteria population occurred in the river (Cole, 1972) while phytoplankton abundances were among the smallest observed.

The consistently low P/R ratios in the study area emphasize the importance of detritus in the system. During this study the average contribution of the phytoplankton to the total particulate organic carbon (Cole, 1972) was minor: 4.8% in the river, 15.2% in the discharge canal, and 27.5% in the lake. The zooplankton contributed much less than the phytoplankton. Zooplankton were rarely observed during phytoplanktonic enumeration. Steele (1969) noted that the role of detritus in aquatic communities may be as important as plankton. It appears that this is particularly true for the near shore areas of western Lake Erie, with the detritus perhaps being more important than the plankton in community energetics.

Regulation of Abundance and Productivity

Phytoplankton productivity has been observed to be regulated by a combination of physical, chemical, and biological environmental factors (Hutchinson, 1967). Primary among the physical parameters are temperature, light, and turbulence. Chemical regulators include nutrient levels and the influence of toxic materials. Competition for

Table 8. Ratios of mean daily phytoplanktonic gross primary productivity to community respiration (P/R) at the sampling stations.

Date	Lake	Discharge Canal	River
5-1	--	--	0.06
5-15	0.26	0.36	0.09
5-27	0.25	0.14	0.02
6-10	0.44	0.21	0.25
6-23	0.55	--	0.18
7-7	0.96	1.21	0.36
7-21	0.54	0.35	0.45
8-4	0.59	0.26	0.11
8-24	0.57	0.42	0.35
9-1	--	0.34	0.15
9-29	1.23	4.54	0.18
10-27	--	0.03	0.07
Mean	0.60	0.79	0.19

nutrients and light plus grazing pressure rank as major biological controls.

Low water temperatures appeared to be a major cause of diatom dominance in the spring and a contributing factor to their increase in the fall. Slightly higher temperatures in the discharge canal, combined with slightly lower light penetration and depressed nitrogen concentrations, also may have contributed to the relatively early occurrence of blue-green algal dominance in the discharge canal. For most of the study period, however, temperatures were quite uniform throughout the study area. Consequently, they could not have been responsible for differences incurred in phytoplanktonic productivity throughout the area.

The role of light appeared to have great importance in the phytoplanktonic regulation in the study area. Daily primary productivity observed in the discharge canal closely followed the photoperiod. Maximum daily primary productivity in the discharge canal was observed about two weeks after the summer solstice. This lag of two weeks may have resulted from the modifying effects of temperature and nutrient concentrations. Thereafter, the primary production in the discharge canal gradually declined for the remainder of the study, except for a second significant peak in September. The river and lake exhibited no obvious relationship to photoperiod, except in possible combination with temperature to reduce early spring and fall algal productivities.

Light penetration was severely limited at all stations, limiting most algal productivity to the upper meter. Below 1.0 m, low light availability appeared to limit photosynthetic activity. The depth of light penetration in the lake appeared to be related to wind induced turbulence. During periods of relative calm when diurnal stratification was observed to develop in the lake (Cole, 1972), settling of suspended particular matter could occur. This permitted increases in the illumination at the lower levels and possibly allowed increases in the primary productivity at the lower levels. Such was the case observed on 1 July 1970, during late morning to mid-afternoon, similar productivities were observed throughout the evaluated water column in the lake. Also on 4 August 1970, during a period of relative calm, the productivities at 0.5 and 1.5 m were observed to generally exceed the values for these levels during more turbulent periods. Surface values did not, however, reflect the calm conditions nor were there obvious differences in the productivity profiles of the inshore areas, indicating that factors other than light were limiting these populations.

Wind induced turbulence in the lake, in addition to increasing turbidity and causing vertical homogeneity of the phytoplankton, appeared to cause a general reduction in the photosynthetic potential of the lake's phytoplankton. Examination of the various physical and chemical parameters analyzed concurrently with this study (Cole, 1972) show that wind-induced severe wave action in the lake had a sufficiently consistent difference from the discharge canal to account for the reduction in the photosynthetic capabilities of the lake from that of the discharge canal. The heavy wave action often experienced by the lake could have caused a disorientation in the lake's plankton that resulted in decreases in their reproductive and photosynthetic abilities. Allen (1920) felt that a similar disorientation caused population reductions in lake plankton discharged into a lotic system. This persistant reduction in production capabilities may partially explain why surface primary productivities in the lake did not significantly increase, as did lower levels of the water column, during periods of relative calm.

Low river primary productivities and phytoplankton abundances may be associated with some unidentified toxic inhibition. Nalepa (1972) felt that adverse environmental conditions, particularly low oxygen concentrations, in conjunction with river discharge were the primary regulators of zooplankton in the river at the time of this study. River velocities do not appear to influence negatively the phytoplankton volumes and primary productivities, because some of the highest phytoplankton populations occur in the river at the time of greatest river discharges in the spring. Changes in the productivity and biomass are not related to changes in oxygen concentration in the river. Nutrient levels are greatest in the river and temperature and light do not differ greatly from the other areas. By deduction toxic inhibitors are most likely limiting river productivity and biomass.

Carbon, of the three nutrients (carbon, phosphorus, and nitrogen) that are most frequently associated with limiting algal production (Hutchinson, 1967), appeared least likely to occur in quantities sufficiently low to limit productivities. Alkalinities in the area range around 100 mg/liter (Beeton, 1963). This is reflected in the generally high dissolved organic carbon concentrations (3-6 mg/liter) observed throughout the study at all stations (Cole, 1972).

Phosphorus concentrations during most of the study do not appear to limit the phytoplanktonic activity in the study area. At no time does the phosphorus concentration fall below a level observed by Sawyer (1947) to possibly limit algal activity. However, total and dissolved phosphorus concentrations were observed to increase in conjunction with the late summer blue-green algae blooms in the study area. This implies that, while phosphorus alone is not limiting, its presence in extremely high concentrations enabled the blue-green algae to optimize existing environmental conditions that permitted a bloom.

Nitrogen concentrations appear to be a major factor controlling algal succession and composition in the river, lake, and, to a lesser extent, the discharge canal. Nitrate-nitrogen appears to be closely related to blue-green algal succession in the study area. The decline of nitrate in July to below 0.3 mg/liter, the often cited level of possible inorganic nitrogen limitation (Sawyer, 1947), coexisted with the dominance (95%) of blue-green algae in the lake. In the river the nitrate concentration remained greater than 0.3 mg/liter into August. There the blue-green dominance was not encountered until August. Blue-green algae are capable of optimizing low nitrogen concentrations only in situations where phosphorus is not limiting, and higher phosphorus concentrations yield higher blue-green algae productivities (Ogawa and Carr, 1969). This accounts partially for the late summer blue-green blooms which occurred in conjunction with a phosphorus pulse in the study area. Some of the major species observed during the bloom were regarded as nitrogen fixers by Ogawa and Carr (1969). Howard, et al. (1970) observed nitrogen fixation to occur in Lake Erie during the summer.

The relatively early dominance of blue-green algae in the discharge canal was possibly caused by an early depression in nitrate concentrations combined with slightly lower light penetrations, associated with high suspended solids concentrations (Cole, 1972), and slightly higher water temperatures.

The possible role of zooplankton as a regulator of phytoplankton abundances is suggested by seasonal changes in phytoplankton, zooplankton, and particulate carbon. The volume and carbon content of the algae did not parallel productivity in the study area. Productivity per unit volume in the discharge canal was lowest for most of the spring and fall, and highest in the summer. The river in contrast had the lowest ratios in late summer. In the lake the highest productivity per unit volume occurred in mid-summer shortly before the August blue-green bloom. Productivities in the lake and discharge canal remained relatively constant during the summer until the bloom, while community respiration and algal volume declined slightly. Productivity was not being stored as detrital carbon in the water because total organic carbon concentrations did not increase during this period (Cole, 1972). Since little net movement of carbon to the sediment is expected in the turbulent lake, much of the produced carbon may have moved to consumers. Nalepa (1972) showed that increases in the biomass of zooplankton were greatest at that time. Zooplankton consumption may have depressed the volume of phytoplankton at a time when the zooplankton were most abundant in the lake and discharge canal, while gross primary productivity was maintained. Zooplankton grazing also may have influenced changes in the mean size of the algae, which increased during the summer as zooplankton abundances increased. The bloom occurred when zooplankton abundance was greatest and indicates that zooplankton did not limit productivity at that time, although they may have influenced algal species composition so that large blue-green algae were favored.

Community Structure

Eutrophication, it has been hypothesized, results in increased sizes of organisms (Hall, *et al.*, 1970) and decreased diversities (Wilhm and Dorris, 1968). The results of this study do not suggest such a simple and direct relationship. The river appears to be the most enriched but productivities are relatively low and diversity relatively high.

Unidentified toxins may be responsible for low productivities, but if so they seem to affect all species equally rather than affecting some species at the expense of other species. Diversities and productivities were both observed to be highest in the discharge canal. Williams' (1964) work has implied that diversity varied indirectly with productivity but that relationship does not appear to hold in this study area.

Diversity differences in this study area appear to be caused primarily by differences in the concentration of rare species; equitability was much less a factor. Rare species, possibly derived from surrounding marsh areas occurred more frequently in the river and discharge canal. It is possible that reproduction of the rare species was limited in the lake and they were diluted out or died by the time they reached the lake stations.

The phytoplankton populations of western Lake Erie exhibit extensive quantitative and qualitative changes from year to year. This stimulated Chandler and Weeks (1945) to write, "General statements concerning phytoplanktonic production in these waters (western Lake Erie) based on observations limited to a season or even a complete year might be very misleading." Part of this variability can be explained in that a body of water the size of western Lake Erie is capable of containing very different populations of phytoplankton at the same time. This was observed by Verduin (1952) in the island region. Studies are continuing to determine annual phytoplanktonic variability in the near-shore areas of Lake Erie, as related to possible regulatory factors. In order to achieve a reasonable level of certainty concerning possible nutrient limitation in the study area analyses such as *in situ* nutrient enrichment bioassays should be performed. These results could then be applied to the field observations to aid in determining the impact of the various parameters.

The only other comprehensive study of the total phytoplankton populations of the River Raisin area of Lake Erie was conducted by Wright and associates (1955) in 1929 and 1930. This early study had only one station in the area "about two miles out form the shore". Class seasonal dynamics exhibited by the early populations were similar to those observed in the 1970 study. The densities, however, were somewhat smaller in the earlier investigation, while vertical distributions, as in this study, were essentially uniform.

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APPENDIX

Table A1. Phytoplankton density (no./ml) arranged in order of increasing abundance at the sampling stations.

<u>2 May 1970</u>

Station	6	3	8	9	1
Mean	678	1381	1482	3277	6478
Multiple Range					

<u>28 May 1970</u>

Station	9	3	1	6	8
Mean	1259	2101	2530	2530	6065
Multiple Range					

<u>23 June 1970</u>

Station	9	6	3	1	8
Mean	1196	1329	1715	2507	6333
Multiple Range					

<u>21 July 1970</u>

Station	6	1	3	8	9
Mean	157	265	512	1156	1289
Multiple Range					

<u>23 August 1970</u>

Station	9	1	8	3	6
Mean	949	1132	1606	2145	2267
Multiple Range					

<u>15 September 1970</u>

Station	3	6	8	1	9
Mean	450	535	673	1091	1509
Multiple Range					

Table A1 (con't.)

10 October 1970

Station	6	3	8	1	9
Mean	667	1126	1598	1621	1865
Multiple Range					

7 November 1970

Station	1	6	3	9	8
Mean	395	434	1224	1320	2191
Multiple Range					

Table A2. Phytoplankton volume (x 10^4 μ^3/ml) arranged in order of increasing abundance at the sampling stations.

2 May 1970

Station	6	8	9	3	1
Mean	392	614	656	859	3956
Multiple Range					

28 May 1970

Station	9	3	1	6	8
Mean	275	785	1204	1486	2928
Multiple Range					

23 June 1970

Station	9	6	3	1	8
Mean	269	700	889	1538	3979
Multiple Range					

21 July 1970

Station	6	1	3	9	8
Mean	56	148	242	269	917
Multiple Range					

23 August 1970

Station	9	1	8	3	6
Mean	2084	2412	2555	7026	7382
Multiple Range					

15 September 1970

Station	3	8	6	9	1
Mean	553	792	941	1004	1804
Multiple Range					

Table A2 (con't.)

10 October 1970

Station	6	9	3	8	1
Mean	404	628	983	1196	1367
Multiple Range					

7 November 1970

Station	1	6	9	3	8
Mean	228	238	291	864	975
Multiple Range					

Table A3. Mean individual planktonic volume (μ^3) arranged in order of increasing volume at the sampling stations.

2 May 1970

Station	9	8	6	1	3
Mean	2,006	4,136	5,706	5,774	6,205
Multiple Range					

28 May 1970

Station	9	3	8	1	6
Mean	2,170	3,742	4,474	4,721	5,885
Multiple Range					

23 June 1970

Station	9	3	6	1	8
Mean	2,209	5,243	5,251	6,077	6,277
Multiple Range					

21 July 1970

Station	9	6	3	1	8
Mean	2,100	3,520	4,867	5,472	7,770
Multiple Range					

23 August 1970

Station	8	1	9	3	6
Mean	16,024	21,367	21,907	32,330	32,506
Multiple Range					

15 September 1970

Station	9	8	3	6	1
Mean	6,828	11,836	13,312	18,238	19,142
Multiple Range					

Table A3 (con't.)

10 October 1970

Station	9	6	8	1	3
Mean	3,421	6,062	7,475	8,325	8,708
Multiple Range					

7 November 1970

Station	9	8	6	1	3
Mean	2,197	4,482	5,537	5,784	7,092
Multiple Range					

Table A4. Volume (x 10^3 μ^3/ml) of blue-green algae arranged in order of increasing abundance at the sampling stations.

2 May 1970

Station	9	1	6	3	8
Mean	0	0	33	59	139
Multiple Range					

28 May 1970

Station	8	9	1	6	3
Mean	0	10	295	722	732
Multiple Range					

23 June 1970

Station	9	3	6	1	8
Mean	588	3,949	4,008	9,960	28,010
Multiple Range					

21 July 1970

Station	6	9	1	3	8
Mean	182	450	564	960	7,605
Multiple Range					

23 August 1970

Station	9	1	8	3	6
Mean	19,642	22,432	23,828	68,960	72,340
Multiple Range					

15 September 1970

Station	3	8	9	6	1
Mean	4,718	6,623	8,087	8,648	17,163
Multiple Range					

Table A4 (con't.)

10 October 1970

Station	6	9	3	8	1
Mean	2,633	3,992	8,019	9,788	10,867
Multiple Range					

7 November 1970

Station	9	6	1	8	3
Mean	529	1,429	1,460	5,157	5,462
Multiple Range					

Table A5. Volume (x 10^3 μ^3/ml) of green algae arranged in order of increasing abundance at the sampling stations.

2 May 1970

Station	3	6	1	8	9
Mean	72	75	108	433	685
Multiple Range					

28 May 1970

Station	9	6	1	3	8
Mean	434	512	728	3383	3476
Multiple Range					

23 June 1970

Station	9	6	3	1	8
Mean	740	1880	3039	4304	5356
Multiple Range					

21 July 1970

Station	6	1	3	8	9
Mean	92	568	826	883	1728
Multiple Range					

23 August 1970

Station	3	8	6	9	1
Mean	485	583	738	768	1022
Multiple Range					

15 September 1970

Station	6	3	1	8	9
Mean	112	138	224	321	456
Multiple Range					

Table A5 (con't.)

10 October 1970

Station	9	1	3	6	8
Mean	515	574	672	1136	1137
Multiple Range					

7 November 1970

Station	9	6	1	3	8
Mean	138	171	193	625	727
Multiple Range					

Table A6. Volume (x 10^3 μ^3/ml) of diatoms arranged in order of increasing abundance at the sampling stations.

2 May 1970

Station	6	8	9	3	1
Mean	3759	4957	5863	8418	14,450
Multiple Range					

28 May 1970

Station	9	3	1	6	8
Mean	2289	3710	7513	9684	25,803
Multiple Range					

23 June 1970

Station	1	6	9	3	8
Mean	1057	1130	1350	1903	6318
Multiple Range					

21 July 1970

Station	6	1	9	3	8
Mean	250	286	489	544	670
Multiple Range					

23 August 1970

Station	9	1	3	6	8
Mean	483	663	703	738	821
Multiple Range					

15 September 1970

Station	1	3	6	8	9
Mean	543	588	608	719	1558
Multiple Range					

Table A6 (con't.)

10 October 1970

Station	3	6	8	9	1
Mean	629	726	1036	1757	2255
Multiple Range					

7 November 1970

Station	1	6	9	3	8
Mean	622	777	2226	2557	3825
Multiple Range					

Table A7. Mean diversity of phytoplankton arranged in order of increasing diversity at the sampling stations.

2 May 1970

Station	1	3	8	9	6
Mean	1.81	2.06	3.24	3.60	3.79
Multiple Range					

28 May 1970

Station	6	8	1	3	9
Mean	1.92	2.78	2.85	3.92	4.11
Multiple Range					

23 June 1970

Station	6	9	3	1	8
Mean	4.15	4.18	4.20	4.31	4.48
Multiple Range					

21 July 1970

Station	6	1	3	9	8
Mean	3.64	3.67	4.25	4.26	4.65
Multiple Range					

23 August 1970

Station	3	6	9	1	8
Mean	3.11	3.13	4.22	4.29	4.30
Mutliple Range					

15 September 1970

Station	1	6	3	9	8
Mean	2.54	3.14	3.42	4.40	4.45
Multiple Range					

Table A7 (con't.)

10 October 1970

Station	1	6	9	3	8
Mean	3.72	3.93	4.19	4.62	4.64
Multiple Range					

7 November 1970

Station	9	8	3	1	6
Mean	3.52	4.22	4.29	4.35	4.56
Multiple Range					

Table A8. Mean equitability of phytoplankton arranged in order of increasing equitability at the sampling stations.

<u>2 May 1970</u>

Station	1	3	8	6	9
Mean	0.108	0.128	0.238	0.385	0.445
Multiple Range					

<u>28 May 1970</u>

Station	6	1	8	3	9
Mean	0.095	0.175	0.180	0.368	0.423
Multiple Range					

<u>23 June 1970</u>

Station	9	3	8	1	6
Mean	0.350	0.405	0.405	0.478	0.485
Multiple Range					

<u>21 July 1970</u>

Station	9	1	3	8	6
Mean	0.373	0.413	0.440	0.463	0.573
Multiple Range					

<u>23 August 1970</u>

Station	6	3	9	1	8
Mean	0.215	0.233	0.375	0.383	0.403
Multiple Range					

<u>15 September 1970</u>

Station	1	3	6	8	9
Mean	0.183	0.305	0.320	0.425	0.463
Multiple Range					

Table A8 (con't.)

10 October 1970

Station	1	6	9	8	3
Mean	0.263	0.338	0.378	0.385	0.473
Multiple Range					

7 November 1970

Station	9	8	3	1	6
Mean	0.313	0.380	0.403	0.503	0.578
Multiple Range					