PHYTOPLANKTON COMMUNITY STRUCTURE AND NUTRIENT RELATIONSHIPS IN LAKE CARL BLACKWELL, OKLAHOMA

By

ALLEN RAY FAUST

Bachelor of Science
Oklahoma State University
Stillwater, Oklahoma
1967

Master of Science
Oklahoma State University
Stillwater, Oklahoma
1972

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Thesis Approved:

Troy C. Dorris
Thesis Adviser

Louis P. Varga

Jerry Wilhm

D. D. Durham
Dean of the Graduate College

PREFACE

The objectives of this study were to: (1) evaluate phytoplankton numbers and species diversity in Lake Carl Blackwell, Oklahoma, and in isolated lake water experiments using nutrient additions and aeration; (2) relate times of major phytoplankton blooms to times of taste and odor; (3) describe limiting effects of phosphorus, nitrogen, and carbon on reservoir phytoplankton; and (4) present a data summary of physico-chemical parameters associated with algal blooms.

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CHAPTER I

INTRODUCTION

The principal objective of the present research was to evaluate blue-green, diatom, and green algal response to aeration and nutrient addition. Lake Carl Blackwell is a 35 year old water supply reservoir for Stillwater, Oklahoma, which annually produces annoying taste and odor. Algae are one of several biotic components which are suspected of imparting malflavors. Algae, phosphorus, nitrogen, carbon, and other physicochemical parameters were studied to provide basic data on limiting factors of planktonic algae. Number-based diversity of phytoplankton enclosed in enriched, isolated columns was compared to diversity in the open water of Lake Carl Blackwell.

The term 'eutrophication' as used in this presentation denotes nutrient accumulation regardless of amount or effect, and is not necessarily equivalent to pollution (Warren 1971, see also Hutchinson 1969, King 1970, Odum 1971, Likens 1972). Jackson (1964) defined an algal bloom as a visible change in the water mass produced by an increased growth of algal cells. Blooms have been investigated mostly in response to phosphorus and nitrogen enrichment (Appendix A). Trace metals have been implicated as growth-limiting nutrients under certain conditions (Gerloff and Skoog 1957). Light, pH, and carbon also may be limiting factors. Qualitative aspects of blooms rather than biomass seems to be of major concern in recent studies (Sirenko et al. 1969, King 1970, Welch et al.

1972, Shapiro 1973, Brock 1973). Bloom hypotheses often have centered on such phenomena as overwintering, symbiotic relationships, and conditions conducive to bloom development.

A generally held hypothesis is that algae remain planktonic and bloom in temperate zone reservoirs in response to nutrients which become available during spring or fall overturns. Upwelling brings mineralized nutrients into the euphotic zone when higher water temperature and light conditions become favorable for high autotrophic production. Nitrogen, phosphorus, carbon, or trace elements may be limiting under these conditions.

A contrasting hypothesis by Russian workers asserts that spring blooms are brought about by overwintered stages that form benthic colonies below the euphotic zone and eventually become planktonic. Algae also may overwinter in clumps blown up on shore from which they re-enter the water when the level rises or when rains occur in spring. Hence, algal cells antecedent to blooms develop earlier on the bottom or shore than in the water mass (Sirenko et al. 1969).

Blue-green algae may form symbiotic relationships with gram-negative bacillus bacteria (Silvey and Roach 1964, Kuentzel 1969, Holm-Hansen 1968, Legge and Dingeldein 1970). Gelatinous covers of blue-greens contain high concentrations of bacteria (Silvey and Roach 1964). Symbiotic bacteria can provide the CO_2 necessary for large blooms which cannot be accounted for by free CO_2 in the water or by CO_2 which diffuses in from the atmosphere (Silvey and Roach 1964, Sirenko et al. 1969). Blooms of blue-greens in Southwestern United States reservoirs continued as long as bacteria were supplied with organic matter and produced CO_2 (Silvey and Roach 1964).

Organic matter seems to be necessary for heterotrophic growth. No excessive algal growths occurred in a 546 ha (1350 acre) Texas reservoir which contained abundant bacteria and algae (Wells 1969). The pH was consistently 8.5, and phosphorus fluctuated between 0.07 and 0.30 mg/1. Lack of growth was due to low dissolved organic matter.

It has been argued that blue-greens require an alkaline medium for optimum growth (Webster and Frenkel 1952, Kratz and Myers 1955, Fogg 1956, Brock 1973), may be sensitive to high free CO_2, and may be dependent on carbonate ion, while forms which compete successfully with blue-greens at pH below 8.4 may not be so inhibited (Jackson 1964). Recent studies reveal that blue-greens can take up CO_2 at lower CO_2 concentration than green algae (King 1970). Blue-green algal production is reduced at CO_2 concentration of less than 2.5μ moles/liter. High CO_2 may cause a shift from blue-green to green algae, especially when other nutrients are abundant (Shapiro 1973). For this reason alkaline bodies of water, which have low free CO_2 concentrations, may support more blue-greens.

Increased algal growth in Lake Medota occurred in areas exposed to winds but not in protected coves (Wohlschlag and Hasler 1951). Winds stirred up nutrients from the sediments and brought in additional CO_2 by aeration. Algal mats were deposited on shore by wind action after the bloom. Cells did not die immediately, but were retained in jelly-like masses which slowly dehydrated. Bacterial action was reduced and actinomycetes increased, feeding on the mass of algae.

Nitrogen fixation can provide much of the nitrogen necessary for blooms. Forty-three percent of annual nitrogen input to Clear Lake, California comes from biological nitrogen fixation (Horne and Goldman,

1972). Another source of nitrogen is ammonia which is formed and nitrified after algal cells die and lyse (Topachevskiy et al. 1969). Autotrophic nitrifying bacteria may compete with algae for available CO_2 (Torpey 1968).

Death of algae is important in cycling of phosphorus since phosphorus is not an atmospheric constituent and algae are known to assimilate 'luxury' phosphorus up to 20% dry weight (Porcella 1969, Fitzgerald 1969, Kuentzel 1971, Azad and Borchardt 1970). Heavy growth can occur in as little as 0.015 mg/l orthophosphate and release from one bloom can produce a second bloom (Kuentzel 1969).

Russian investigations have shown that large blue-green growths are relatively short-lived because the algae are not euplanktonic, but have a long wintering period on mud bottoms where anaerobic, richly organic conditions exist (Topachevskiy et al. 1969). Microcystis aeruginosa colonies reached a maximum in early spring when oxygen content was low or undetectable by the Winkler method, but where a high concentration of organic substances existed (Sirenko et al. 1969). Cell multiplication occurred first on a mud bottom in the dark and increased rapidly in light near the surface after densely packed colonies floated loose. Heterotrophic nutrition was reduced and autotrophic production increased. Although this reversal has been documented for Microcystis aeruginosa (Sirenko et al. 1969), Holm-Hansen (1967, 1968) and Van Baalen et al. (1971) believe that heterotrophic growth is possible only in light. Growth of blue-green algae in clear water often is excessive (Hergenrader and Hammer 1971). Turbidity slowed growth of Nostoc muscorum (Lazaroff and Vishniac 1961) and inhibited photosynthesis of Aphanizomenon sp., and Microcystis aeruginosa (Hergenrader and Hammer 1971). Anabaena sp.

decreased in clear, aerated water (Malueg et al. 1971), and was observed blooming with *Microcystis sp.* in low turbidity (Krishnamoorthi et al. 1971).

CHAPTER II

THE STUDY AREA - LAKE CARL BLACKWELL

Lake Carl Blackwell is located 11 km west of Stillwater, Payne County, Oklahoma. Construction was completed in 1938, and the reservoir was filled in 1945 by intermittent flow of Stillwater Creek. Drainage area was 173 km^2 of blackjack oak, shortgrass prairie, and grain-crop farm land. No urban or industrial runoff and a minimum of domestic waste originates in the watershed. Surface area was 1400 ha (3460 acres) at spillway elevation of 288.0 m M.S.L. in 1945. Spillway level was 283.1 m M.S.L. at the time of the present study with storage of 19.7 million m^3 and surface area of 665 ha (1643 acres) (Ree, W., Director, Outdoor Hydraulic Laboratory, U.S.D.A., personal communication concerning water level of Lake Carl Blackwell). Mean depth was approximately 3 m (Norton 1968). Suspended particles of montmorillonite clay cause Lake Carl Blackwell to be turbid most of the time (Leonard 1950). Clay particles are kept in suspension by wind-induced wave action. The Oklahoma State University Geology Department found that the capacity of the reservoir basin had been reduced 6% by 1959 by erosion and runoff from road beds and trails (Ree, personal communication).

Maximum depth of the reservoir during the study was 12 m near the dam. Depth at the experimental station was 4 m. Wind action and basin topography prevented thermal stratification except during brief periods. Lake Carl Blackwell is considered to be a chemically stable system in

that major changes normally occur slowly (Rice 1972). Mass transport occurs mainly by wind-induced currents.

CHAPTER III

MATERIALS AND METHODS

Sampling Station and Design of Experiments

One sampling station consisting of a raft with an instrument shelter was anchored approximately 40 m upstream from the dam (Fig. 1). A submerged cable provided power for pumps and analytical equipment.

Isolating columns are commonly used to study *in situ* natural plankton communities of lakes and reservoirs (Goldman 1962, Stepanek 1965, Slack and Ehrlich 1967, Kemmerer 1968, McLaren 1967, Schlinder et al. 1971, Powers et al. 1972, Schelske and Stoermer 1972, Shapiro 1973). Four columns of 12 mil polyethylene sheet extended from 40 cm above the surface to the reservoir bottom (Fig. 2). Volume of each column was approximately 7,000 liters. Water in columns was continuously circulated by submersible pumps. Water from 3 m was released near the surface to mix nutrients and to simulate reservoir circulation. Six experiments of aeration and nutrient addition were performed from June to October, 1972 (Table I). Two columns simultaneously received aeration or a nutrient while the other two columns served as controls. Experiments involving aeration and phosphorus were repeated while those involving nitrate and glucose were performed once.

Duplicate samples of net algae and surface algae were removed from the reservoir and each column immediately after nutrients were added and

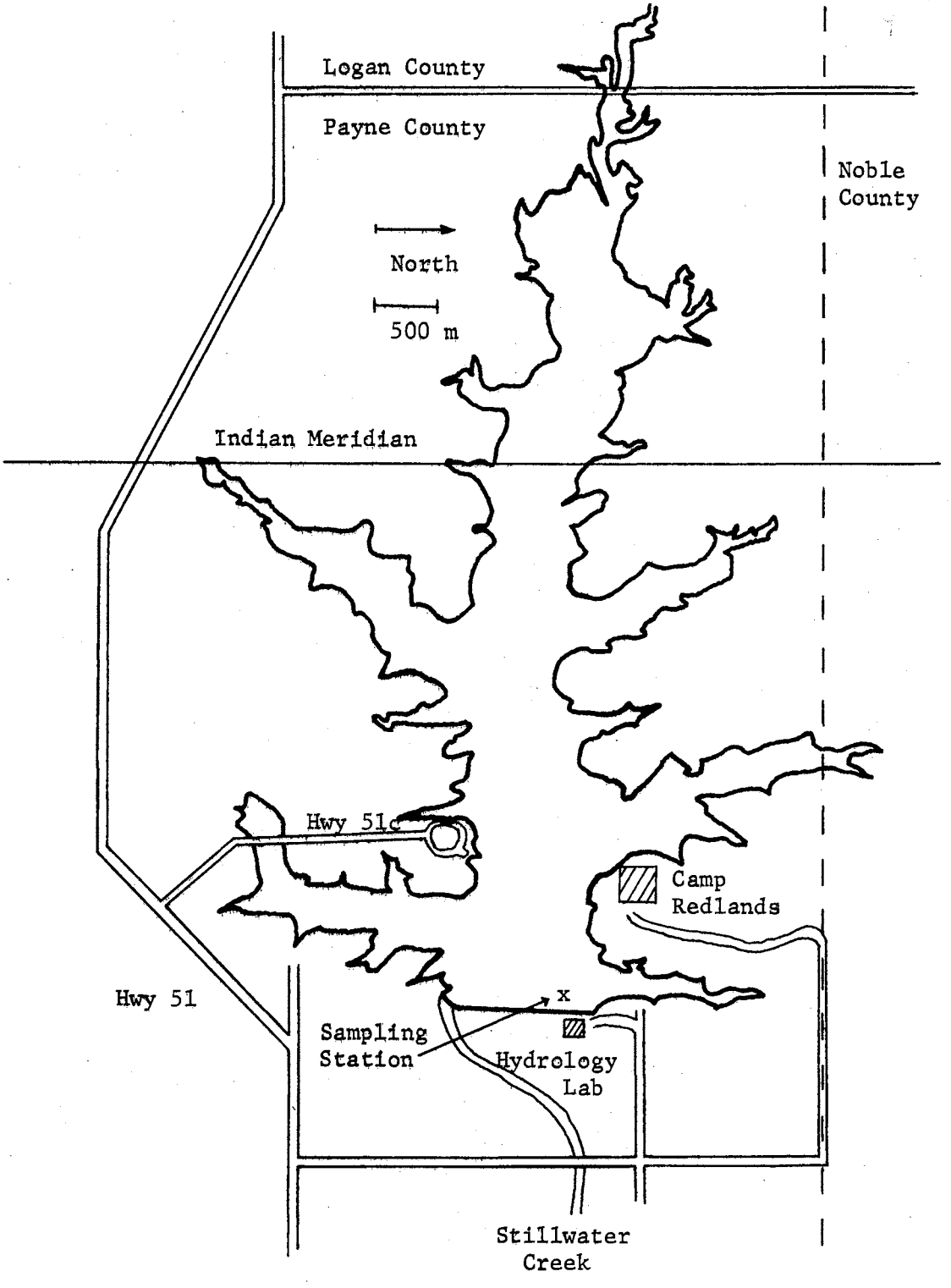

Figure 1. Lake Carl Blackwell, Payne County, Oklahoma

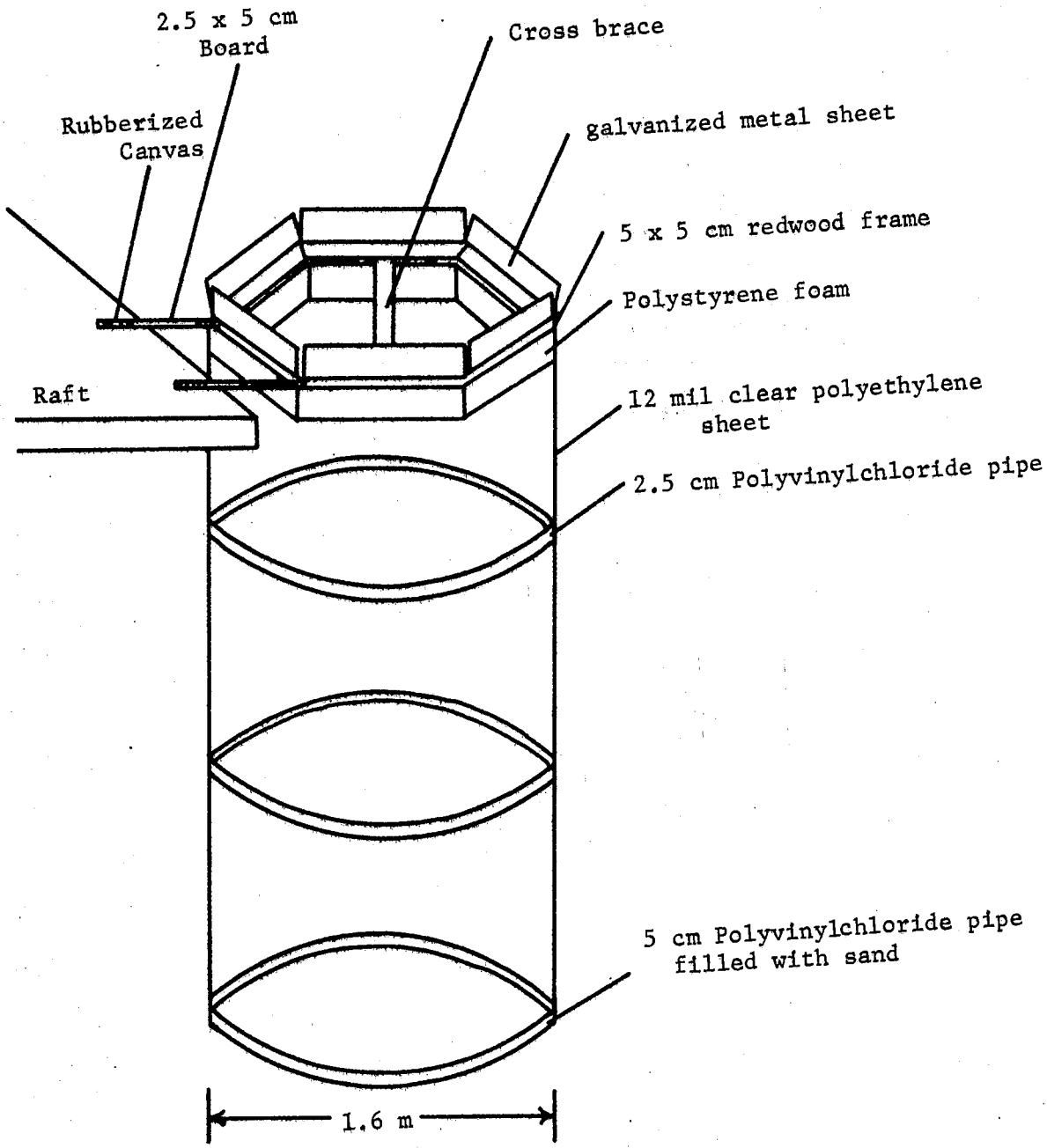

Figure 2. Structure of Polyethylene Column

TABLE I

DATES AND CONDITIONS OF FIELD EXPERIMENTS

Experiment	Inclusive Dates	Experimental Units*	
		Treatment	Control
1 - Aeration	6-21-72 to 6-27-72	Two columns aerated, circulated	Two columns circulated
2 - Phosphorus	7-14-72 to 7-22-72	Two columns phosphorus added, circulated	Two columns circulated
3 - Nitrate	7-25-72 to 8-02-72	Two columns nitrate added, circulated	Two columns circulated
4 - Glucose	8-08-72 to 8-18-72	Two columns open at bottom, glucose added, circulated	Two columns closed bottom, glucose added, circulated
5 - Aeration	9-03-72 to 9-09-72	Two columns aerated, circulated	Two columns circulated
6 - Phosphorus	9-12-72 to 9-21-72	Two columns phosphorus added, circulated	Two columns circulated

*Two replicates for each experimental unit.

every other day for 8 days. Oxygen, temperature, and light penetration were measured each time algae were sampled. Duncan's new multiple range test was used to determine significant differences among treated columns, control columns, and the reservoir (Steele and Torrie 1960).

An experiment was performed to identify algal forms which overwinter on bottom muds in Lake Carl Blackwell. Mud was collected by dredge from 2 m and 5 m depths. Approximately 500 g of undisturbed bottom mud was placed in each of two 30 liter aquaria with modified Gorham's medium (Appendix B). Temperature was held at 24 ± 2 ^{o}C during a 12 hour light-dark regime under Sylvania Gro-Lux lamps. The aquaria were stirred twice daily. Algal samples were counted every 2 days for 35 days.

A green alga (Chlorella pyrenoidosa) and a blue-green alga (Dactylococcopsis sp.) were added to filtered Lake Carl Blackwell water in a second laboratory experiment. Added nutrients (0.496 g/l $NaNO_3$ plus 0.063 g/l Na_3PO_4), added CO_2 (bubbled 10 min twice daily), and low pH (6.0 for 10 days and 3.3 for 10 days) served as treatments. Filtered lake water served as a control.

Physicochemical Parameters

Dissolved oxygen concentration was measured with a galvanic cell oxygen probe and special metering circuit. The probe was calibrated by the Alsterberg azide modification of the Winkler method. Aerations were made at the rate of 0.056 m^3/min/column. Temperature was measured by a thermistor which was calibrated with a mercury thermometer accurate to ± 0.1^{o}C. Light penetration was observed using a Secchi disc. pH was measured with an Orion Model 407 portable meter and Beckman 39000 combination electrode. A standard curve was prepared from buffers of pH

3.0 to 10.0 and millivolt readings were converted to pH from the curve.

Phosphorus additions were calculated to provide 1.0 mg/l PO_4-P after precipitation in the reservoir by divalent calcium and magnesium ions. Ca^{++} plus Mg^{++} concentration was 50 mg/l in Lake Carl Blackwell (Rice 1972). Other precipitating elements were present in much lower concentrations and were omitted in calculations. Each treated column received 538 g HPO_4^{-}. Water samples for phosphorus analyses were taken from 0.5 m in 1 liter polyethylene bottles and kept on ice for 6 hr until analysis (A.P.H.A., 1971).

Orthophosphate was determined by the single-solution method of Murphy and Riley (1962). Particulate matter was removed by filtration with 0.22μ Millipore filters (Eley 1970). Filtered and unfiltered samples were converted to orthophosphate by digestion in a boiling water bath for 1 hr with 5% potassium persulfate (Menzel and Corwin 1965). Absorbance was read after 15 min color development in 4 cm cells on a Beckman DB-G spectrophotometer at 720 nm. Color was stable for up to 30 min, then began to fade slightly.

Determination of phosphorus in bottom mud at the site of the columns was made by adding 1 g of mud to 1 liter of distilled water, agitating, and further treating the sample as a water sample. Samples were filtered before reading absorbance.

Standard curves of digested and undigested phosphorus concentrations from 0.0025 to 0.1666 mg/l were prepared in triplicate. Undigested standards followed Beer's Law over the range of concentrations used. Digested standards also followed Beer's Law at concentrations encountered in Lake Carl Blackwell. Higher concentrations gave a non-linear response. Digested and undigested absorbances were averaged to produce

one standard curve. Sample values were obtained from the linear regression of the curve. Absorbance values varied no more than 0.003 units between duplicates within columns.

Five forms of phosphorus were calculated from unfiltered-digested, filtered-digested, and filtered-undigested samples as follows:

Unfiltered-digested equals total phosphorus

Filtered-digested equals total soluble phosphorus (inorganic plus organic)

Filtered-undigested equals soluble orthophosphate (inorganic)

Filtered-digested minus filtered-undigested equals soluble organic phosphorus

Unfiltered-digested minus filtered-digested equals particulate phosphorus

Nitrate additions were calculated to increase NO_3-N concentration to 5.0 mg/l. Nitrate ion produces negligible complexes and precipitates because of its molecular size, polarization, and electron-accepting properties (Kolthoff et al. 1969). Dissolved $NaNO_3$ (49.1 g) was added to treated columns. Water for nitrate analysis was taken from 0.5 m and addition of 40 mg/l of $HgCl_2$ and refrigeration at $4^{\circ}C$ preserved the samples (E.P.A. 1971). Duplicate nitrate analyses were performed within 4 days by the method of Mullin and Riley (1955). Absorbance was read at 540 nm. A standard curve was prepared using concentrations from 0.0037 to 3.700 mg/l NO_3-N. The standard curve obeyed Beer's Law over the range of concentrations used. Sample concentrations were converted from linear regression of the standard curve.

Carbon has been increased in algal nutrition studies by adding soluble organic compounds (Hobbie and Wright 1965), bicarbonate ion (Allen 1972), or carbon dioxide gas (Shapiro 1973). Continuous addition of CO_2

gas to large volume columns was prohibitively expensive, while bicarbonate addition produced almost no free CO_2 since reservoir pH was as high as 8.4. Thus, algal community dynamics were monitored for 10 days after addition of 1600 mg/l glucose.

Algal Sampling

Algae were sampled by duplicate vertical net hauls using a 16 mesh/cm net and a retrieval rate of 0.5 m/sec. Net algae were preserved with FPA (Prescott 1970). Surface algae were settled and stained for 5 days by Lugol's iodine (Lund et al. 1958). McNabb's (1960) method was used to enumerate algae.

Phytoplankton Diversity

A species diversity index for mixed populations is useful as an indicator of changes in water conditions (Margalef 1965). The quantitative index: $\bar{d} = -\sum_{i=1}^{n} n_i/N \log_2 n_i/N$ represents diversity per individual and is independent of sample size. $\bar{d}$ is dimensionless and any units of numbers or biomass can be used (Wilhm and Dorris 1968).

Independent samples of size 120 to 420 individuals of phytoplankton from Lake Carl Blackwell did not produce significantly different diversities (Table II). Two pooled samples or at least 240 individuals were counted. It is not necessary to classify organisms to species to calculate $\bar{d}$, but specimens must be placed in categories of like individuals. Algae were not identified to species in every case (Appendix C).

TABLE II

$\bar{d}$ OF INDEPENDENT ALGAL SAMPLES

Species	Sample Size						
	60	120	180	240	300	360	420
Melosira sp. A	10	19	34	56	49	69	86
Melosira sp. B	32	61	90	116	165	180	202
Cyclotella sp.	7	15	22	25	31	29	42
Aphanizomenon sp.	6	7	13	15	14	22	32
Anabaena sp.	1	4	5	7	10	14	20
green micro cells	1	4	4	3	6	10	14
Microcystis sp.	1	3	4	2	5	3	4
unknown diatom	2	2	6	8	6	16	9
Oscillatoria sp.		1	1	2	4	2	3
flagellate		1	1	1	1	2	4
Closterium sp. A		3		3	6	9	3
Pediastrum sp.				1	1	1	
Staurastrum sp.				1		1	
Ceratium sp.					1		
Closterium sp. B					1		
Nodularia sp.						2	
Spirulina sp.							1
S =	8	11	10	13	14	14	12
$\bar{d}$ =	2.07	2.34	2.23	2.27	2.24	2.38	2.33

CHAPTER IV

RESULTS AND CONCLUSIONS

Algae and Taste and Odor in Lake Carl Blackwell

Counts of algae were made from April, 1971, to January, 1972, to determine general population trends and to identify predominant forms. Counts were made in summer, 1972, coincident with nutrient experiments. Different species of algae were dominant at different times making it impossible to conduct each nutrient experiment with a similar community.

Diatoms peak first in many reservoirs (Baklanovskaya 1969, Lin 1972, McDaniels 1973). The normal sequence of events in European reservoirs has been described as: spring - diatoms, early summer - greens, late summer - blue-greens, autumn - second diatom peak (Knoppert et al. 1970). Lake Carl Blackwell did not follow this regime during either year of the study (Figs. 3, 4). Variation also existed in the sequence of algal peaks in 1971 and 1972.

Taste and odor is most prevalent in Lake Carl Blackwell water in early September. Diatoms and green algae were abundant in August and September, 1971. Blue-green and green algae dominated in August and September, 1972. All three groups of algae probably contribute to taste and odor problems in September. Laboratory cultures of Lake Carl Blackwell blue-green algae emitted a fishy, rotting grass odor, with the fish odor more prevalent as cultures aged. Diatom cultures produced a musty, grassy odor.

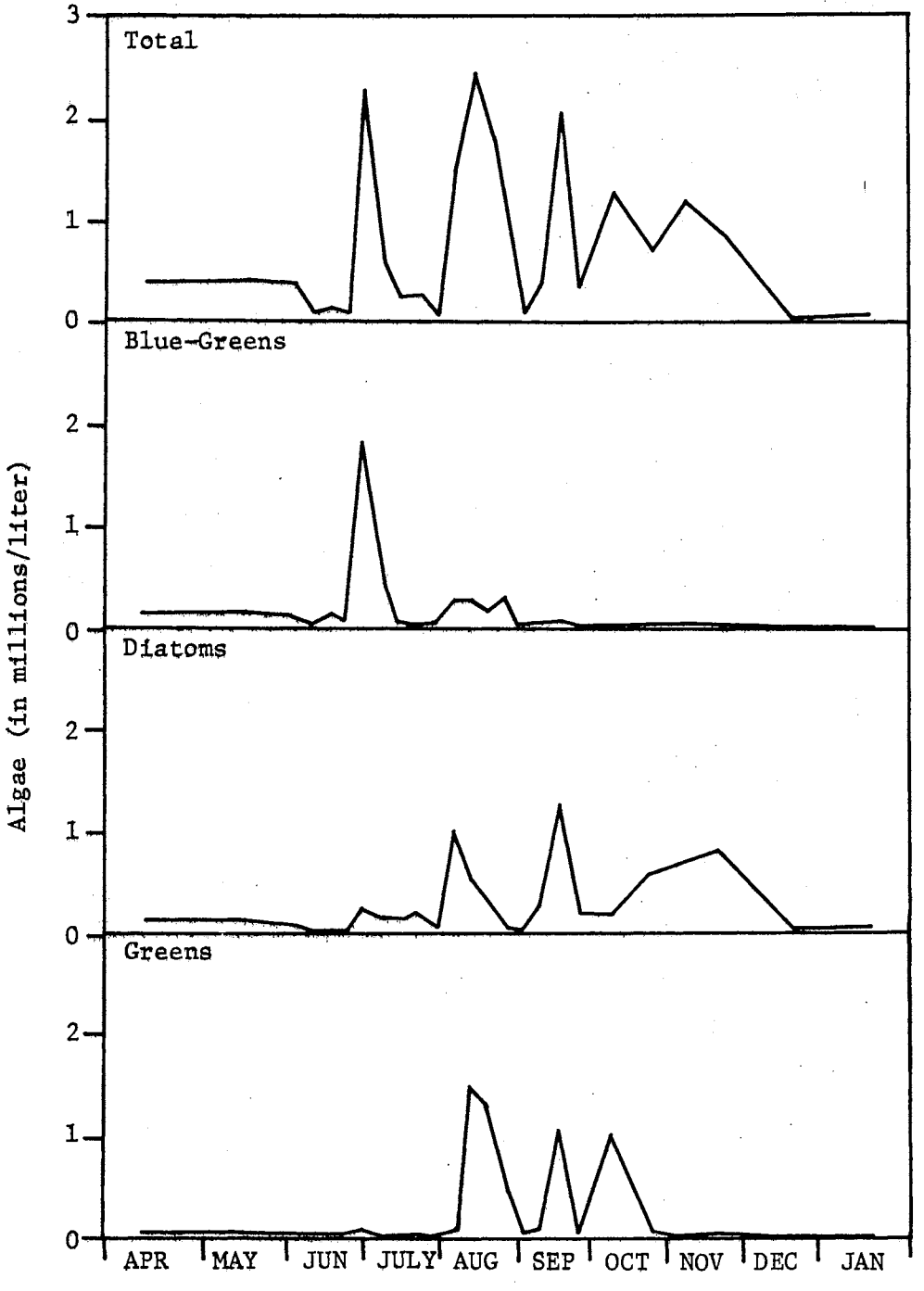

Figure 3. Phytoplankton Numbers in Lake Carl Blackwell, April, 1971 - January 1972

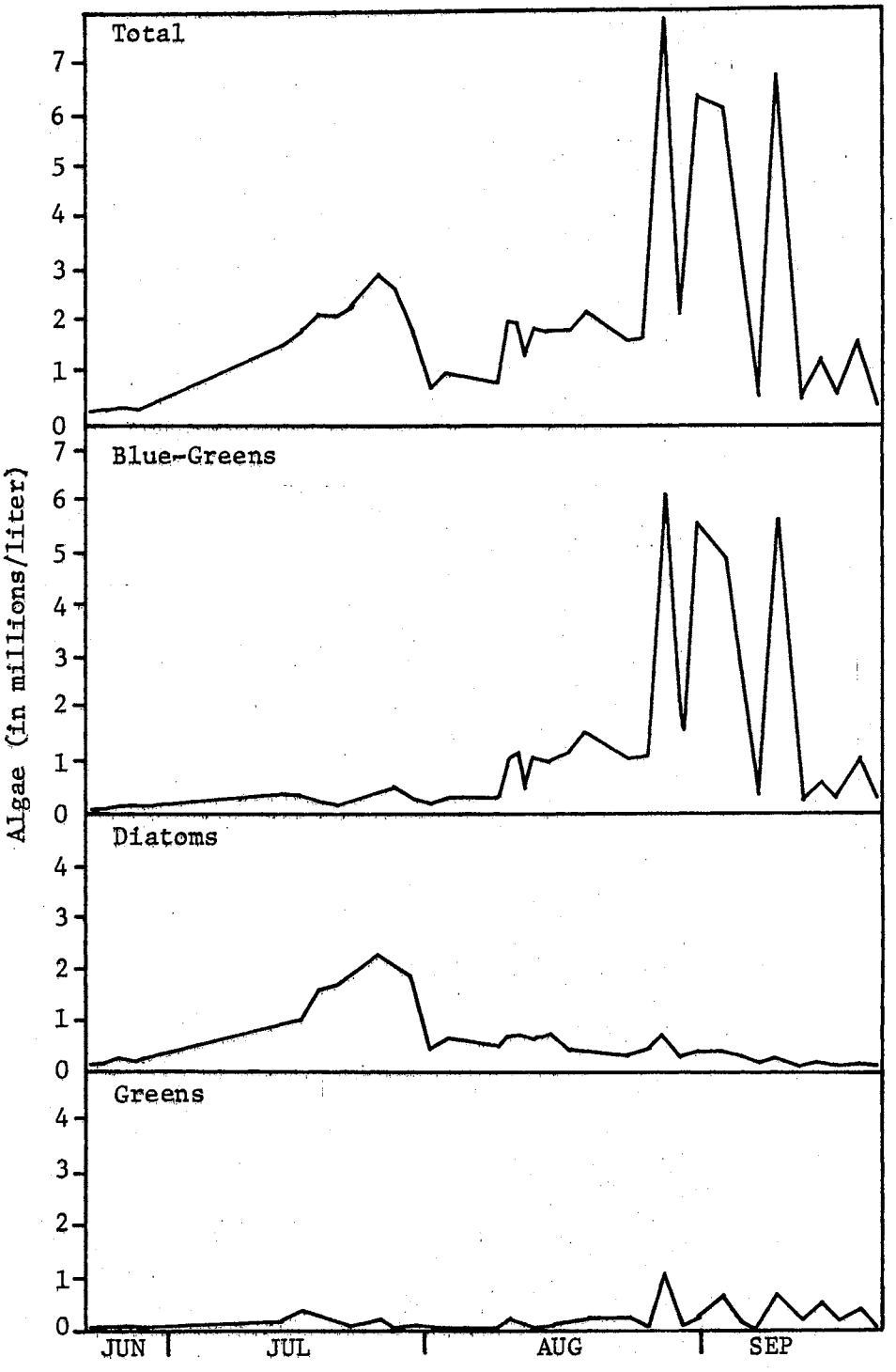

Figure 4. Phytoplankton Numbers in Lake Carl Blackwell, Summer, 1972

Response of Phytoplankton to Aeration

Oxygenation of reservoirs by forced air injection resulted in reduction of numbers of summer phytoplankton (Symons et al. 1967, Robinson et al. 1969, Knoppert et al. 1970). Blue-green phytoplankton abundance increased during aeration while other phyla decreased (Lackey 1973). In a reservoir aerated for periods of 3 to 8 days surface clarity was not impaired, oxygen content increased, and blue-green and green algae decreased (Symons et al. 1967). Algal numbers increased after aeration was terminated. Oxygen content in a Stockholm reservoir was reduced by air injection because of vertical transport of oxygen-depleting mud (Bernhardt 1967). Aeration was shown to be a negligible carbon source unless at least 0.5% CO_2 was added (Kratz and Myers 1955). Aeration and circulation may favor algal species that normally sink rapidly and, depending on species present, could result in increases or decreases in overall algal abundance (Lackey 1973).

Algal populations of Lake Carl Blackwell were dominated by diatoms during the first aeration experiment. The second aeration experiment was performed near the end of a blue-green bloom. It was expected that diatoms would increase in all columns because of substrata supplied by the sides of columns. Diatom numbers were slightly lower in number in columns during the first experiment and higher in number during the second experiment (Table III). Blue-greens and greens were lower in number in aerated columns and higher in control columns during both experiments. It appears that aeration may be capable of reducing numbers of blue-green and green algae in Lake Carl Blackwell.

Aeration and circulation in columns reduced mean Secchi disc light penetration from approximately 40 cm to 30 cm. Circulation alone in con-

TABLE III

MEAN NUMBERS* OF ALGAE DURING AERATION EXPERIMENTS

Parameter	Reservoir	Non-aerated Columns	Aerated Columns
		Experiment No. 1	
Total algae	266.7	247.2	218.1
Blue-greens	39.8	42.2	34.4
Diatoms	182.0	162.4	174.1
Greens	45.0	42.6	32.1
		Experiment No. 2	
Total algae	3871.5	5194.0	2873.9
Blue-greens	3125.4	4046.4	2147.7
Diatoms	276.9	385.5	398.6
Greens	469.1	762.1	327.8

*Number of algae x 10^3 per liter, N = 16.

trol columns reduced mean light penetration to 37 cm. Mean temperature of aerated columns was about 1°C cooler than the reservoir. Dissolved oxygen concentration was near saturation at the surface in the reservoir and all columns, but was significantly increased near the bottom in aerated columns. Forced air injection of Lake Carl Blackwell probably would not lower water temperature sufficiently to reduce summer evaporation. Bottom water in the relatively shallow reservoir contains enough oxygen for fish except for brief summer periods so that aeration would seldom be beneficial for the sole purpose of maintaining high oxygen levels.

Inorganic Phosphorus Relationships

Serruya (1971) suggested that montmorillonite particles may adsorb phosphorus and that montmorillonite added to reservoir waters might sediment phosphorus thereby removing it from possible planktonic uptake. Montmorillonite clay particles constitute most of the turbidity and sediment in Lake Carl Blackwell (Leonard 1950). Lake Carl Blackwell sediment contains 0.980 mg/g phosphorus of which 0.965 mg/g is particulate. Particulate organic and inorganically bound phosphorus fractions were not distinguished by the determination method used since persulfate digestion and acid hydrolysis probably convert phosphorus adsorbed onto montmorillonite particles into orthophosphate.

Sediments may lose 18 to 65% of phosphorus to overlying water (Li et al. 1973). Slight stirring of bottom sediment by pumps in control columns during phosphorus addition experiments appears to have increased orthophosphate by approximately 0.06 mg/l. Release of orthophosphate from only 0.5 cm of Lake Carl Blackwell sediment would be sufficient to

produce the observed orthophosphate increase in control columns. Bacterial solubilization of precipitated aluminum-phosphorus complexes such as montmorillonite can occur in water of high pH (Gahler 1969), and might provide sufficient orthophosphate to produce algal blooms in Lake Carl Blackwell water which has a high pH (Table IV). It is doubtful that application of montmorillonite to reservoirs would be useful in reducing phosphorus.

TABLE IV

pH OF LAKE CARL BLACKWELL, 1940 TO 1973

Reference	Sample Year	pH
Leonard (1950)	1940 - 1941	7.1 - 8.3
U. S. Geol. Survey (1947)	1947	7.3 - 7.8
Leonard (1950)	1949 - 1950	7.4 - 8.4
Cooper (1965)	1963 1964	7.8 - 8.8 8.3 - 8.8
Norton (1968)	1967	8.4
Rice (1972)	1971	8.1 - 8.6
Orr (unpublished)	1972	8.1 - 8.5
Faust (present study)	1973	8.2 - 8.6

Organo-Phosphorus Relationships

Organo-phosphorus is excreted by phytoplankton and released upon death (Lean 1973), but algae also may take up organo-phosphorus compounds, perhaps even preferentially (Ryther and Guillard 1959). Interpretation of results of algal assay tests are complicated by the fact

that all organo-phosphorus may not be formed biologically. Lean (1973) reported that two forms of organically bound phosphorus were present 3 min after radioactive phosphate enrichment of a lake water sample. One form was a molecular aggregate or colloid for which he postulated no biologically important role, but which may be the so-called "particulate organic phosphorus" commonly included as a living cellular constituent. Colloidal organo-phosphorus cannot be distinguished by present methods from phosphorus bound within living cells. A rapid increase of particulate phosphorus in assay cultures cannot necessarily be equated with an uptake by algae.

Particulate phosphorus increased within 1 hr after orthophosphate addition in columns (Table V). Algae may have absorbed part of the orthophosphate, but it is probable that some orthophosphate was converted to the colloidal organo-phosphorus form.

Lean (1973) described a second form of organically bound phosphorus which had a relatively low molecular weight of 250. Formation of such a compound may be a cellular response to low orthophosphate or high biomass (Lean 1973). Soluble organo-phosphorus increased temporarily in columns (Table V). The increase cannot be attributed to high algal biomass and, although orthophosphate was in low concentration in Lake Carl Blackwell water, no evidence exists to show that cellular phosphorus was low. Conditions under which the low molecular weight organo-phosphorus compound may be formed have not been ascertained and more study is needed of phosphorus kinetics and biotic relations in the aquatic environment.

Response of Phytoplankton to Phosphorus

Algae increased significantly in numbers in response to added ortho

TABLE V

MEAN OF FIVE FORMS OF PHOSPHORUS* BEFORE AND DURING PHOSPHORUS ADDITION EXPERIMENTS

Parameter	Time (hrs)	Reservoir	Columns	
			No P Added	P Added
Total P	Before addition	0.0620	0.0650	0.0623
	1	0.0682	0.1225	1.0280
	48	0.0570	0.0518	0.0545
	96	0.0578	0.0643	0.0606
	144	0.0652	0.0733	0.0715
	192	0.0824	0.0733	0.0730
Soluble P	Before addition	0.0100	0.0103	0.0114
	1	0.0105	0.0805	0.9494
	48	0.0076	0.0085	0.0113
	96	0.0098	0.0121	0.0118
	144	0.0125	0.0123	0.0113
	192	0.0136	0.0111	0.0104
Ortho P	Before addition	0.0040	0.0042	0.0040
	1	0.0040	0.0711	0.9237
	48	0.0046	0.0038	0.0055
	96	0.0032	0.0077	0.0064
	144	0.0058	0.0061	0.0060
	192	0.0091	0.0057	0.0050
Sol. Org. P	Before addition	0.0060	0.0063	0.0074
	1	0.0065	0.0094	0.0259
	48	0.0028	0.0047	0.0058
	96	0.0067	0.0044	0.0054
	144	0.0066	0.0062	0.0053
	192	0.0044	0.0054	0.0064
Partic. P	Before addition	0.0610	0.0547	0.0509
	1	0.0577	0.0420	0.0786
	48	0.0494	0.0433	0.0432
	96	0.0467	0.0522	0.0438
	144	0.0527	0.0610	0.0605
	192	0.0688	0.0622	0.0626

*Concentrations in mg/liter, N = 8.

phosphate and to phosphorus released from bottom sediments in 2 days in one experiment (Fig. 5) and in 4 days in a second experiment (Fig. 6). Numbers also increased in control columns where phosphorus concentration was increased by sediment stirring. Blue-greens responded to a lesser extent than greens in both experiments and diatoms did not respond in either experiment. Increase of cell numbers was short-lived which may indicate a turnover time of less than 4 days in enriched columns.

Mineral deficiencies cause specific symptoms in algae including different abilities to recover if viability is not entirely lost (Soeder 1965), so that it is important to know whether a phytoplankton community is 'juvenile' or 'senile'. A juvenile community is actively growing and increasing in numbers while a senile community consists of degenerative cells. Production of new material may come to a complete standstill in a senile community. The response of cell numbers to phosphorus addition in 2 days probably is indicative of a juvenile community which was beginning active cell multiplication. The response in 4 days during a second experiment occurred in a community which had just produced a large blue-green bloom.

Response of Phytoplankton to Nitrate

Depletion of inorganic nitrogen can be the main cause for termination of spring algal blooms (Pechlaner 1970). Nitrate and ammonia concentration decrease almost to zero at the surface in Lake Carl Blackwell by the end of June and remain low throughout the summer (Toetz 1972). Even though nitrate concentration was extremely low in reservoir water (Table VI), addition of 5.0 mg/l of nitrate had no effect on the senile, diatom-dominated community which was present initially. Diatoms in the

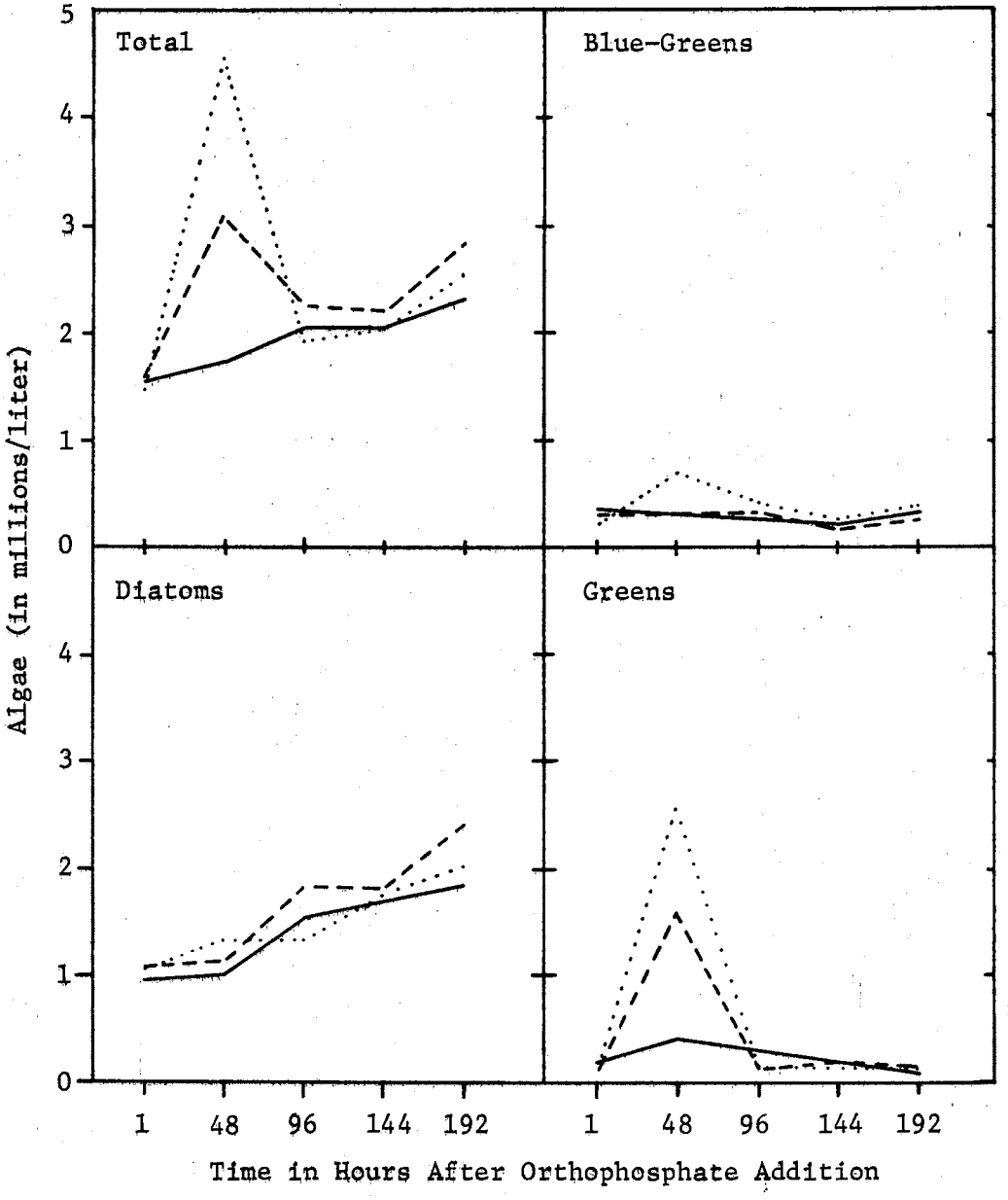

Figure 5. Total, Blue-Green, Diatom, and Green Algae During Phosphorus Experiment One (———— Reservoir, ------ Phosphorus Added, ... Control)

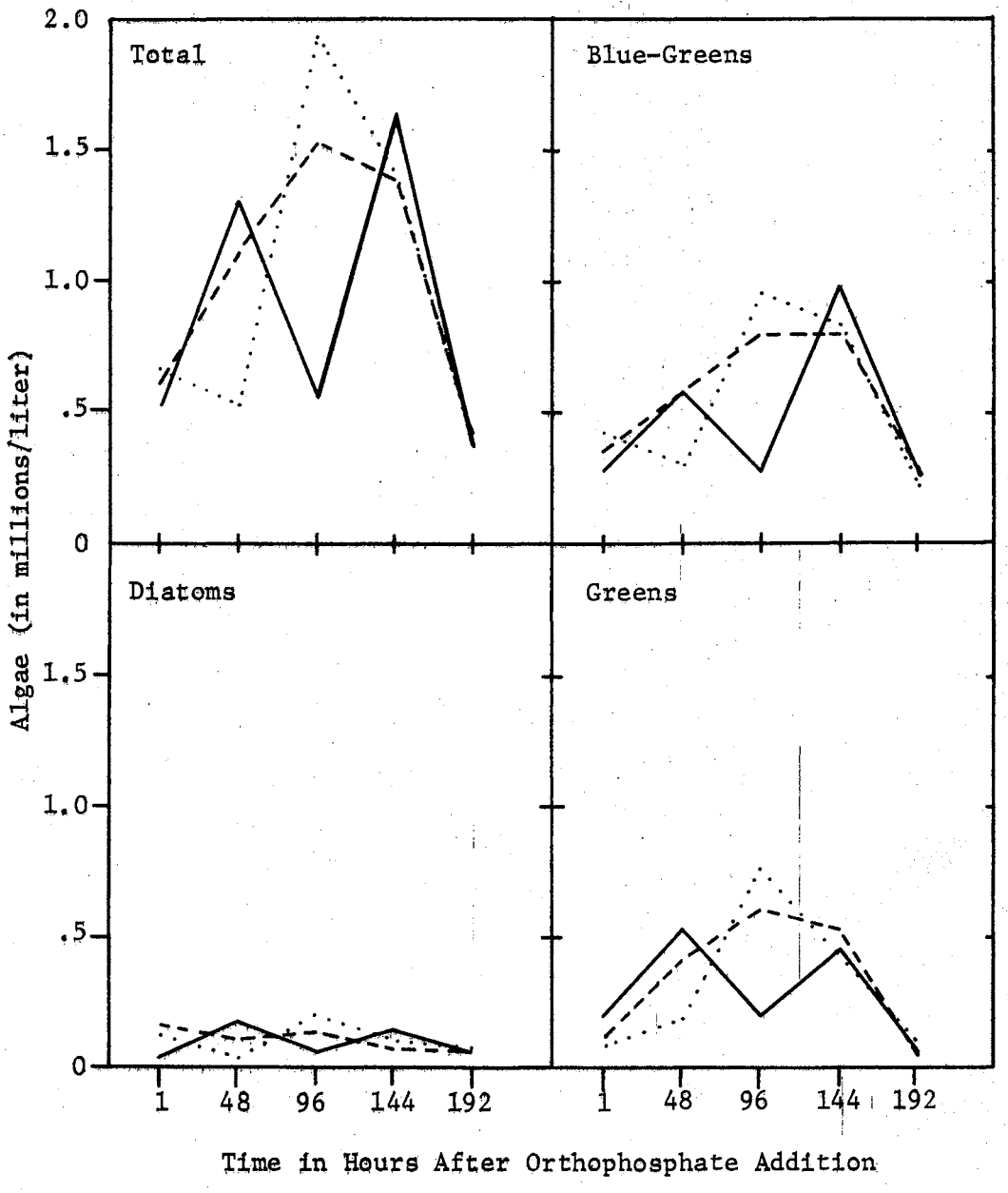

Figure 6. Total, Blue-Green, Diatom, and Green Algae During Phosphorus Experiment Two (—— Reservoir, ---- Phosphorus Added, ····· Control)

columns and the reservoir decreased from 2,200,000 to 500,000 cells/liter in 7 days (Fig. 7). A slight increase in numbers of diatoms after day 7 may have been a delayed response initiated by a release of other nutrients such as silicon or phosphorus from the previous bloom.

TABLE VI

SOLUBLE NITRATE*, JULY, 1972

Time After Addition (Hrs)	Reservoir	No Nitrate Added	Nitrate Added
1	0.0135	0.0136	> 2.000
48	Undetectable	Undetectable	Undetectable
96	0.0025	0.0017	0.0022
144	0.0025	0.0018	0.0017
192	Undetectable	0.0021	0.0030

*Concentration in mg/l, N = 4.

Blue-greens and greens remained low in number with less than 500,000 cells/liter. It was expected that nitrate addition would increase green algal numbers, but rapid uptake of nitrate by periphyton could have prevented increased green algal numbers. Some blue-greens in Lake Carl Blackwell can fix atmospheric nitrogen (Toetz 1972), and addition of inorganic nitrogen probably would not increase blue-green algal numbers above usual summer bloom abundance in Lake Carl Blackwell.

Response of Phytoplankton to Organic Carbon

Blue-green algal growth can increase in high concentration of organic matter (Vinyard 1967, Sirenko et al. 1969), and some green algae may

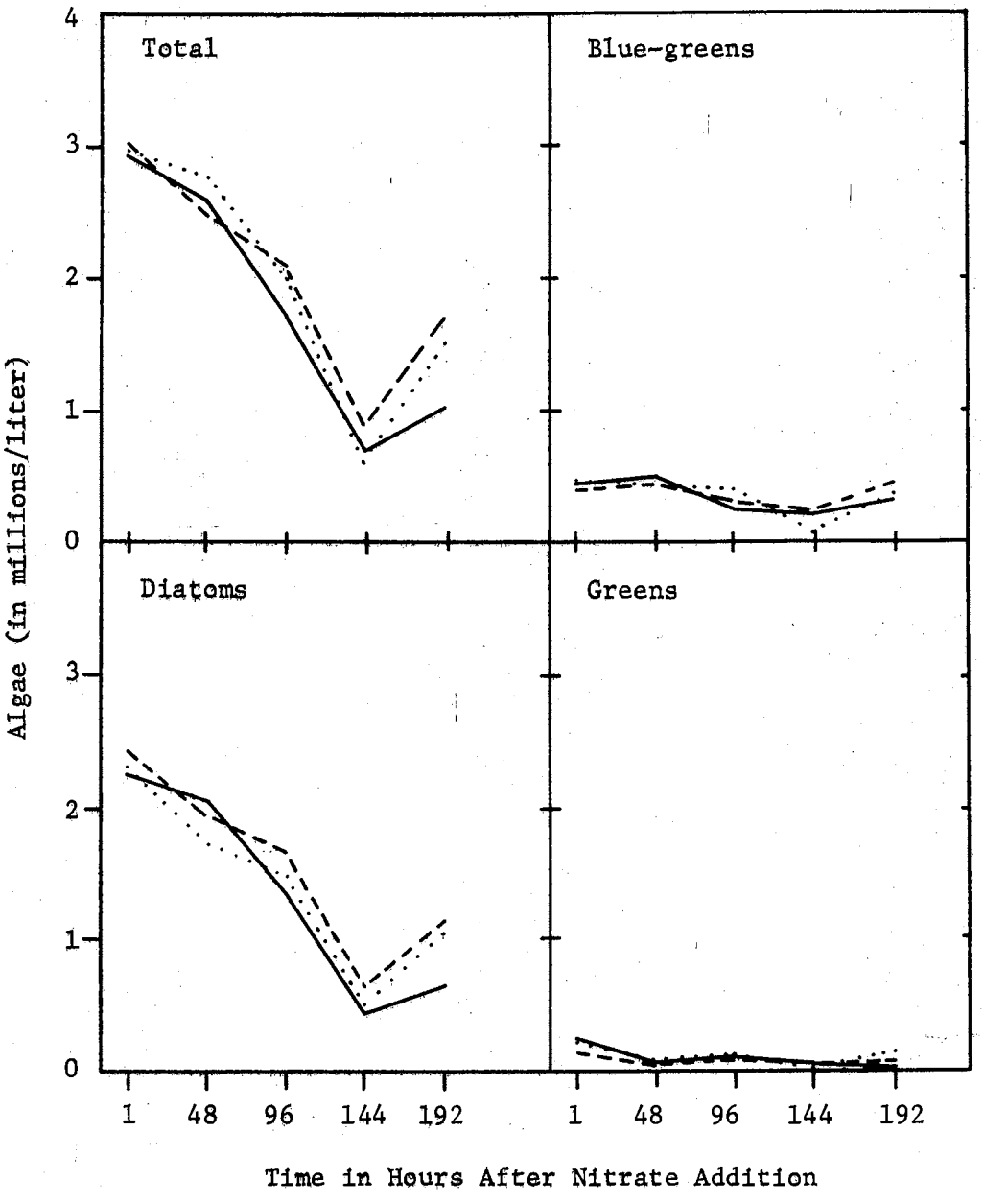

Figure 7. Total, Blue-Green, Diatom, and Green Algae During Nitrate Experiment (—— Reservoir, ----- Nitrate Added, ····· Control)

use dissolved organic compounds through passive uptake (Hobbie and Wright 1965). Total dissolved organic carbon in Lake Carl Blackwell was about 15 mg/l in 1971 (Kelly, J., Chemistry Department, Oklahoma State University, personal communication). Mean organic content of sediment was 1.23% in June and 1.94% in October, 1967 (Norton 1968). Organic detrital material was in low concentration in net samples taken during the present study.

Organic carbon as glucose was added in an experiment when blue-green numbers were increasing. Surface algal numbers in enriched columns slightly increased in 72 hrs and remained more abundant than reservoir algae for 5 days (Fig. 8). Net algal numbers increased in enriched columns in 72 hrs and remained more abundant than reservoir net algae for 8 days. Release of CO_2 by bacterial action rather than direct algal uptake of glucose may have increased algal growth. Bacteria increased and glucose was reduced to low levels in all enriched columns within 4 days after glucose addition (Orr, J., Biology Department, Cameron State College, personal communication concerning unpublished bacteria data from Lake Carl Blackwell). Turnover time of small surface algae probably was more rapid than that for larger species thereby causing surface algal numbers in columns to return to reservoir levels before the end of the experiment.

Phytoplankton Diversity

Phytoplankton has been proposed as an indicator of total ecosystem diversity because of its ubiquity and abundance. One proposed use of phytoplankton diversity measures is to reveal acceleration or deceleration in the rate of production (Margalef 1965). In order to be a useful

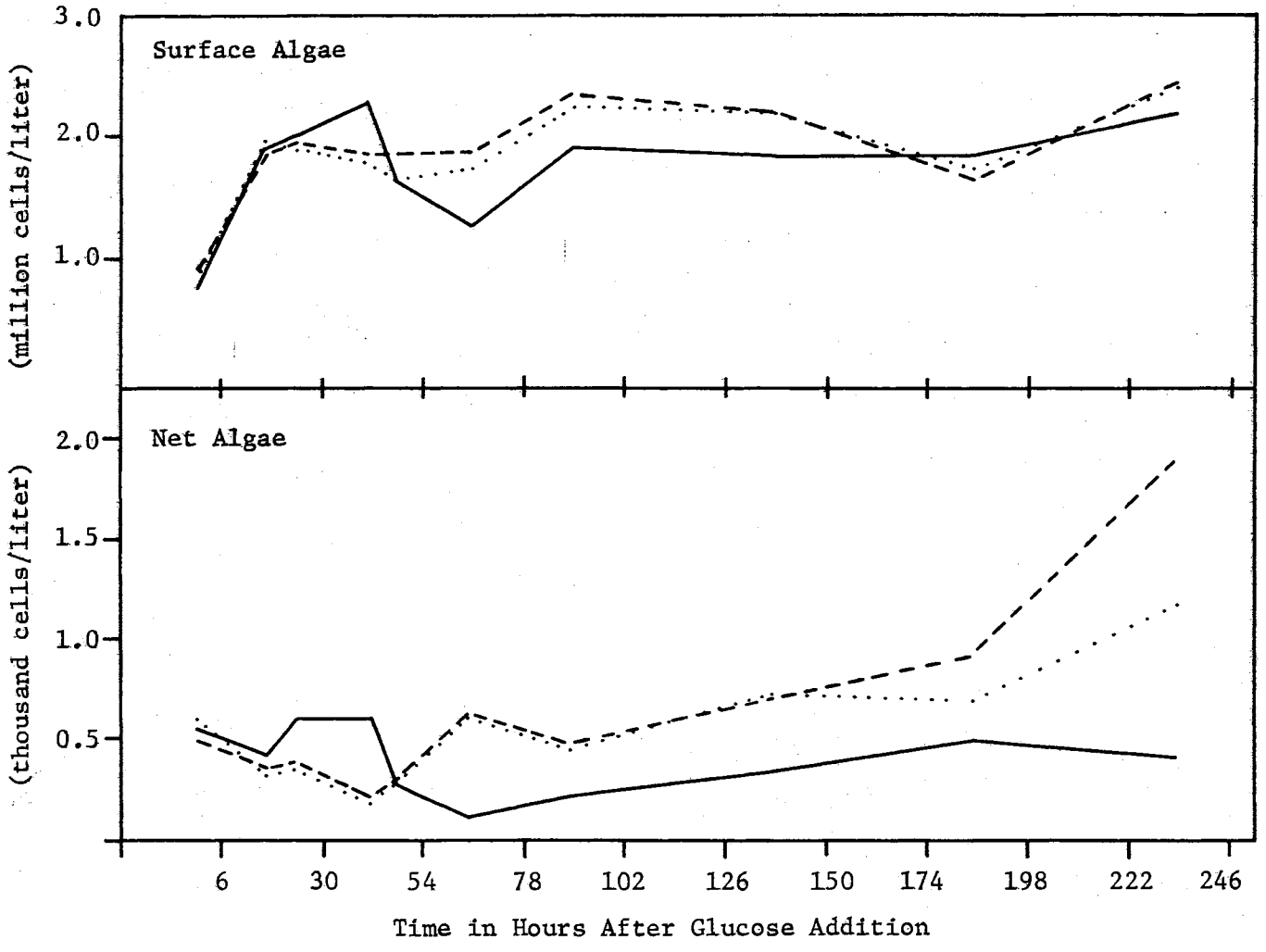

Figure 8. Total Surface and Total Net Phytoplankton During Glucose Experiment (—— Reservoir, ----- Columns Open at Bottom, ····· Columns Closed at Bottom)

index of eutrophication changes, species diversity must discriminate between changes associated with different levels of nutrient enrichment (Hooper 1969).

Species diversity was calculated for surface phytoplankton and net phytoplankton for the reservoir for the summers of 1971 and 1972 and for enriched and untreated columns during experiments in 1972. Net $\bar{d}$ generally was lower than surface $\bar{d}$ because of the loss of small species through the net (Table VII). Several species of diatoms in Lake Carl Blackwell are similar and may not have been distinguished taxonomically, but this uncertainty probably caused only a small understimation of species diversity. Phytoplankton communities in general are characterized by a large number of species, omission of several rare species has little effect in calculating phytoplankton diversity provided some critical number of species is exceeded in the census (Sager and Hasler 1969). Maximum contribution to total diversity occurs when a species contributes 37% of the sample (Wilhm and Dorris 1968). Diversity of 1032 phytoplankters in 21 species was reduced from 2.4 to only 2.3 by omitting ten species with four or less individuals.

Species diversity ranges from 1.0 to 2.5 in eutrophic lakes and up to 4.5 for oligotrophic lakes (Margalef 1968). Lake Carl Blackwell can be classified as a eutrophic lake since $\bar{d}$ varied from 0.50 to 2.82.

Diversity of phytoplankton in 1971 did not correlate well to total algal numbers ($r = + .05$) because algal peaks were caused by abundance of several species within a group rather than by dominance of one or two species (Fig. 9a). In contrast, diversity in 1972 was inversely correlated to total algal numbers ($r = - .84$) because algal peaks were dominated by blooms of only a few species (Fig. 9b). The low correlation of

TABLE VII

MEAN AND RANGE OF $\bar{d}$ FOR LAKE CARL BLACKWELL SURFACE AND NET PHYTOPLANKTON, 1971, 1972

Month	Surface $\bar{d}$		Net $\bar{d}$	
	Mean	Range	Mean	Range
June, 1971	2.11	1.77-2.70	1.87	1.72-2.02
July, 1971	2.02	1.71-2.17	1.90	1.79-1.98
August, 1971	2.36	1.75-2.64	1.96	1.51-2.31
September, 1971	2.57	2.25-2.76	1.52	1.06-1.92
October, 1971	1.91	1.68-2.25	1.25	1.23-1.27
June, 1972	2.46	2.35-2.82	1.93	1.30-2.48
July, 1972	2.38	2.25-2.65	2.44	1.93-2.73
August, 1972	2.22	1.34-2.58	1.89	1.31-2.23
September, 1972	1.93	1.39-2.58	1.05	0.50-1.82

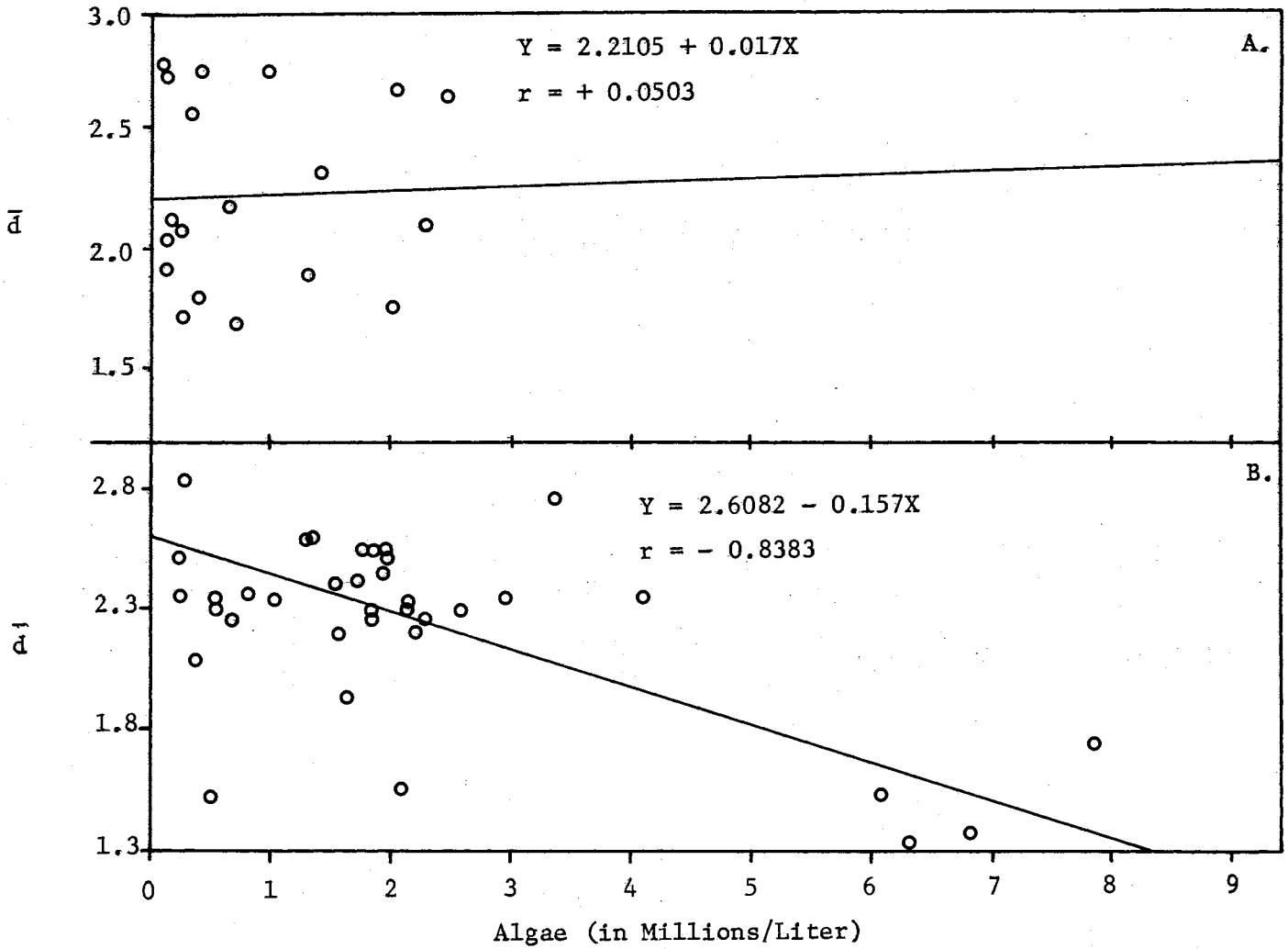

Figure 9. Regression of Species Diversity ($\bar{d}$) on Total Algal Number

$\bar{d}$ with algal counts indicates that phytoplankton diversity may not always be a good indicator of algal bloom conditions.

Enrichment of isolated water columns was expected to reduce species diversity if only a few species were able to use added nutrients and reproduce more rapidly (Lund 1969, Schindler et al. 1971). Diversity of net algae was significantly different only after phosphorus addition and after glucose addition (Table VIII). In the first phosphorus experiment $\bar{d}$ of net algae in enriched columns was less (2.28) than the reservoir (2.54) because of an increase in large but relatively scarce species such as Melosira spp., Oscillatoria sp., and Bacillaria sp. In the second phosphorus experiment net algal $\bar{d}$ increased toward 2.0 because several large species responded to phosphorus. Surface algal $\bar{d}$ in enriched columns was not significantly different from reservoir surface algal $\bar{d}$ during either phosphorus experiment since many greens and bluegreens increased for brief periods.

Net algal $\bar{d}$ increased 3 days after glucose enrichment and remained higher than reservoir $\bar{d}$ until the end of the experiment 8 days later (Fig. 10). Large species such as Pediastrum spp., Bacillaria sp., Melosira spp., and Aphanizomenon sp. colonies became twice as abundant in enriched columns to produce the significantly higher diversity. Diversity of surface algae was not influenced by addition of glucose.

Numbers of many species of phytoplankton increased by an order of magnitude in only a few days when conditions were favorable in the reservoir. Sometimes many species responded to nutrient enrichment. Diversity of phytoplankton seems to be of little value as a sensitive index to changes produced by different levels of a nutrient or to increased or decreased production rates. More study is required to determine if $\bar{d}$

TABLE VIII

DUNCAN'S MULTIPLE RANGE TEST ON $\bar{d}$ FOR AERATION AND NUTRIENT ADDITION EXPERIMENTS

Experiment	Parameter	Reservoir		Columns	
				Untreated	Treated
Aeration No. 1	Surface $\bar{d}$	2.53		2.55	2.38
	Net $\bar{d}$	1.94		2.13	2.16
Aeration No. 2	Surface $\bar{d}$	1.67		1.77	1.88
	Net $\bar{d}$	1.10		1.29	1.28
Phosphorus No. 1	Surface $\bar{d}$	2.39		2.34	2.36
	Net $\bar{d}$	2.54		2.41	2.28
Phosphorus No. 2	Surface $\bar{d}$	2.24		2.25	2.16
	Net $\bar{d}$	1.00	*	2.08	1.83
Nitrogen	Surface $\bar{d}$	2.30		2.42	2.48
	Net $\bar{d}$	2.29		2.29	2.24
Glucose	Surface $\bar{d}$	2.45		2.53	2.50
	Net $\bar{d}$	1.88	*	2.32	2.17

*Indicates significant difference ($\alpha = .05$) between reservoir and untreated columns; _____ indicates significant difference ($\alpha = .05$) between reservoir and treated columns, N = 16.

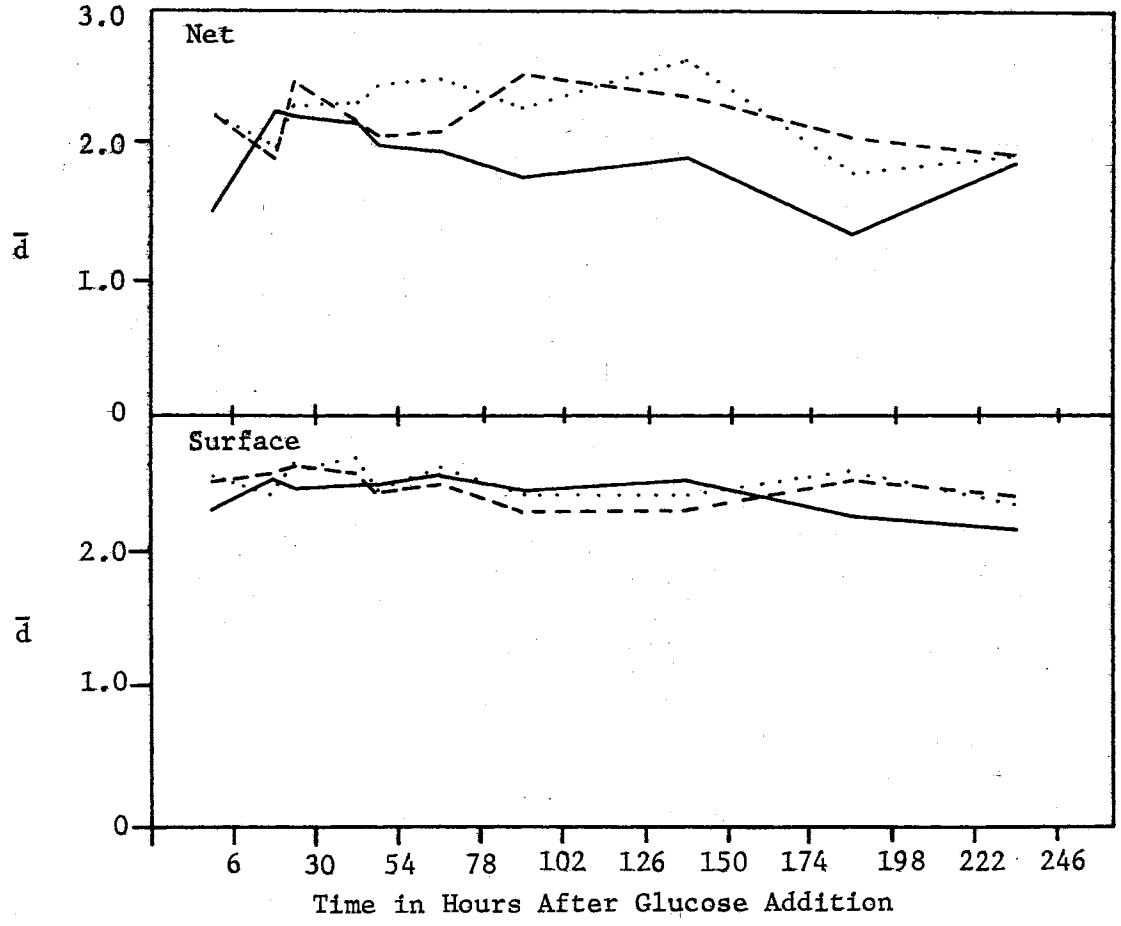

Figure 10. Diversity ($\bar{d}$) of Surface and Net Phytoplankton After Glucose Enrichment (—— Reservoir, ---- Columns Open at Bottom, ···· Columns Closed at Bottom)

might indicate phytoplankton community changes induced differentially by various nutrients.

Laboratory Experiments

Response of Algae on Winter Bottom Mud

Algal blooms which are noted in spring may originate as a few cells or compact colonies on shore or winter bottom mud rather than from planktonic individuals (Sirenko et al. 1969, Topachevskiy et al. 1969). Benthic algae from Lake Carl Blackwell produced a planktonic bloom when winter bottom muds from 2 m and 5 m depths were introduced into nutrient medium and temperature was increased. Diatoms and blue-greens bloomed after day 18 in the cultures with mud from 2 m (Fig. 11). Algal numbers remained lower in the cultures with mud from 5 m and produced smaller peaks after about 25 days. Populations fluctuated after 28 days. Green algae did not increase in either culture.

Diatoms on bottom mud consisted mostly of Navicula spp., Gyrosigma sp., Bacillaria sp., and an unidentified form. Cyclotella sp., Melosira spp., Gyrosigma sp., and a naviculoid diatom were the abundant diatoms in reservoir water in winter. The dominant blue-greens on bottom mud consisted of Oscillatoria spp., Spirulina major, and a tiny sigmoid organism. Anabaena spp., Microcystis sp., and Aphanizomenon sp. were not produced from either benthic sample. Anabaena spp., Oscillatoria spp., and Aphanizomenon sp. were observed in reservoir water in winter. Microcystis sp. was not present on bottom mud or in the water and probably overwintered on shore in crusts. Microcystis aeruginosa was abundant in 1971 summer blooms, but seldom was seen in 1972 summer samples. Little rainfall and runoff into Lake Carl Blackwell occurred in 1972 and

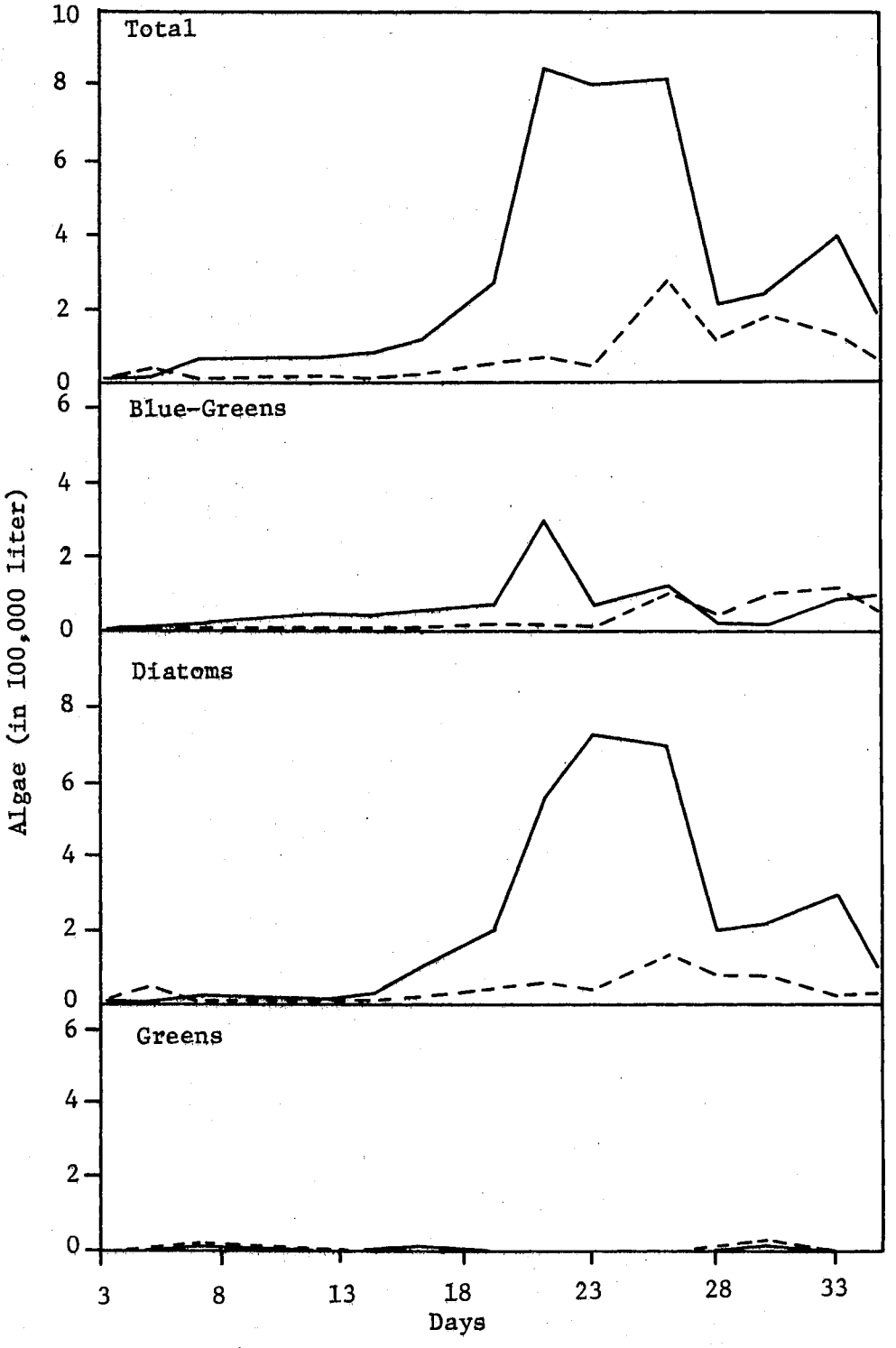

Figure 11. Algal Numbers Grown From Bottom Mud in Winter in Laboratory Cultures (—— 2 m, --- 5 m)

perhaps overwintered crusts of Microcystis sp. cells were not washed into the reservoir in abundance. A few small green coccoid cells and desmids were present on winter bottom mud. Green coccoid cells, Pediastrum spp., and several other green algae existed in planktonic forms in the water. Blue-greens and diatoms seem to be capable of overwintering on bottom below the euphotic zone while green algae probably overwinter as planktonic individuals.

Response of Phytoplankton to Nutrient Addition, Bubbled CO_2, and Low pH

Injection of CO_2 and addition of nitrogen and phosphorus to a lake community dominated by blue-green algae result in a rapid shift to dominance by green algae (Shapiro 1973). Blue-green algae can take up CO_2 at lower CO_2 concentrations than green algae and thus predominate in waters with high pH (King 1970). The lower pH limit for blue-greens is 5.0 in natural water and 4.1 in cultures (Brock 1973). Lake Carl Blackwell water has been slightly alkaline during observations taken since 1940 (Table IV), with a low free CO_2 concentration of approximately 1×10^{-5} mg/l (Rice 1972).

Filtered Lake Carl Blackwell water was seeded with the green alga Chlorella pyrenoidosa and the blue-green alga Dactylococcopsis sp. Part of this mixture served as a control, while the remainder was divided equally among three treatments. Population numbers of the two species in untreated controls oscillated synchronously (Fig. 12). Dactylococcopsis sp. maintained greater numbers until the fourteenth day in control and nutrient-enriched cultures and remained dominant in numbers throughout the experiment in low pH and CO_2-enriched cultures (Table IX).

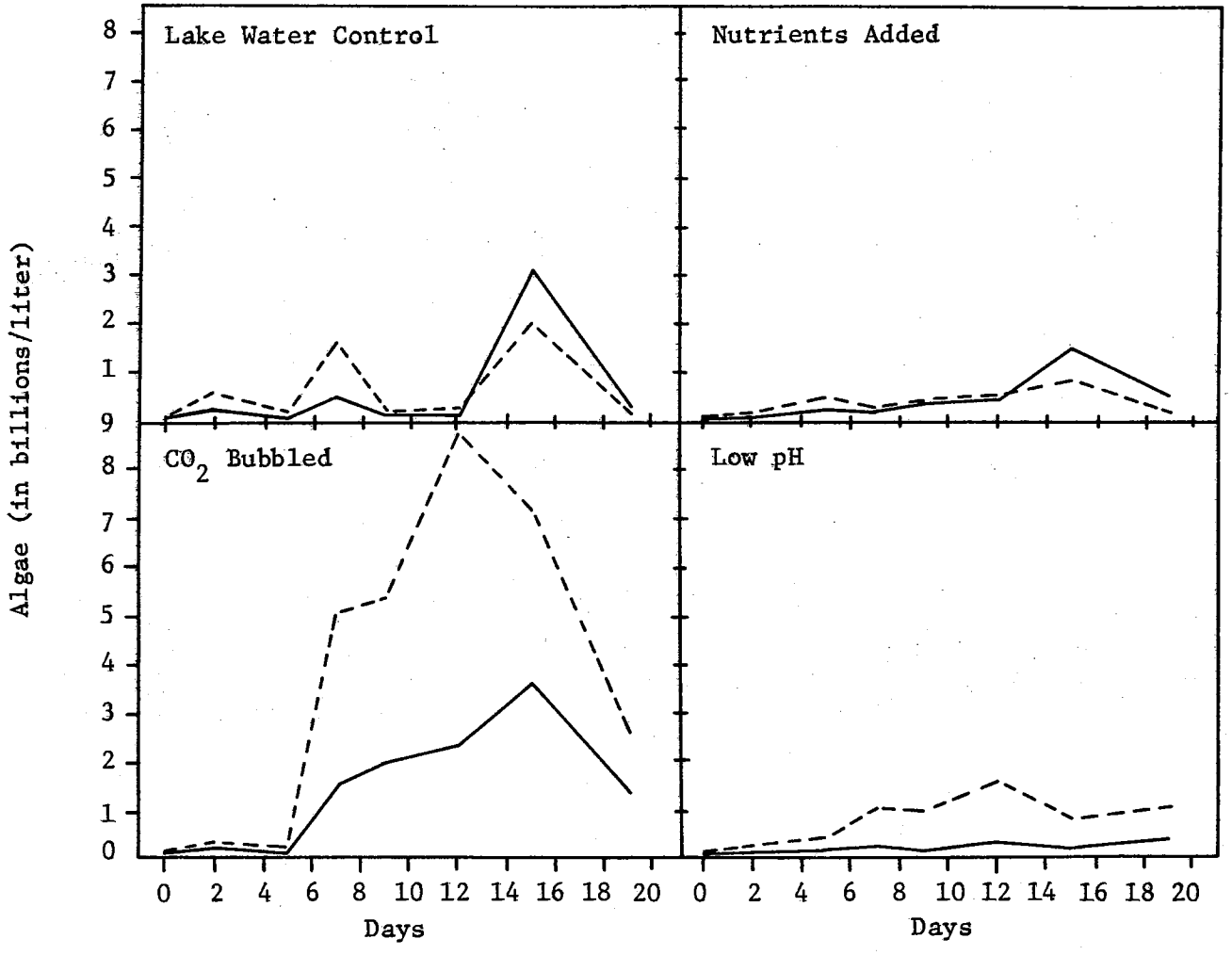

Figure 12. Green and Blue-Green Algae in Lake Water, Low pH, Bubbled CO_2 and Added Nutrients (——— Chlorella sp., ----- Dactylococcopsis sp.

TABLE IX

pH AND RATIO (R) OF NUMBER OF GREEN ALGAE TO BLUE-GREEN ALGAE IN LAKE WATER, LOW pH, BUBBLED CO_2, AND ADDED NUTRIENTS

Day	Lake Water		Low pH		Bubbled CO_2		Nutrients	
	pH	R	pH	R	pH	R	pH	1
1	8.5	.586	6.5	.586	6.4	.586	8.2	.586
3	9.1	.398	6.4	.373	6.1	.724	8.8	.617
6	9.5	.143	6.5	.289	6.3	.258	9.1	.501
8	9.3	.272	6.4	.234	6.1	.294	9.1	.796
10	8.8	.264	3.3	.136	5.9	.365	8.9	.877
13	8.8	.589	3.3	.225	5.9	.264	8.4	.890
16	9.0	1.581	3.4	.198	6.3	.509	8.7	1.739
20	8.8	2.433	3.5	.353	6.5	.512	8.9	2.775

Algal numbers only slightly increased in cultures to which nutrients were added indicating that additional nutrients had little or no effect on the two populations. Diffusion of atmospheric CO_2 can be sufficient to produce an algal bloom in any body of water which receives an adequate supply of phosphorus and nitrogen (Schindler and Brunskill 1972). CO_2 influx apparently was not rapid enough to significantly increase numbers of algae in the nutrient medium, and CO_2 probably was limiting to algae in both the lake water control and nutrient medium (Fig. 12).

Algal numbers increased rapidly in CO_2-enriched cultures to which no additional nutrients were added. The blue-green algal species remained higher in number than the green algal species even though pH was consistently near 6.0. Algal numbers in the low pH cultures increased slightly as in the controls and nutrient-enriched medium. Blue-greens maintained higher numbers even in pH as low as 3.3 to 3.5 for 10 days. Dactylococcopsis sp. grew linearly in a medium with no bicarbonate rather than logarithmically and growth appeared to be related to low influx of atmospheric CO_2 (Rice 1972). Some blue-greens may be more efficient at obtaining CO_2 at low CO_2 concentration, but Dactylococcopsis sp. grew even better in high CO_2 concentration. Blue-green forms in Lake Carl Blackwell are reputed bloom formers and probably take advantage of low CO_2 (i.e. high pH) in the reservoir. Carbon dioxide appears to be limiting to the two species of algae grown in filtered Lake Carl Blackwell water.

Discussion

Stirring of bottom sediments in control columns by circulating pumps during phosphorus addition experiments apparently caused an in-

crease in orthophosphate concentration since algal numbers increased in both the phosphorus-enriched and control columns. No increase of algal numbers occurred in control columns during nitrate addition even though control columns were stirred. Instead, phytoplankton rapidly decreased in number during most of the nitrate experiment. The increase from day 7 to day 9 probably was not a response to initial stirring of sediments. The increase in algal numbers during the glucose addition experiment was not caused by stirring of sediments alone. Columns enriched with glucose but separated from bottom sediments also produced increased algal numbers.

Lake Carl Blackwell algae appear to be limited by phosphorus since orthophosphate is usually about 0.004 mg/l in the reservoir water and added orthophosphorus produced increased numbers of algae. Other forms of phosphorus may not be available for algal nutrition (Lean 1973, McDaniel 1973).

Inorganic nitrogen sometimes was undetectable in Lake Carl Blackwell surface water in spring and summer and was shown to be limiting to algae in other southwestern United States reservoirs (McDaniel 1973). Nitrogen may be limiting to some algal species in summer in Lake Carl Blackwell even though many species of blue-greens in the reservoir are nitrogen-fixers.

Carbon is a limiting factor to algae in Lake Carl Blackwell. CO_2 bubbling in Lake Carl Blackwell water produced excessive growth in laboratory experiments. Since the reservoir is shallow and subject to complete mixing by wind action, CO_2 input from atmospheric sources probably is large but is not sufficient to produce maximal growth. CO_2 from bacterial decomposition can account for large blooms and increased algal

growth should be proportional to CO_2 released from organic matter decomposition. This natural phenomenon probably is limiting algal growth in Lake Carl Blackwell more than other sources of CO_2. Bicarbonate alkalinity is usually 1×10^{-3} mg/l (Rice 1972), and probably does not limit algae which can use bicarbonate ion readily.

Light may limit phytoplankton growth in Lake Carl Blackwell since average summer light penetration was only 0.5 m as measured by Secchi disc.

Blue-green algae may absorb phosphorus at low concentration (Shapiro 1973), can fix nitrogen (Wyatt 1971), and assimilate CO_2 at low concentration (King 1970), thereby making blooms of blue-green algae inevitable in even slightly eutrophic bodies of water. No empirical data base exists to substantiate a single limiting factor hypothesis for the growth of Lake Carl Blackwell phytoplankton.

CHAPTER V

SUMMARY

1. Phytoplankton peaks in Lake Carl Blackwell during 1971 and 1972 were compared. Columns of clear polyethylene sheet enclosed reservoir algal communities and were used to monitor algal numbers and diversity after orthophosphate, nitrate, and organic carbon additions, and during aeration. Taste and odor in the water supply were related to algal blooms. Species diversity of phytoplankton as an indicator of eutrophic conditions was reviewed. Data was presented to support the data that no single limiting nutrient hypothesis is applicable to Lake Carl Blackwell.

2. Blue-green algae peaked earliest in 1971 and diatoms peaked earliest in 1972. Multiple peaks of blue-greens occurred in 1972. Green algae were the most abundant group during late summer of 1971, while blue-green algae were most abundant during late summer of 1972. Blue-greens, diatoms, and greens may contribute to taste and odor problems in late summer.

3. Aeration in reservoirs has been used to reduce algal numbers, oxygenate the water, and lower surface water temperature in order to decrease evaporation. Aeration lowered blue-green and green algal numbers in Lake Carl Blackwell. Diatom numbers were not affected greatly. Surface temperature and water clarity were slightly reduced, and oxygen content of the bottom water increased.

4. Total phosphorus concentration in Lake Carl Blackwell water

ranged from 0.040 to 0.085 mg/l during summer months. Orthophosphate and soluble organic phosphorus ranged from 0.003 to 0.010 mg/l. Most phosphorus was bound in particulate form, but organic and inorganic particulate forms were not distinguishable. Sedimentary phosphorus in Lake Carl Blackwell was 99% particulate. Stirring of bottom sediment and perhaps bacterial solubilization released phosphorus from montmorillonite sediment and increased dissolved orthophosphate in the columns by 0.060 mg/l.

Release of sedimentary phosphorus and addition of orthophosphate produced significant increases in numbers of algae in 2 days for a juvenile community and in 4 days for a senile community. Blue-greens responded less than greens to added phosphorus. Diatoms did not respond. Orthophosphate in the water disappeared rapidly and probably was partly absorbed by periphyton or precipitated by calcium and magnesium ions.

Particulate phosphorus increased within 1 hr in the columns indicating that the algae might have assimilated phosphorus or that organophosphorus colloidal particles were formed in the water. Soluble organophosphorus was detected within 1 hr after phosphorus addition indicating that perhaps excretion of soluble organo-phosphorus occurred rapidly as a cellular response to low orthophosphate in the water. Some species of algae in Lake Carl Blackwell are phosphorus limited since orthophosphate is less than 0.010 mg/l.

5. Soluble inorganic nitrogen reached an undetectable level and probably was limiting to some algal species during summer months. Nitrate nitrogen concentration ranged from undetectable to 0.057 mg/l in July, 1972. Blue-green algae which fix nitrogen are abundant in Lake Carl Blackwell. Addition of dissolved nitrate produced no increase in

algal numbers in a senile diatom-dominated community. Added nitrate disappeared rapidly and may have been partly taken up by periphyton on sides of the columns.

6. Organic carbon is low in concentration in Lake Carl Blackwell. The allochthonous organic carbon sources are intermittent flows from natural and agricultural sources. No domestic or industrial wastes originate in the watershed. Addition of 1600 mg/l glucose increased blue-greens and diatoms after 3 days. Green algae remained low in number throughout the experiment. Numbers of algae were increased by organic enrichment probably because of bacterial release of CO_2 rather than direct uptake of glucose by the algae.

7. Surface algal $\bar{d}$ ranged from 1.34 to 2.82 and net algal $\bar{d}$ ranged from 0.50 to 2.73 indicating that the reservoir is eutrophic. Correlation of $\bar{d}$ with algal counts was low in 1971 ($r = +.05$) when algal peaks were caused by abundance of many species and high in 1972 ($r = -.84$) when algal peaks were caused by abundance of only one or two species. Phytoplankton $\bar{d}$ may not always be a good indicator of bloom conditions. Enrichment of columns did not significantly change $\bar{d}$ of surface algae but increased $\bar{d}$ of large net algae in phosphorus and glucose addition experiments. $\bar{d}$ may be of minimal value as a sensitive index to changes produced by different levels of a nutrient or to increased or decreased production rates.

8. Overwintering benthic algae collected from bottom mud in midwinter produced blooms when cultured in the laboratory. Naviculoid diatoms made up most of the biomass from a shallow sample and Gyrosigma sp. constituted most of the organisms from the deep sample. Anabaena sp., Oscillatoria sp., and Aphanizomenon flosaquae also were noted.

Microcystis sp. was not seen and may overwinter in crusts on shore. The blue-greens Anabaena sp., Oscillatoria spp., Spirulina major, and Aphanizomenon flosaquae and the green algae apparently overwinter as planktonic individuals. Algae grew faster and more abundantly from samples taken from mud at 2 m than from mud taken at 5 m. Both samples produced a musty, rotting grass odor after the blooms.

9. The green alga Chlorella pyrenoidosa and the blue-green algae Dactylococcopsis sp. were placed together in filtered Lake Carl Blackwell water and treated with low pH, CO_2, and added nitrate and orthophosphate. The blue-green alga grew well in pH as low as 3.3. Both algae bloomed within 1 week when CO_2 concentration was increased by bubbling. Added nitrate and orthophosphate had no effect on algal numbers. Apparently, filtered lake water contained sufficient nitrate and orthophosphate for some algal growth and atmospheric CO_2 influx was limiting. CO_2 provided through bacterial decomposition in addition to atmospheric diffusion may provide sufficient CO_2 for excessive growth.

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APPENDIX A

FACTORS INFLUENCING BLUE-GREEN ALGAL GROWTH

GENERAL FACTORS

Taxonomic Groups Contributing to Major Blooms

U.S.S.R. - Microcystis aeruginosa (Sirenko et al. 1969, Topachevskiy et al. 1969, Baklanovskaya 1969, Butorin et al. 1971) Aphanizomenon flosaquae (Sirenko et al. 1969, Baklanovskaya 1969, Butorin et al. 1971) Anabaena spp. (Topachevskiy et al. 1969, Baklanovskaya 1969) Coelosphaerium dubium (Baklanovskaya 1969) Microcystis pulverea (Baklanovskaya 1969).

Other - Anabaena flosaquae (Whitford and Kim 1971) Anabaena spp. (Robinson et al. 1969; Malueg et al. 1971, Kratz and Myers 1954, 1955, Hergenrader and Hammer 1971, Krishnamoorthi et al. 1971, Henley et al. 1971, Lange 1971) Microcystis spp. (Robinson et al. 1969, Kratz and Myers 1954, 1955, Hergenrader and Hammer 1971, Krishnamoorthi et al. 1971, Adeniji 1971, Meyer 1971, Lange 1971) Oscillatoria sp. (Robinson et al. 1969, Lange 1971) Cylindrospermum sp. (Robinson et al. 1969) Aphanizomenon flosaquae (Wyatt 1971, Hergenrader and Hammer 1971, Meyer 1971, Lange 1971) Coelosphaerium sp. (Meyer 1971) Merismopedium sp. (Meyer 1971) Microcystis sp., Aphanizomenon sp., and Anabaena sp. followed early diatom peaks (Lin 1972).

Number of Species Encountered

U.S.S.R. - No specific references.

Other - Eight Cyanophyta of 81 species (Robinson et al. 1969) 13 Cyanophyta of 72 species (Lin 1972) 11 Cyanophyta of 44 species (Faust, present study).

Reservoir Distribution

U.S.S.R. - Summer: surface-few meters and bottom (Sirenko et al. 1969) Winter: less than 20-30 meters deep (Sirenko et al. 1969) 10-15 meters on mud bottom, bloom June to September (Topachevskiy et al. 1969).

Other - All depths, summer vacuolated and at surface; bottom unknown but suspected in winter (Wixson et al. 1971). Most luxurious blooms from mid-June to July (King 1970). Different species form epilimnetic blooms than Oscillatoria sp. which are more often in hypolimnetic blooms (Eberly 1967) Microcystis sp. not found on winter bottom muds as were other blue-greens (Faust, present study).

PHYSICAL FACTORS

Currents

U.S.S.R. - Most abundant in slow or calm water (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - Subject to currents, decrease (Wohlschlag and Hasler 1951, Oskam 1971).

Wind

U.S.S.R. - Driven ashore in mats, pushed off by spring rains; stirs bottom nutrients (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - Directly affects algal distribution (Langford and Jermolajev 1966) Suspected stirring of silt, organics, nutrients, and planktonic forms (Jackson 1964, Faust, present study) Increased growth in areas exposed to winds (Wohlschlag and Hasler 1951).

Temperature

U.S.S.R. - 20 C plus (Microcystis spp.) (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - 24 C (Anabaena sp.)(Webster and Frenkel 1952) 24 C (Nostoc muscorum)(Lazaroff and Vishniac 1961) 25 - 30 C abundant Cyanophyta (Faust, present study) May exist at up to 70 C (Brock 1973).

Biological Oxygen Demand

U.S.S.R. - No specific references.

Other - Low BOD - Microcystis sp. and Anabaena sp. observed in a bloom (Krishnamoorthi et al. 1971).

Turbidity (Light)

U.S.S.R. - Light not necessary for abundant growth anaerobically, early spring on bottom muds (Microcystis sp., Aphanizomenon sp.), much greater in more light at surface (Microcystis sp.) (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - Slow growth in absence of light for Nostoc muscorum (Lazaroff and Vishniac 1961) Anabaena sp. grew under only 50 ft candles (Webster and Frenkel 1952) Removal of light inhibited photosynthesis of Aphanizomenon sp., Anabaena sp., and Microcystis

aeruginosa (Hergenrader and Hammer 1971) Microcystis sp. and Anabaena sp. observed blooming under low turbidity (Krishnamoorthi et al. 1971) Anabaena sp. susceptible to light (Wyatt 1971) Anabaena sp. growth decreased in clear, aerated water (Malueg et al. 1971).

CHEMICAL FACTORS

Oxygen

U.S.S.R. - More dead cells in high O_2, in low O_2 survival on bottom muds and shore mats (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - High pO_2 inhibits respiration by Anabaena sp. as well as photosynthesis by Anabaena sp. and Phormidium sp. which does not fix nitrogen (Stewart and Pearson 1970) Anabaena sp bloom in 16 mg/liter O_2 (Malueg et al. 1971) O_2 near saturation during bloom (Joyner 1971) Decreased O_2 increased acetylene reduction and nitrogen fixation (Wyatt 1971).

Red-ox Potential

U.S.S.R. - Microcystis aeruginosa grew best in low red-ox conditions (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - No specific references.

Carbon Dioxide

U.S.S.R. - High CO_2 required, sources are free atmospheric, inorganics, bacterial symbionts (Sirenko et al. 1969).

Other - Anabaena sp., Anacystis sp., and Nostoc sp. appear restricted to CO_2 as a carbon source (Kratz and Myers 1955) At CO_2 concentration less than 2.5 micromoles/liter algal photosynthesis decreases rapidly (King 1970) Atmospheric CO_2 permits blooms with adequate nitrogen and phosphorus (Schindler et al. 1971) Anacystis nidulans grew better with added CO_2, required 10^{-5} micrograms of CO_2 per cell (Kerr et al. 1970) High CO_2 required (Kuentzel 1969, Lange 1971) Carbonate ion may be essential to some Cyanophyta (Jackson 1964) CO_2 addition resulted in shift to green algae (Shapiro 1973).

Phosphorus

U.S.S.R. - No specific references.

Other - Cyanophyta grow in 0.015 mg/l (Kuentzel 1969) No growth in 0.07-0.30 mg/l, but little organics, pH 8.5 (Wells 1969) PO_4 decreased in a bloom of Microcystis sp., Anabaena sp., and Aphanizomenon sp. (Hergenrader and Hammer 1971) PO_4 produced a bloom (Schindler et al. 1971, Kalff, 1972a, Nyquist and Sigler 1967, McCombie 1953) 0.010 mg/l is minimum concentration for growth (Bowen 1970) Phosphorus has been limiting element in Lake Michigan (Schelske and Stoermer 1972) Phosphorus is low in water, average in sediments of Lake Carl Blackwell, orthophosphate limiting at times (Faust, present study).

Sodium

U.S.S.R. - No specific references.

Other - Oscillatoria sp. favored more by high Na levels (deNoyelles 1967) Anabaena variabilis required 40 mg/l (Kratz and Myers 1954, 1955) Anacystis nidulans required Na (Kratz and Myers 1955).

Calcium

U.S.S.R. - No specific references.

Other - Low requirement by blue-greens (Hasler 1966).

Cobalt

U.S.S.R. - No specific references.

Other - An essential element for blue-greens (Hasler 1966).

Zinc

U.S.S.R. - No specific references.

Other - Aphanizomenon sp. and Anabaena sp. incorporated Zn salts into cells with no effects except morphological changes (unknown).

Copper

U.S.S.R. - Blooms of Cyanophytes occurred only when water became enriched by copper (Telitchenko 1971).

Other - Copper used as algacide in U.S. (cupric sulfate).

Potassium

U.S.S.R. - No specific references.

Other - Blue-greens, especially Oscillatoria spp. favored by high K levels (deNoyelles 1967) Anacystis nidulans requires K (Kratz and Myers 1955).

Iron

U.S.S.R. - No specific references.

Other - Iron may be limiting (Goldman 1971) Iron in chelated forms only produced increased photosynthesis (Sakamoto 1971) 100 mg/l iron was growth limiting to cultured blue-greens (Gerloff and Skoog 1957) May be limiting (Schelske 1962, Wetzel 1965).

pH

U.S.S.R. - High pH, alkaline conditions required (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - Oscillatoria aghardhii in medium at pH 7.1 - 7.3 produced bloom which increased pH to 9.2 (Eberly 1967) CO_2 uptake by algae increased pH, blue-greens take advantage, extract CO_2 at lower concentrations (King 1970) Cyanophytes common at pH 5 or 6 but absent below pH 4.1 in natural lakes (Brock 1973) Anabaena flosaquae optimum at pH 7.5 (Gorham et al. 1964) No bloom in pH 8.5 but few organics (Wells 1969) pH 7.4 - 9.0 required for Anabaena variabilis and Anacystis nidulans (Kratz and Myers 1954, 1955) Nostoc spp. grew in pH 6.9 - 9.0 (Kratz and Myers 1954, 1955) Anabaena sp. cultures had pH of 9.5 (Webster and Frenkel 1952) Anabaena sp. bloomed with a pH of 9.0 (Malueg et al. 1971) Microcytis sp. required at least pH 7.4 (Jackson 1964) Dactylococcopsis sp. grew in pH 3.3 - 3.5 for 10 days, bloomed vigorously in pH 6.0 (Faust, present study).

Nitrogen

U.S.S.R. - Blue-greens grew in 0.06 - 0.17 mg/l NH_4 and 0.21 - 0.23 mg/l NO_3 (Baklanovskaya 1969) Growth in 0.02 - 1.00 mg/l NH_4 and 0.27 - 1.45 mg/l NO_3 (Topachevskiy et al. 1969).

Other - N_2 fixation occurs in Wisconsin lakes, 2.4 kg N/ha/yr with nitrogen limiting in some lakes and is light dependent (Stewart 1971) Spring bloom of Aphanizomenon flosaquae and autumn bloom of Anabaena circinalis occurred in Clear Lake, Cali-

fornia and 43% of yearly inflow of nitrogen was due to fixation (Horne and Goldman 1972) Dense Anabaena sp. bloom occurred in 0.045 mg/1 NO_3 (Smith 1969) Nitrogen added produced bloom (Schindler et al. 1971) Blue-greens have reputation for needing organic nitrogen source (Edmondson 1967) 5.0 mg/1 N was limiting to Microcystis aeruginosa (Gerloff and Skoog 1957) Anabaena sp. and Aphanizomenon flosaquae can fix nitrogen (Wyatt 1971) NH_4 preferred if NO_3 present also (Toetz 1971) Anabaena sp. fix more molecular nitrogen under decreased oxygen (Wyatt 1971) Anabaena flosaquae and Nostoc muscorum reduce acetylene (Stewart and Pearson 1970) Blue-greens not N limited (Faust, present study).

Organics

U.S.S.R. - Growth good in biogenic, organic bottom ooze (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - Anabaena sp. capable of oxidizing several organic substrates (Webster and Frenkel 1952) Microcystis sp. and Anabaena sp. will grow well in water free of organics (Krishnamoorthi et al. 1971) Monomolecular hexadecanol and octodecanol layers acted as added nutrients for growths of filamentous and non-filamentous types (Wixson et al. 1971) Anabaena sp. and Aphanizomenon sp. can reduce acetylene (Wyatt 1971) Carbon material is controlling nutrient in eutrophication (Legge and Dingeldein 1970) Organic carbon source altered numbers of individuals of large species (Faust, present study).

BIOLOGICAL FACTORS

Production of Growth Inhibitors

U.S.S.R. - Postivie, suppress green algae, exoproducts help remove oxygen from colony along with bacterial symbionts (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - Anabaena circinalis produced exoproduct, may not be inhibiting; Oscillatoria spp. also produced (Henley et al. 1971) Aphanizomenon flosaquae toxin killed Anabaena sp. and Microcystis sp. but not Selenastrum sp. (Lange 1971).

Development (Miscellaneous)

U.S.S.R. - Winter: few cells in large clumps, 15% alive, on dry shore (Topachevskiy et al. 1969) Spring: colonies earlier on bottom than in water, bloom June-September, may bloom and return to bottom several times during summer, cycle materials (Sirenko et al. 1969, Topachevskiy et al. 1969) Dense winter colonies

of 6-15 million cells/liter of Microcystis sp., cells loose in slime colonies at surface in aerobic conditions. Aphanizomenon sp. and Microcystis sp. make up 70 - 90% of phytoplankton (Butorin et al. 1971) 2.3 - 2.6 million colonies of Microcystis sp. per liter (Sirenko et al. 1969) As neuston, greater than 10 kg/m^3 (Topachevskiy et al. 1969) 171,000 blue-green cells per ml (Baklanovskaya 1969).

Other - Aphanizomenon sp. dominant in July (Joyner 1971) Aphanizomenon sp. greater than 100 mg C/m^3 (Hergenrader and Hammer 1971) Microcystis sp. dominant after rainy season (Adeniji 1971) Anabaena sp. chlorophyll a of 110 mg/m^3 (Malueg et al. 1971).

Predation

U.S.S.R. - Very little to none on blue-greens (Topachevskiy et al. 1969).

Other - Blue-green forms especially are not utilized (Provasoli 1969, Lund 1969) Seen in abundance in carp ponds (Lund 1969) Bloom of Aphanizomenon sp. was controlled by zooplankton feeding (Billaud 1967).

Photosynthesis

U.S.S.R. - Microcystis aeruginosa transfers from heterotrophic to autotrophic, moves from bottom up and changes, slime envelope provides anoxic conditions (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - Anabaena variabilis, Microcystis sp. and Nostoc muscorum are obligate photoautotrophs (Kratz and Myers 1954, 1955) Aphanizomenon sp. is a photoautotroph (Hergenrader and Hammer 1971) Bloom originates on bottom - implies change (Wyatt 1971) Anabaena sp. able to oxidize organic substrates (Webster and Frenkel 1952) Lyngbya lagerheimii is obligate photoautotroph (Van Baalen et al. 1970).

Bacterial Symbionts

U.S.S.R. - Abundant in mucus on bottom, take up oxygen, produce carbon dioxide (Sirenko et al. 1969).

Other - Positive in blue-greens (Silvey and Roach 1964) Greens - complete overlapping seldom seen because of competition for nutrients and because of antibiotic activity (Oswald et al. 1952, Legge and Dingeldein 1970, Kuentzel 1969) Symbiotic with lichens, cycads, bryophytes, and pteridophytes (Holm-Hansen 1968).

CONTROL FACTORS

Mechanical and Chemical Methods

U.S.S.R. - Remove organic ooze and silt, oxygenate water, reduce eutrophicating runoffs, strip reservoir bottom muds before filling, remove reducing conditions on bottom (Sirenko et al. 1969, Topachevskiy et al. 1969).

Other - Mixing decreased blue-greens more than greens (Robinson et al. 1969) Removal of light, added turbidity inhibits Aphanizomenon sp. (Hergenrader and Hammer 1971) Even with lower BOD and turbidity blooms of Microcytis sp. and Anabaena sp. were still observed (Krishnamoorthi et al. 1971) Aerated, clear water decreased bloom of Anabaena sp. (Malueg et al. 1971) Turbidity may be a major factor in control of algal growth (Joyner 1971, Faust, present study) Increased oxygen concentration, especially on the bottom decreases blooms (Wyatt 1971) Aphanizomenon sp. blooms removed and reduction of summer algal biomass by high water replacement rate (dilution) (Welch et al. 1972) Sealing lake bottoms, flushing by large volumes of water, and diverting organic inflows could reduce blooms (Dollar et al. 1967) Aeration reduced greens and blue-greens but not diatoms (Faust, present study).

APPENDIX B

FORMULA FOR MODIFIED GORHAM'S MEDIUM

Chemical Formula	mg/l in Solution
$NaNO_3$	496
K_2HPO_4	39
Fe Citrate	6
$MgSO_4 \cdot 7H_2O$	75
$Na_2SiO_3 \cdot 9H_2O$	58
Na_2CO_3	20
Citric Acid	Omitted
EDTA	Omitted
$CaCl_2$	27
KCl	1
$NaHCO_3$	260

APPENDIX C

PLANKTONIC ALGAE ENCOUNTERED IN LAKE CARL

BLACKWELL, OKLAHOMA

CHLOROPHYTA	
Volvocaceae	*Volvox sp.*
Hydrodictyaceae	*Hydrodictyon reticulatum* *Pediastrum duplex* *Pediastrum simplex*
Desmidiaceae	*Closterium gracile* *Closterium sp.* (moniliferum ?) *Cosmarium sp.* (subcrenatum ?) *Staurastrum sp.* (chaetoceros ?)
Zygnemataceae	*Spirogyra sp.*
Oocystaceae	*Chlorella sp.* (?) *Oocystis sp.* *Nephrocytium sp.* (limnetica ?)
Clorococcaceae	*Clorococcum sp.* (humicola ?) *Planktosphaeria gelatinosa*
Chaetophoraceae	*Stigeoclonium sp.*
CYANOPHYTA	
Nostocaceae	*Aphanizomenon flosaquae* *Anabaena affinis* *Anabaena sp.* (planctonica ?) *Anabaenopsis sp.* *Nodularia sp.* (harveyana ?)
Oscillatoriaceae	*Spirulina major* *Oscillatoria princeps* *Oscillatoria sp.* (limosa or nigra ?)
Chroococcaceae	*Coelosphaerium sp.* (naegelianum ?) *Merismopedium sp.* (punctatum ?) *Microcystis aeruginosa*
PYRROPHYTA	
Peridiniaceae	*Peridinium sp.*
Ceratiaceae	*Ceratium hirundinella*

EUGLENOPHYTA

Euglenaceae	*Euglena sp.*
	Phacus sp.

CHRYSOPHYTA

Coscinodiscaceae	*Melosira italica*
	Melosira distans
	Melosira sp. (granulata ?)
	Cyclotella sp.
Nitzschiaceae	*Bacillaria paradoxa*
Fragilariaceae	*Fragilaria sp.*
	Synedra sp.
	Tabellaria sp.
Naviculaceae	*Gyrosigma sp.*
	Navicula sp.
	Frustulia sp.
	Amphipleura sp.
Gomphonemaceae	*Gomphonema sp.*
Cymbellaceae	*Cymbella sp.*

VITA

Allen Ray Faust

Candidate for the Degree of

Doctor of Philosophy

Thesis: PHYTOPLANKTON COMMUNITY STRUCTURE AND NUTRIENT RELATIONSHIPS IN LAKE CARL BLACKWELL, OKLAHOMA

Major Field: Zoology

Biographical:

Personal Data: Born in Clinton, Oklahoma, January 11, 1945, the son of Jacob S. and Elvira L. Faust.

Education: Graduated from Midwest City High School, Midwest City, Oklahoma, 1963; received the Bachelor of Science degree, Oklahoma State University, Stillwater, Oklahoma, May, 1967, with a major in Zoology; completed requirements for Master of Science degree, May, 1972, Oklahoma State University; completed requirements of Doctor of Philosophy degree, July, 1973, Oklahoma State University.

Professional Experience: Undergraduate research assistant, Cooperative Fishery Unit, Oklahoma State University, 1967; graduate research assistant, Reservoir Research Center, Oklahoma State University, June, 1967 - January, 1969; biomedical research technician, U.S. Army Aeromedical Research Laboratory, Fort Rucker, Alabama, April, 1969 - November, 1970; graduate research assistant, Reservoir Research Center, Oklahoma State University, January, 1971 - July, 1973; National Defense Education Act Fellow, September, 1967 - January, 1969, and September, 1970 - March, 1972.

Member: American Society of Limnology and Oceanography, Phi Sigma Society, American Institute of Biological Sciences, Water Pollution Control Federation, Society of the Red, Red Rose, International Association of Theoretical and Applied Limnology.