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# Primary Productivity in Lake Cochrane, South Dakota, During and After Sediment-Control Dam Construction

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# PRIMARY PRODUCTIVITY IN LAKE COCHRANE, SOUTH DAKOTA, DURING AND AFTER SEDIMENT-CONTROL DAM CONSTRUCTION

BY

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PRIMARY PRODUCTIVITY IN LAKE COCHRANE, SOUTH DAKOTA

DURING AND AFTER SEDIMENT-CONTROL DAM CONSTRUCTION

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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# INTRODUCTION

The acceleration of human activities in the prairie lake environment and the resulting introduction of various chemical substances and silt into lake water has prompted expanded interest in quantitative freshwater ecology. Some of the biologically active chemicals introduced in the lake water can cause an imbalance in the lake ecosystem, and together with silt may result in increased eutrophication of the lake. Because of the many factors involved in freshwater ecology and the complexity of biological phenomena, study of these pollutants requires a multivariant statistical approach.

Approximately 240 natural prairie lakes are located in northeastern South Dakota (State Lakes Preservation Committee 1976). Increased agricultural and municipal development in the watershed has caused many of the lakes to experience rapid and perhaps irreversible deterioration (Steinberg 1972; Haertel 1972, 1976a; State Lakes Preservation Committee 1976). Natural eutrophication may be accelerated by the influx of silt and nutrients from agricultural runoff waters (Felderman and Eno 1977). The nutrients add to the fertility of the water and often result in nuisance algal blooms. The problem is further compounded by the addition of silt which causes a reduction in the lake depth (Felderman and Eno 1977).

Lake Cochrane was selected for this study because of its

history of superior water transparency (Haertel 1972, 1976b). Significant amounts of silt and chemicals enter the lake with runoff at 3 locations (Haertel unpublished data). Restriction or impediment of runoff at these locations should result in improved water transparency (Haertel 1976b, Siegel 1975). Therefore, East Dakota Conservancy Sub-District and the South Dakota Department of Wildlife, Parks, and Forestry decided to impede runoff waters by means of 3 sediment-control dams incorporated into the perimeter road system of the lake and financed through a grant from the Environmental Protection Agency (Siegel 1975) (Figure 1). The dams were designed to slow the movement of runoff water allowing sediment particles and sorbed nutrients to "settle out".

The objectives of this study were to:

(1) evaluate the oxygen light and dark bottle method as a means of estimating primary productivity, and

(2) estimate, during the open-water seasons, spatial and temporal variation of certain water quality parameters in Lake Cochrane during and after construction of the sediment-control dams.

The water quality parameters evaluated included patterns of spatial and temporal variation of: selected inorganic plant nutrients, algal standing crop, and zooplankton distribution. The results are compared to previous data collected from Lake Cochrane in 1970-73 and 1975 (Steinberg 1972; Haertel 1972, 1976a,

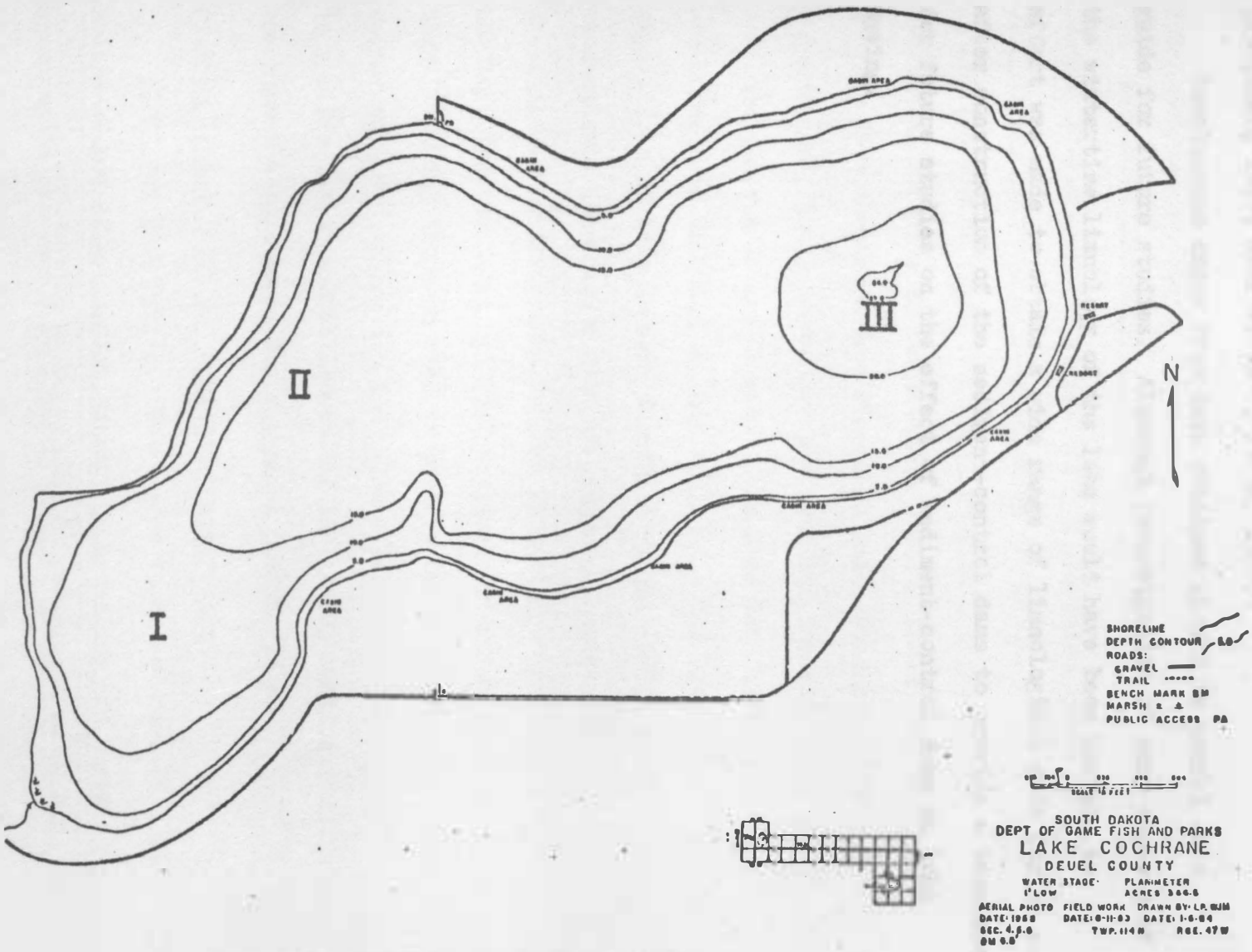


Figure 1. Lake Cochrane Study Area.
I, II, and III depict sampling locations

(Steinberg 1972; Haertel 1972, 1976a, 1977).

Conclusions drawn from data obtained should be useful as a guide for future studies. Although investigation of many aspects of the wintertime limnology of the lake would have been useful, an effort was made to obtain a wide range of limnological data during and after construction of the sediment-control dams to provide a baseline for future studies on the effect of sediment-control dams on lake ageing.

# LITERATURE REVIEW

## Water Quality in Prairie Lakes

Extensive literature exists on water quality in prairie lakes. Nickum and Schoenthal (1967), estimated water quality and primary production in 48 selected South Dakota lakes; Hauber (1969) and Nickum (1970) monitored chemical, physical and biological dynamics of two northern prairie lakes; Megard (1972) studied photosynthesis in a Minnesota lake; Steinberg (1972) reported on primary production and nutrient limitation in two northern prairie lakes; Churchill and Brashier (1972) examined the effects of dredging on nutrient levels and biological populations of Lake Herman; Churchill et al. (1975) evaluated a recreational lake rehabilitation project; Haertel (1972) investigated environmental factors affecting water quality in northern prairie lakes, (1976a) estimated nutrient limitation of algal standing crops in shallow prairie lakes, (1977) evaluated comparative eutrophication and primary production measurements in prairie lakes; and Felderman and Eno (1977) monitored sediment and runoff measurements for a typical prairie lake.

## Primary Productivity and Community Respiration

Light and Dark Bottle. The oxygen light and dark (L & D) bottle method of estimating primary productivity and community respiration has been investigated in great detail and reviewed by Lund and Talling (1957). Comparisons with the carbon-14

method have been discussed (Steeman-Nielsen 1951; Vaccaro and Ryther 1954; Ryther 1956; McAllister 1961; Eley 1970; and others).

Advantages of the L & D bottle method include: (1) convenience of measurement, and (2) a reasonable approximation of the natural production rate since the bottles are returned to the same depth, maintained at the same temperature, and receive the same illumination as the surrounding water (Vollenweider 1968). Criticisms of the L & D bottle method include: (1) variation of the rate of respiratory uptake of oxygen with light intensity (Gessner and Pannier 1958), (2) provision of a substrate suitable for bacterial growth: bacteria can become abundant and can influence respiration rates in long exposure times (Vollenweider 1968), (3) possible large respiratory uptake of oxygen if active zooplankton are numerous (Vaccaro and Ryther 1954), (4) absorption of the shorter wavelengths of light by glass (Vollenweider 1968), (5) inhibition of algal growth near a smooth surface (Vollenweider 1968), and (6) differences in the respiration rate between light and dark bottles (Strickland 1960). The L & D bottle method of estimating primary productivity may also be thought of as an estimate of "community metabolism" (Odum 1971) because of the respiration from microscopic organisms and bacteria present in the bottles. Respiration from these organisms is assumed to be negligible (Vollenweider 1968) for short exposure times.

The estimates of gross productivity and community respiration by the bottle method are based on the assumption that the rate of

respiration is constant during both light and dark periods. If light respiration exceeds dark respiration, both gross productivity and community respiration are underestimated. A convincing amount of evidence has accumulated to indicate that the average rate of respiration in the light is higher than the average rate of respiration in the dark (Jackson and McFadden 1954; Ryther 1954; Verduin 1960; Odum and Wilson 1962; Odum, Beyers, and Armstrong 1963; Beyers 1963a, 1963b). This conclusion is based primarily on observations that the maximum rate of respiration often occurs immediately after sunset and that the rate declines through the night to a minimum before sunrise. It is assumed that the rate of respiration increases during the day from a pre-sunrise minimum to a post-sunset maximum. The mathematical function describing this increase is not known.

Oxygen curve. The diurnal curve method[1] of estimating primary productivity and community respiration has been investigated to a lesser extent (Winberg 1963; Vollenweider 1968; Eley 1970). Direct comparisons between the L & D bottle and $O_2$ curve method have been made (Talling 1957; Verduin et al 1959; Sreenivasan 1965; Eley 1970).

Advantages of the $O_2$ curve method include (Vollenweider 1968):

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[1] Diurnal normally refers to day events only, while the diurnal oxygen curve method involves measurements of dissolved oxygen concentration over a 24-hr period. Therefore, in this discussion the method will be referred to as the $O_2$ curve method (Eley 1970).

(1) avoidance of artificial enclosures, (2) the measurement of photosynthesis and respiration of both planktonic and attached forms of vegetation, and (3) the measurement of respiration of larger planktonic animals. Criticisms of the $O_2$ curve include: (1) difficulty of accurately estimating $O_2$ exchange with the atmosphere during the strong but variable wind conditions that usually are present in prairie lakes, (2) limited sensitivity to small oxygen changes, (3) possible errors from temporary fluctuations in respiration rates, and (4) inconvenience, since measurements must be made over a 24-hr period. For estimates made in deep water, the relative contributions of the phytoplankton and atmospheric diffusion are quantitatively more important than other components of the community (Vollenweider 1968). Thus, the $O_2$ curve method, corrected for atmospheric diffusion, approximates the relative changes in the metabolism of the phytoplankton and can be compared with the L & D bottle method as an estimate of primary productivity. Lake Cochrane has a large mean depth (3.9 m) and small littoral area, hence the oxygen changes are probably mostly caused by photosynthetic activity of the phytoplankton.

Few comparisons have been made between bottle and free-water methods, although it is generally conceded that bottle methods underestimate actual metabolic rates (Ryther 1956; Talling 1957; Rodhe 1958; Verduin et al 1959; Verduin 1960; Eley 1970). Talling (1957) found gross productivity estimated from $O_2$ changes to be

greater than L & D bottle rates by 1.9 for Gebel Aulia Reservoir and 1.6 for a bay of Lake Victoria. L & D bottle Pg rates were found to be less than one-half rates measured under natural conditions in Lake Erie (Verfuin et al 1959). Eley (1970) recorded $O_2$ curve Pg estimates to be 1.95 greater than bottle rates for Keystone Reservoir.

Not all investigators agree that higher rates obtained by free-water methods are correct. Winberg (1963) defended the L & D bottle method and concluded that differences between free-water and bottle methods were due to incorrect adjustments for atmospheric reaeration and lack of consideration of gas exchange with bottom sediments. Gross productivity estimates by L & D bottle methods for Amaravathy Reservoir, India were higher than estimates made from natural $O_2$ changes, but the techniques of measurements and calculation were not described adequately (Sreenivasan 1965).

Stepwise Multiple Regression

Stepwise multiple regression analysis (Little 1966) can be used to investigate the relative importance of selected environmental variables on the observed levels of any selected variable. It deals with linear relationships among more than 2 variables, and selects the set of independent variables that best predicts the dependent variable with the minimum number of independent variables. Evaluation of the relative contribution of each independent variable is obtained by examination of the individual coefficients

in the regression equation. Because of the lack of complete data in most environmental investigations, the number of published papers involving multivariate analysis is few. In recent years, some papers on the application of stepwise multiple regression procedures to oceanography (Platt and Rao 1970; Hameedi 1976) and limnology (Brylinsky and Mann 1973; Brown 1973; Haertel 1972, 1976a, 1977; Thoreson et al 1976) have been published.

## RESEARCH AREA

Lake Cochrane, a shallow, non-stratified, closed basin lake located in the Coteau des Prairies in southern Deuel County, was formed during the Mankato Substage of the Wisconsin glaciation (approximately 10,000 years b.p.) (White personal communication). The lake lies in a small basin, running in a southwest-northeast direction. There is little surface drainage or agricultural runoff except in spring and fall; the watershed is small, 202 hectares (500 acres, Deuel County Soil Conservation Service 1972). The major soil type in the watershed area is Foreman, a type of clay loam (Soils of South Dakota 1967).

In the past, Lake Cochrane has been only moderately eutrophic when compared to other lakes in the area (Steinberg 1972; Haertel 1972, 1976a, 1977; State Lakes Preservation Committee 1976). Mean depth of the lake is approximately 3.9 m. and maximum depth is 8.23 m. Maximum volume is $5.69 \times 10^6$ $m^3$ and this is subject to annual precipitation and groundwater levels (during the summer of 1976 the lake was approximately 2 m. low due to a drought-ridden summer and winter). The lake lies in a natural glacial valley, somewhat buffered from strong prairie winds by a belt of trees and coteau hills. The closed basin concentrates ions, particularly magnesium and sulfate, resulting in slightly brackish water with a measured conductivity of approximately 2800 micromhos/$cm^2$ (Haertel 1976a). The lake has moderate

groundwater recharge (State Lakes Preservation Committee 1976). Approximately three-fourths of the shoreline is occupied by summer cottages, houses, and resorts and the lake is utilized for sport fishing, boating, swimming, and recreation throughout the summer months.

# MATERIALS AND METHODS

## Sampling Schedule

Water quality in Lake Cochrane was sampled approximately every 18 days from 13 April to 14 October 1976, and 30 April to 26 September 1977. Samples were collected from 3 sites and 2 depths at one of the sites in 1976 and from 2 sites and 2 depths at one site in 1977. Surface (5 to 10 cm) water samples were collected at stations I, II, and III (Figure 1) in 1976 and at stations I and III in 1977. Bottom samples (0.5 m off bottom) were collected from station III both years. Chemical and biological parameters and methods used were selected to give a comparison with two previous studies conducted on Lake Cochrane (Haertel 1972, 1976a).

## Determination of Physical Parameters

Triplicate temperature and depth measurements were made at all stations. Temperature values, in degrees Celsius, were obtained by use of a bucket thermometer. Depth values, in meters, are based on measurements obtained from a calibrated, lead-weighted sounding line.

Depth of the euphotic zone (EZ) is defined as the depth to which 1% of the surface light intensity penetrates. It is derived from the extinction coefficient of light measured with a submarine photometer (Kahlsico, Inc. model no. 268WA310). Secchi depth (SD) measurements of water transparency were obtained with a 20 cm. black and white Secchi disc. Depth of the EZ was

measured at stations I and III and SD was measured at all stations in duplicates.

Wind speed and direction by hour and daily solar radiation were obtained from the National Weather Service located on the campus of South Dakota State University, Brookings, South Dakota. Conversion to wind stress was calculated (Small 1963). Solar radiation was measured with a 50 Junction Epply Radiometer equipped with a circular chart recorder. Solar radiation values are presented as calories per square centimeter (langleys) per day. Solar radiation and wind stress of the previous seven days represents the previous seven day average and was used in the statistical correlations together with the solar radiation and wind stress on the morning of sampling. Precipitation data was obtained from the National Weather Service located at Clear Lake, South Dakota. Lake Cochrane is 88.5 kilometers north-northeast of Brookings, South Dakota and 6.7 kilometers south-southeast of Clear Lake, South Dakota.

Determination of Chemical Parameters

Triplicate samples of water for chemical analyses were collected with a modified VanDorn PVC (polyvinylchloride) sampler (4 liter capacity) and placed in opaque, plastic 2 liter bottles. Parameters measured, methods of analyses, minimum detectable concentration and sampling intervals appear in Table 1. All chemical tests were in accordance with American Public Health Association (1973).

Table 1. Water Chemistry Analyses; Methods used, Minimum Detectable Concentrations, and Sampling Intervals.

| Test | Method | Minimum Detectable Conc. (mg/l) | Sampling Interval |
|---|---|---|---|
| $NO_3$-N | Brucine | .01 | 18 days |
| Org-N | Kjeldahl | .40 | 18 days |
| $PO_4$-P | Stannous Chloride | .01 | 18 days |
| Total $PO_4$-P | Acid hydrolysis | .01 | 18 days |
| $HCO_3$ | Calculated from alkalinity | - | 18 days |
| $CO_3$ | Calculated from alkalinity | - | 18 days |
| Si | Heteropoly Blue | 1.00 | 18 days |
| $O_2$ | Winkler (Azide Modification) | .02 | 18 days |

Determination of Biological Parameters

Zooplankton Standing Crop Measurements. Triplicate oblique tows of zooplankton were collected with a Clarke-Bumpus automatic plankton sampler equipped with a #12 mesh net (12.5 cm diameter, 90 cm long, 120 micrometer aperture opening) on 9 dates in 1976 and on 9 dates in 1977 at all stations. Quantitative counts were made according to the method in Edmonson and Winberg (1971). Zooplankton filtering rate is defined as the % of water volume filtered by zooplankton and is calculated by multiplying the abundance of zooplankton (by species) times the experimentally determined filtration rate for that species or genus (Haney 1970) (Haertel M.S. submitted to Ecology).

Phytoplankton Standing Crop Measurements. Triplicate surface and bottom water samples were collected from the same bottle casts as the chemical parameters. Chlorophyll a samples were collected from each station and later analysed at the laboratory according to the method in (Strickland and Parsons 1968). Samples for algal cell counts were immediately preserved with Lugols solution and stored for identification and enumeration. Approximately 250 ml of sample were concentrated to 5 ml in a plankton centrifuge; 1 ml of the preserved, centrifuged sample was placed in a Sedgewick Rafter counting chamber and inverted for 15 to 20 minutes to allow settling. The strip count method was used and 3 slides (300 individuals) were examined at each station on each date. Fields were randomly selected at 100X on a Nikon inverted microscope until 100 of the most abundant large taxon were

counted (Lund et al 1958). Smaller organisms were counted at 400 X until 100 of the most abundant taxon were recorded (Lund et al 1958). A colony of Anacystis incerta or A. cyanea, and a tetrad of Agmenellum quadruplicatum or Agmenellum sp. were recorded as one unit.

Gross Productivity and Community Respiration. Terminology pertaining to primary productivity and community respiration has been reviewed (Odum and Hoskin 1958; Davis 1963; Beyers 1963b; and Eley 1970). However, variations in the definitions occur and the common terms used in this discussion will be abbreviated and are defined as (Eley 1970):

Gross Productivity (Pg) - The rate of energy stored as reduced organic material or the liberation of oxygen as a by-product of photosynthesis by photoautotrophic organisms.

Community Respiration (Rt) - The rate of oxidation of organic matter to provide energy for the life processes of the biota and the chemical oxygen demand of the abiotic components of the community.

Net Productivity (Pn) - The net rate of energy storage by the community or the difference between Pg and Rt.

Gross Productivity to Community Respiration Ratio (Pg/Rt) - The ratio of gross productivity to community respiration must be unity (Pg/Rt = 1.0) in a balanced steady state system, if no export or

import occurs (Beyers 1963a). If some event should disturb this ratio in such a manner that it becomes greater or less than unity, an increase or reduction of the biomass will take place.

Primary productivity and community respiration were measured by the L & D bottle method (Vollenweider 1968) at stations I and III (Figure 1), on 11 dates one season and 6 dates during the second season. Samples were collected with a non-toxic Van Dorn PVC (polyvinyl chloride) sampler (4 liter capacity) immediately after the physical, biological, and chemical data was collected (± 800 hr). All L & D bottle experiments were run during the morning hours to coincide with the pre-noon maximum productivity rate (Shalar and Untura 1970) and to lessen air bubble effects.

Quadruplicate sets of standard 300 ml BOD bottles, four clear (LB) and four dark (DB), were suspended separately at 4 depths in stations III and 3 depths in station I. Two initial (IB) bottles from surface and bottom depths were preserved immediately to prevent $O_2$ changes. All treatments (4LB, 4DB, and 2 IB) were taken from the same Van Dorn cast. The L & D bottles were suspended from 4 to 6 hours. Determination of oxygen concentration was made by the Azide modification of the Winkler method (American Public Health Association 1973). A value for Pg is calculated by subtracting the mean oxygen concentration of the DB from that of

its corresponding LB mean oxygen concentration. Pn values are calculated by subtracting the mean oxygen concentration of the IB from that of its corresponding LB mean oxygen concentration. Rt values are similarly calculated by subtracting the mean oxygen concentration of the DB from that of its corresponding IB mean concentration. Final figures were expressed as production of carbon per square meter of lake surface by the method described in Haertel (1977). Milligrams of carbon assimilated per hour were calculated according to the equation (Strickland 1966):

$$(\text{mg } O_2 \text{ evolved/hr.})(0.375/\text{photosynthetic quotient}).$$

A value of 1.2 was chosen for the photosynthetic quotient (Ryther 1956). Values of Pg and Rt were converted into specific forms according to the method in Haertel (1977).

The effect of incubation time on L & D bottle experiments was tested on 2 dates. L & D bottles were exposed to solar radiation for periods of one-half and full exposure (6 hours) times. The studies were conducted at station I on 18 May and at station III on 3 June 1977. Comparison of Pg, Rt, and Pn values for the different exposure times were made.

A modification of the $O_2$ curve method of Eley (1970) was used to estimate the rate of primary production and community metabolism at station III on 23 May and 20 August 1976 and 11 July 1977. Comparisons of Pg and Rt were made between the $O_2$ curve method and the L & D bottle method which was run at the same time. The

concentration (g $O_2/m^3$) of dissolved oxygen was determined at 1.5 m depth at 4 hour intervals. Concentrations of oxygen at the 1.5 m depth were summed over the EZ to obtain g $O_2/m^2$. The average rate-of-change (g $O_2/m^2hr$) was calculated for each 4 hour interval. A correction for atmospheric reaeration was calculated by multiplying a diffusion constant (k) by the average oxygen saturation deficit of the surface waters during each 4 hour interval. The diffusion constant (k) was estimated by averaging k values determined for each nighttime sampling interval by the formula (Eley 1970):

$$k = q_n - q_{n+1} \; / \; s_n - s_{n+1}$$

where, k = g $O_2/m^2$ hr at 0% Oxygen saturation,

n = any nighttime sampling period (i.e. after sunset and before sunrise),

n + 1 = the subsequent 4 hr nighttime sampling period,

$q_n$ = rate-of-change of the surface g $O_2/m^3$ at nighttime n,

$q_{n+1}$ = rate-of-change of the surface g $O_2/m^3$ at nighttime n+1,

$s_n$ = the oxygen saturation deficit of the surface water at nighttime n, and

$s_{n+1}$ = the oxygen saturation deficit of the surface water at nighttime n+1.

The corrected average oxygen rate-of-change for each 4 hour interval was plotted against time, and a daytime respiration line was extrapolated between pre-sunrise and post-sunset negative rate-of-change points (Figure 2) (Odum and Wilson 1962;

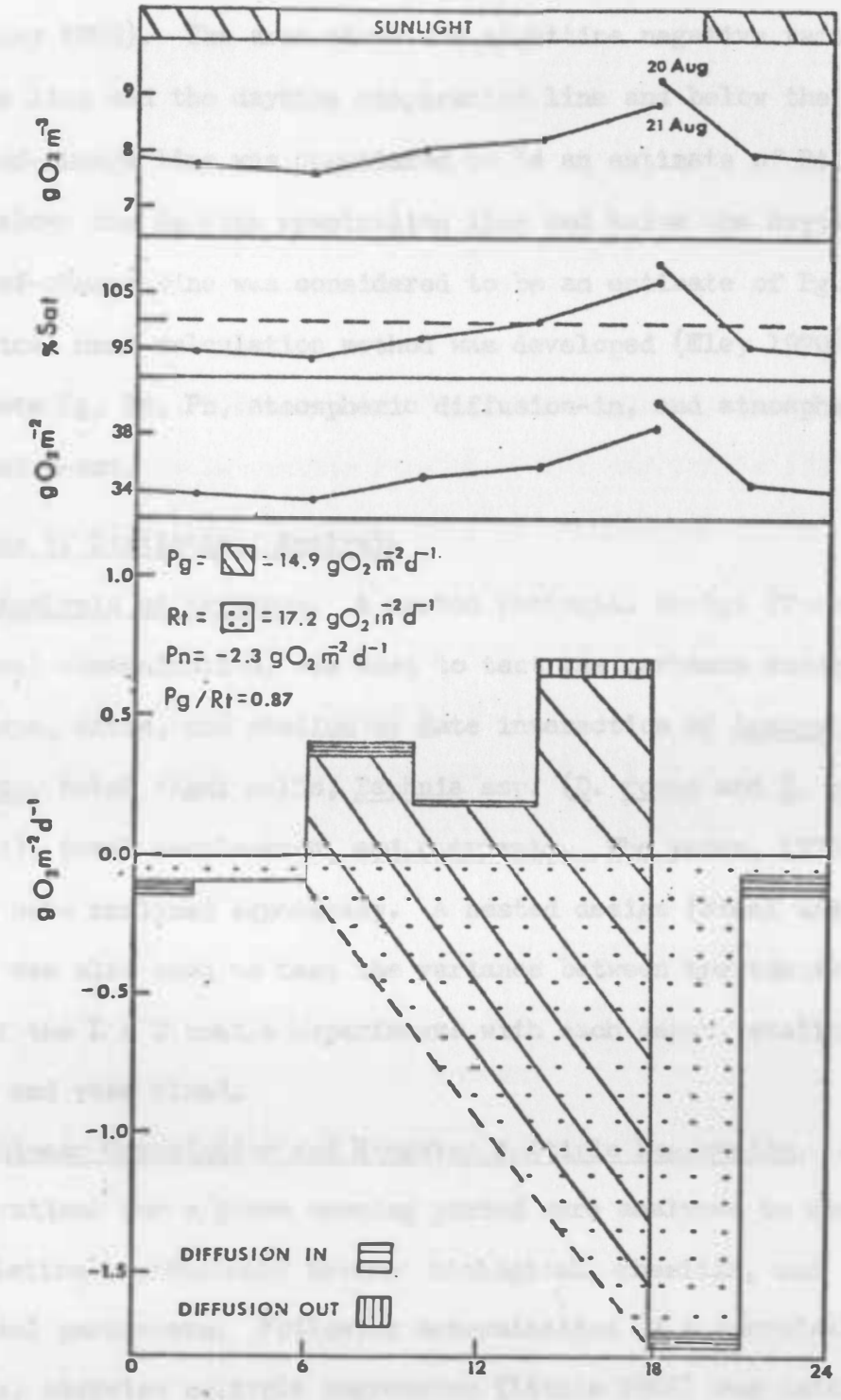



Figure 2. $O_2$ curve on 20-21 August 1976, Lake Cochrane.

and Eley 1970). The area above the nighttime negative rate-of-change line and the daytime respiration line and below the zero rate-of-change line was considered to be an estimate of Rt. The area above the daytime respiration line and below the daytime rate-of-change line was considered to be an estimate of Pg. A graphical hand calculation method was developed (Eley 1970) to estimate Pg, Rt, Pn, atmospheric diffusion-in, and atmospheric diffusion-out.

Methods of Statistical Analysis

Analysis of Variance. A nested factorial design (Tucker personal communication) was used to test the variance among stations, dates, and station by date interaction of Anacystis incerta, total algal cells, Daphnia ssp. (D. rosea and D. galeata pooled), total zooplankton, and nutrients. The years, 1976 and 1977, were analyzed separately. A nested design (Steel and Torrie 1960) was also used to test the variance between treatments (LB, DB) of the L & D bottle experiments with each depth, station, date, and year fixed.

Linear Correlation and Stepwise Multiple Regression. All observations for a given testing period were analyzed to obtain linear correlation coefficients between biological, chemical, and physical parameters. Following determination of a correlation matrix, stepwise multiple regression (Little 1966) was initiated on certain variables to determine the relative importance of each

variable and its predictive value. Dependent and independent parameters used in multiple regression appear in Table 2.

Sampling dates were tested according to the following schedule:

1) Combined by seasons, each year run separately;

2) years combined.

Seasons were "coded in" as "dummy" independent variables in a logarithmically increasing fashion (Steel and Torrie 1960) (Tucker personal communication) defined as (Haertel 1976):

a) Spring-defined as the period from ice-out until the water temperature reached approximately 20 degrees Celsius, usually early to mid-June;

b) Early Summer-defined as the period of time from mid-June to mid-July, the period of abundant bluegreen algae;

c) Late Summer-defined as the period of time from mid-July to mid-September, the period of consistently high algal blooms;

d) Fall-defined as early September to mid-October (1976 only).

Table 2. Dependent and Independent Parameters Used In Stepwise Multiple Regression Analysis

| | Dependent Parameters | Independent Parameters[a] |
|---|---|---|
| 1. | Chlorophyll a (C) | P, N, Si, R, EZ, T, WD, L-7, W-7, FR |
| 2. | Algal cells (A) | P, N, Si, R, S, T, WD, L-7, W-7, FR |
| 3. | Orthophosphate (P) | A, R, T, WD, L-7, W-7, FR |
| 4. | Nitrate-N (N) | A, R, T, WD, L-7, W-7, FR |
| 5. | Euphotic Zone (EZ) | C, R, T, WD, L-7, W-7, FR |
| 6. | Secchi Depth (SD) | A, R, T, WD, L-7, W-7, FR |

[a] Independent parameters used in multiple regression analysis: silicate (Si) rain (R), temperature (T), water depth (WD), solar radiation-average of prior seven days (L-7), solar radiation on day of sampling (L), wind stress-average of prior seven days (W-7), wind stress on day of sampling (W), zooplankton filtering rate (FR).

# RESULTS

## Environmental Measurements

The 1976 climatic conditions varied greatly from 1977 conditions at Lake Cochrane. Little rain fell in 1976 and the lake was approximately 2 m below normal, however mid- and late-summer rains during 1977 replenished the lake level to about 1.5 m below normal by the end of the 1977 sampling period. A drastic decline in secchi depth occurred in both 1976 and 1977 when compared with 1975 (Table 3) and 1970 (Haertel 1977). Between the years 1976-77 secchi depth and euphotic zone values were similar. However, maximum and mean secchi depth values at all stations were slightly greater in 1976 than 1977 (Table 4). The silicate values between both years were lowest on the first sampling date (Table 4). The reduced silicate values correspond with periods of maximum diatom abundance. Silicate values gradually increased through the sampling period to maximum values in late summer, as bluegreens increased and diatoms decreased.

Total kjeldahl nitrogen mean values were fairly consistent during the years 1975-76-77 (Table 3). Total $PO_4$ mean values decreased in 1976 and then rose in 1977 to the previous 1975 levels (Table 3). Nitrate-N ($NO_3$-N) and orthophosphorus (ortho $PO_4$-P) were present in very low concentrations during all years measured, however larger amounts of both were present in 1977 than 1976 at all stations, possibly because of the larger amounts of nutrients carried with runoff when rainfall levels increase

Table 3. CHANGES WITH TIME IN SELECTED WATER QUALITY PARAMETERS IN LAKE COCHRANE, 1975-76-77

| Year | Seasonal variation | $NO_3$ (mg/l) | TKN (mg/l) | Ortho $PO_4$ (mg/l) | Total $PO_4$ (mg/l) | Temp (°C) | Depth (m) | Secchi depth (m) | Euphotic zone (m) | Filter rate (%) | Total Zooplankton (#/l) | Total Daphnia (#/l) | Total Algal cells ($10^3$/ml) | Chloro a ($mg/m^3$) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1975[a] | low | 0.00 | 0.00 | 0.00 | 0.00 | 6.0 | | 1.0 | 2.0[b] | 13[b] | 46[b] | 1[b] | 1[b] | 4.5 |
| | mean | 0.02 | 1.27 | 0.04 | 0.16 | 19.5 | | 1.6 | 3.7 | 89 | 232 | 30 | 5[a] | 14.4 |
| | high | 0.13 | 3.45 | 0.13 | 0.62 | 26.0 | | 2.8 | 7.6[b] | 337[b] | 858[b] | 200[b] | 10[b] | 19.0 |
| 1976 | low | 0.00 | 1.08 | 0.00 | 0.04 | 10.0 | 3.6 | 0.7 | 3.1 | 13 | 64 | 0 | 5 | 6.6 |
| | mean | 0.00 | 1.30 | 0.02 | 0.04 | 17.7 | 4.2 | 1.2 | 4.4 | 42 | 118 | 13 | 50 | 12.7 |
| | high | 0.03 | 1.67 | 0.04 | 0.08 | 24.0 | 4.5 | 2.1 | 5.8 | 145 | 215 | 72 | 111 | 18.8 |
| 1977 | low | 0.00 | 0.64 | 0.00 | 0.12 | 14.0 | 4.15 | 0.7 | 3.5 | 1 | 16 | 0 | 11 | 4.8 |
| | mean | 0.04 | 1.31 | 0.03 | .19 | 19.7 | 4.40 | 1.1 | 4.3 | 60 | 165 | 7 | 52 | 12.1 |
| | high | 0.16 | 1.99 | 0.07 | 0.32 | 23.5 | 4.8 | 2.0 | 6.0 | 242 | 647 | 34 | 90 | 21.6 |

[a] Haertel 1977

[b] Haertel unpublished data

Table 4. MEAN AND EXTREME VALUES OF SELECTED WATER QUALITY PARAMETERS OF THE STUDY AREAS, APRIL TO OCTOBER, 1976-77

| Station | Seasonal Variation | $NO_3$ mg/l | TKN mg/l | Ortho-P mg/l | Tot-P mg/l | Silicate mg/l | Temp C | Depth (m) | Secchi depth (m) | Euphotic zone (m) | Filter Rate % | Total Zoopl (#/l) | Total Daphnia (#/l) | Chla ($mg/cm^3$) | Total algal cells/ml |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **1976** | | | | | | | | | | | | | | | |
| I | low | 0.00 | 1.19 | 0.00 | .03 | 4.1 | 10.0 | 2.0 | .7 | 2.0 | 9 | 31 | 0 | 8.7 | 1 |
| | mean | 0.0 | 1.5[illegible] | 0.02 | .05 | 8.1 | 17.5 | 2.7 | 1.2 | 2.7 | 45 | 83 | 2 | 13.6 | 58 |
| | high | 0.03 | 1.87 | 0.04 | .09 | 13.1 | 24.0 | 3.0 | 2.2 | 3.0 | 163 | 234 | 68 | 20.3 | 164 |
| II | low | 0.00 | 1.08 | 0.00 | .03 | 3.7 | 10.0 | 3.2 | .7 | --- | 9 | 65 | 0 | 7.4 | 2 |
| | mean | 0.0 | 1.53 | 0.02 | .04 | 7.5 | 17.7 | 4.1 | 1.2 | --- | 40 | 133 | 12 | 14.6 | 45 |
| | high | 0.03 | 2.12 | 0.04 | .06 | 12.5 | 24.0 | 4.6 | 1.95 | --- | 149 | 230 | 64 | 25.0 | 99 |
| III- sfc | low | 0.00 | 0.64 | .01 | .04 | 3.1 | 10.0 | 5.5 | .7 | 3.1 | 7 | 72 | 0 | 8.5 | 3 |
| | mean | 0.0 | 1.53 | .02 | .05 | 8.0 | 17.6 | 5.9 | 1.2 | 4.4 | 50 | 140 | 17 | 14.5 | 41 |
| | high | 0.02 | 1.70 | .03 | .08 | 14.2 | 24.0 | 6.0 | 2.1 | 5.8 | 179 | 260 | 83 | 30.0 | 65 |
| III-Bot | low | 0.00 | 0.99 | 0 | .03 | 3.2 | 10.0 | --- | --- | --- | 7 | 72[a] | 9 | 8.6 | 1 |
| | mean | 0.0 | 1.57 | .02 | | 7.5 | 17.3 | --- | --- | --- | 50 | 140 | 17 | 13.2 | 46 |
| | high | 0.04 | 2.29 | .04 | .13 | 12.0 | 24.0 | --- | --- | --- | 79 | 260 | 83 | 27.3 | 93 |
| **1977** | | | | | | | | | | | | | | | |
| I | low | 0 | 1.05 | .01 | .11 | 5.3 | 14.0 | 2.3 | .7 | 2.3 | 9 | 19 | 0 | 4.5 | 12 |
| | mean | .03 | 1.75 | .04 | .18 | 11.7 | 19.6 | 2.7 | 1.1 | 2.7 | 61 | 178 | 8 | 10.7 | 52 |
| | high | .11 | 2.40 | .07 | .31 | 19.0 | 23.5 | 3.0 | 2.0 | 3.0 | 241 | 632 | 29 | 16.2 | 78 |
| III-sfc | low | 0 | 1.03 | 0.0 | .12 | 4.9 | 14.5 | 6.0 | .8 | 3.5 | 1 | 11 | 0 | 4.2 | 6 |
| | mean | .05 | 1.75 | .03 | .19 | 12.0 | 19.7 | 6.1 | 1.2 | 4.3 | 59 | 154 | 9 | 12.1 | 54 |
| | high | .18 | 2.41 | .07 | .32 | 19.5 | 23.5 | 6.5 | 1.9 | 6.0 | 242 | 661 | 40 | 22.8 | 115 |
| III-Bot | low | 0 | 0.82 | 0.0 | .12 | 4.8 | 14.0 | --- | --- | --- | 1 | 11[a] | 0[a] | 5.6 | 13 |
| | mean | .04 | 1.64 | .03 | .19 | 11.9 | 19.7 | --- | --- | --- | 59 | 154 | 9 | 13.5 | 48 |
| | high | .23 | 2.44 | .07 | .32 | 18.8 | 23.0 | --- | --- | --- | 242 | 661 | 40 | 25.9 | 88 |

[a] oblique zooplankton tows sampled the entire water column (i.e. no differtiation between surface and bottom).

(White 1977). Between the years 1976-77 total kjeldahl nitrogen levels were consistent, with the lowest values occurring at station III both years (Table 4).

Analysis of variance was performed on ortho $PO_4$-P and $NO_3$-N values and indicated nonsignificant differences among stations and among station by date interaction for both years (Table 5). Differences among dates for both years were highly significant for ortho $PO_4$-P and $NO_3$-N. The nonsignificant differences among station by date interaction meant that stations responded essentially the same on all the dates.

Phytoplankton Standing Crop Measurements

The following algae were common during the 1976 and 1977 summer seasons: five diatoms, Chaetoceros elmorei (Figure 3), Synedra ulna, Cyclotella glomerata (Figure 4), Cyclotella michiganiana (Repsy, personal communication), and Amphora spp. (Figure 5); two dinoflagellates, Peridium bipes, and Glenodinium gymnodinium; two desmids, Pediastrum sp. and Cosmarium sp.; three green algae, Sphaerocystis sp., Oocystis spp., and Scenedesmus spp.; six bluegreens, Anacystis incerta (Microcystis sp.), Anacystis cyanea (Microcystis aeruginosa) (Figure 6), Gomphosphaeria spp., Agmenellum quadruplicatum (Merismopedia sp.), Agmenellum sp. (Merismopedia sp.), and Lyngbya contorta.

Mean summer total algal cell counts were greater in 1976-77 than 1975 (Table 3). Analysis of variance was performed on

Table 5. ANALYSIS OF VARIANCE ON SELECTED PARAMETERS, 1976 AND 1977 SEPARATELY.

| Year | Parameters | F (Station) | F (Date) | F (Station by Date) |
|---|---|---|---|---|
| 1976 | *A. incerta* | 16.6*** | 93.6*** | 19.0*** |
| | Total cells | 10.2*** | 48.7*** | 13.7*** |
| 1976[a] | *A. incerta* | 1.3 | 74.5*** | 2.3* |
| | Total cells | 2.1 | 65.9*** | 2.3* |
| 1977 | *A. incerta* | 5.4** | 31.8*** | 3.8*** |
| | Total cells | 1.4 | 20.5*** | 2.4* |
| 1976 | Chlorophyll *a* | 4.7*** | 40.1*** | 3.7*** |
| 1977 | Chlorophyll *a* | 11.4*** | 87.3*** | 4.2*** |
| 1976 | Ortho-$PO_4$ | 0.51 | 138.0*** | 1.04 |
| | Nitrate-N | 0.31 | 15.6*** | 1.00 |
| | $NH_3$-N | 0.70 | 154.6*** | 0.39 |
| 1977 | Ortho-$PO_4$ | 1.40 | 14.2*** | 0.76 |
| | Nitrate-N | 0.60 | 10.9*** | 1.01 |
| | $NH_3$-N | 1.50 | 62.0*** | 1.33 |
| 1976 | *Daphnia* | 5.34* | 78.5*** | 11.7*** |
| | Total Zoopl. | 1.68 | 12.73*** | 7.6*** |
| 1977 | *Daphnia* | 1.97 | 13.1*** | 4.2* |
| | Total Zoopl. | 3.69* | 25.5*** | 1.28 |

[a]1976 16 July collection data was omitted from the variance test

*denotes significance at the 0.05 level
**denotes significance at the 0.01 level
***denotes significance at the 0.001 level

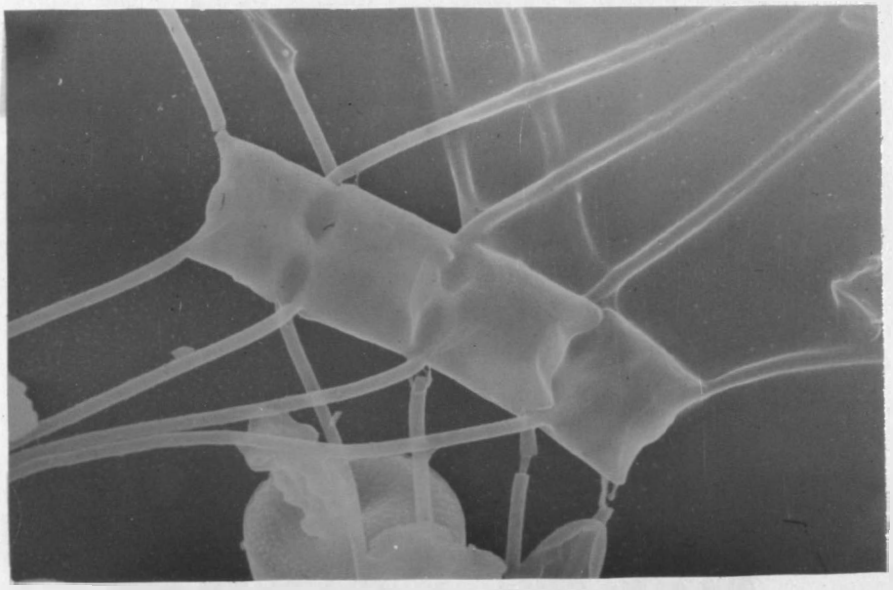
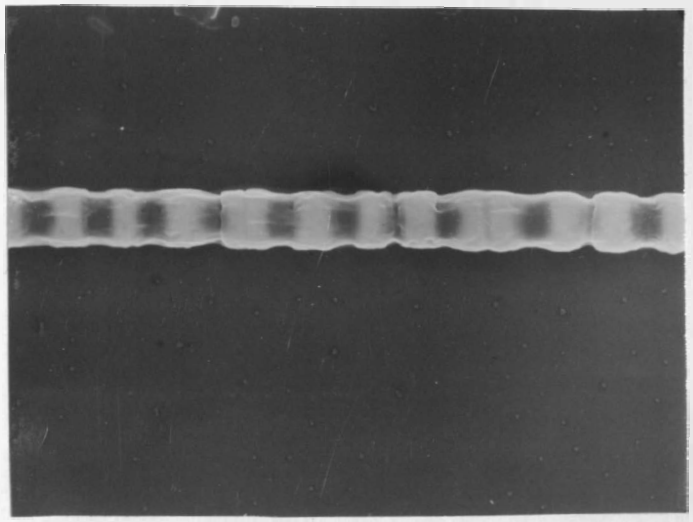
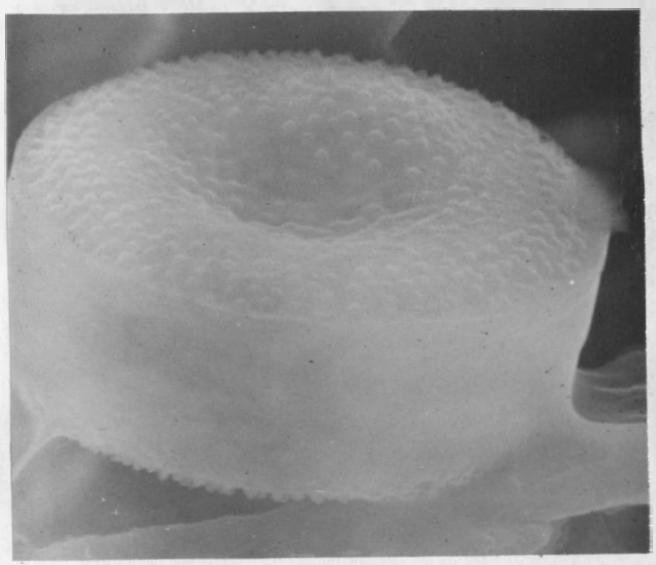


Figure 3. Chaetoceros elmorei, diatom, 4300X. Scanning electron microscope (SEM) picture courtesy of Marcus Johnshoy.



A. Chain of C. glomerata, 2400X.



B. Single C. glomerata, 9130X.

Figure 4. Cyclotella glomerata, diatom.
Scanning electron microscope (SEM)
picture courtesy of Marcus Johnshoy.

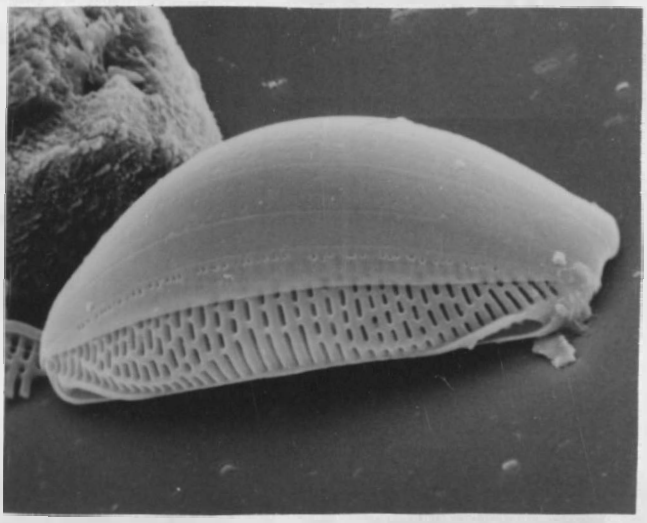


Figure 5. Amphora sp., diatom, 5400X.
Scanning electron microscope (SEM)
picture courtesy of Marcus Johnshoy.

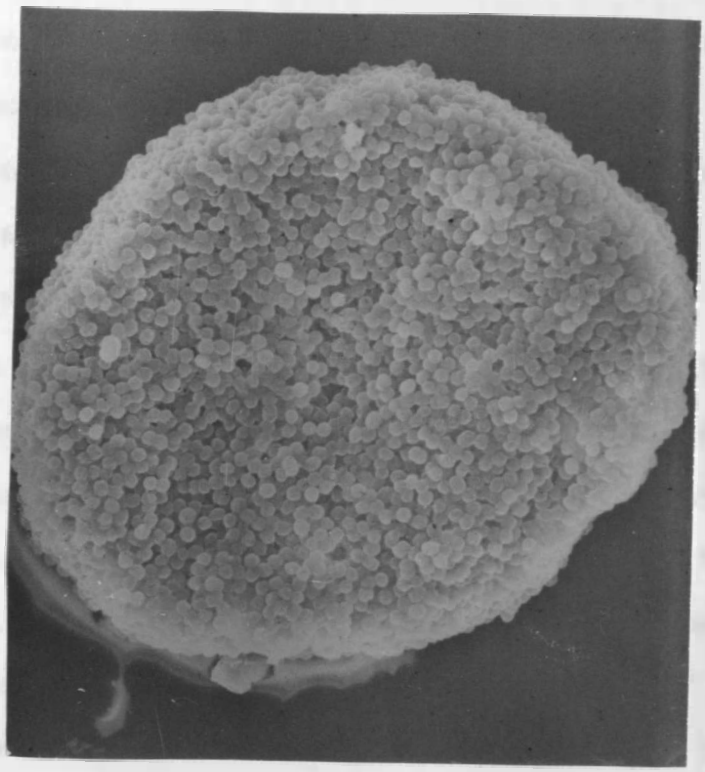


Figure 6. Anacystis cyanea, bluegreen, 828X. Scanning electron microscope (SEM) picture courtesy of Marcus Johnshoy.

total algal cell counts and the most abundant bluegreen species, Anacystis incerta (Table 5). Highly significant differences among stations existed in Anacystis incerta for both years, and in total algal cell counts in 1976; highly significant differences among dates and among station by date interaction (stations responded differently on the same dates) for both years were noted in both A. incerta and total cell counts. Since station by date interaction was significant no attempts could be made to determine which stations or which dates were significantly different (Steel and Torrie 1970).

Nonsignificant differences among stations for A. incerta and total algal cell counts were found when the 16 July 1976 sampling date was removed from the variance test. Comparison of environmental conditions on 15 July 1976 revealed that a strong north wind (gusts up to 56 kph) prevailed throughout the previous day and night. The physical effect of the circulating surface waters apparently resulted in a significant "pile-up" of algal cells at the south station (station I), a phenomenon frequently reported by other investigators (Small 1963; Steinberg 1972; Wetzel 1976).

Algal cell count estimates exhibited the greatest seasonal variation at all stations in 1976 and at station III in 1977. Cell numbers were low in spring and increased to peak concentration during mid- or late-summer (Figure 7).

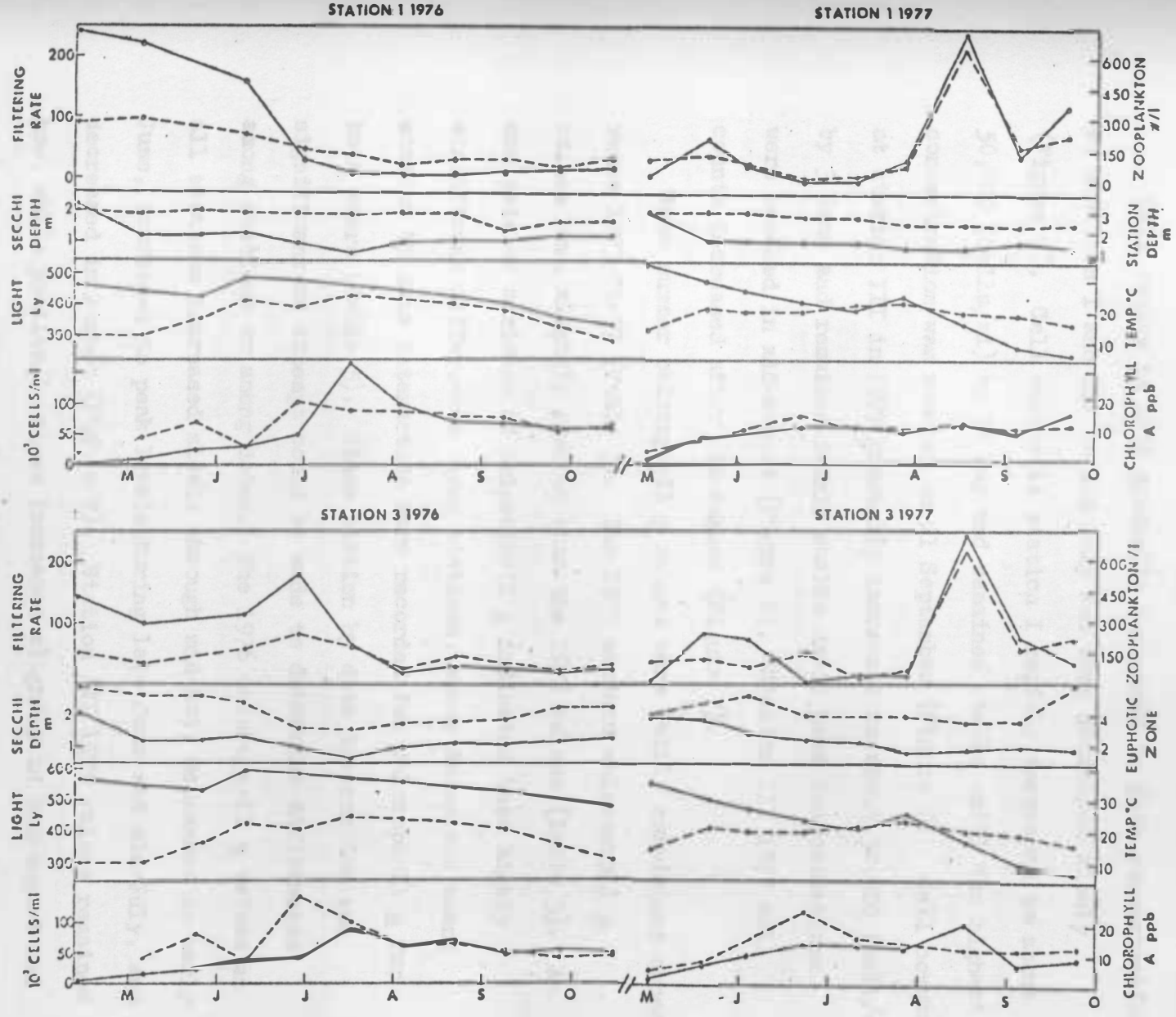



Figure 7. Mean values of selected parameters during open-water seasons, 1976-77: light = average of seven days before sampling, filtering rate = % of the water column, dashed line designates right hand parameter

Cell counts in 1976 gradually increased to peak concentrations at stations I and III in mid-July and then decreased slowly (Figure 7). Cell counts at station I rapidly increased to about 50,000 (cells/ml) by 18 May and remained stable until the highest concentration was reached on 21 September (Figure 7). Cell counts at station III in 1977 gradually increased to about 50,000 (cell/ml) by 3 June and remained fairly stable until peak concentrations were reached in mid-August (Figure 7). Station III 1977 cell counts decreased after mid-August (Figure 7).

Mean summer chlorophyll a values were fairly consistent among years 1975-76-77 (Table 3). The 1977 maximum chlorophyll a values were slightly greater than the 1976 values (Table 3). An analysis of variance of chlorophyll a indicated that highly significant differences among stations, among dates and among station by date interaction were recorded for chlorophyll a for both years (Table 5). Since station by date interaction was significant no attempt could be made to determine differences among stations or among dates. The 1976 chlorophyll a values at all stations increased slowly through mid-May, decreased in early June, increased to peak levels during late June and mid-July, and decreased in August (Figure 7). Station III 1976 values remained low, while station I values increased slightly in mid-August and early September (Figure 7). Station I values decreased slightly in late September and mid-October (Figure 7). The 1977 chlorophyll

*a* values at all stations increased rapidly to peak concentrations in late June and then decreased (Figure 7).

Zooplankton Standing Crop Measurements

Total zooplankton counts and total *Daphnia* mean values were highly variable among the years (Table 3) and stations (Table 4). An analysis of variance indicates significant differences among stations for *Daphnia* in 1976 and for total zooplankton in 1977 (Table 5). Differences among dates were significant for *Daphnia* and total zooplankton both years (Table 5). Highly significant differences among station by date interaction for *Daphnia* and total zooplankton were recorded in 1976, while significant differences were recorded for *Daphnia* in 1977 (Table 5).

A *Daphnia* pulse occurred in 1976 on 10 June at stations I and III and remained high on 28 June at station III (Figure 8). A drastic decline in *Daphnia* at all stations immediately followed, and values remained low for the remainder of the sampling period. In 1977 *Daphnia* pulsed on 18 May at stations I and III and remained high at station III through 3 June. *Daphnia* then suffered a collapse and remained at low levels through the remainder of the sampling period.

Total zooplankton were lowest on 26 September and highest on 13 April in 1976 (Table 3) (Figure 7). Total zooplankton were lowest on 11 July and highest on 16 August in 1977 (Figure 7).

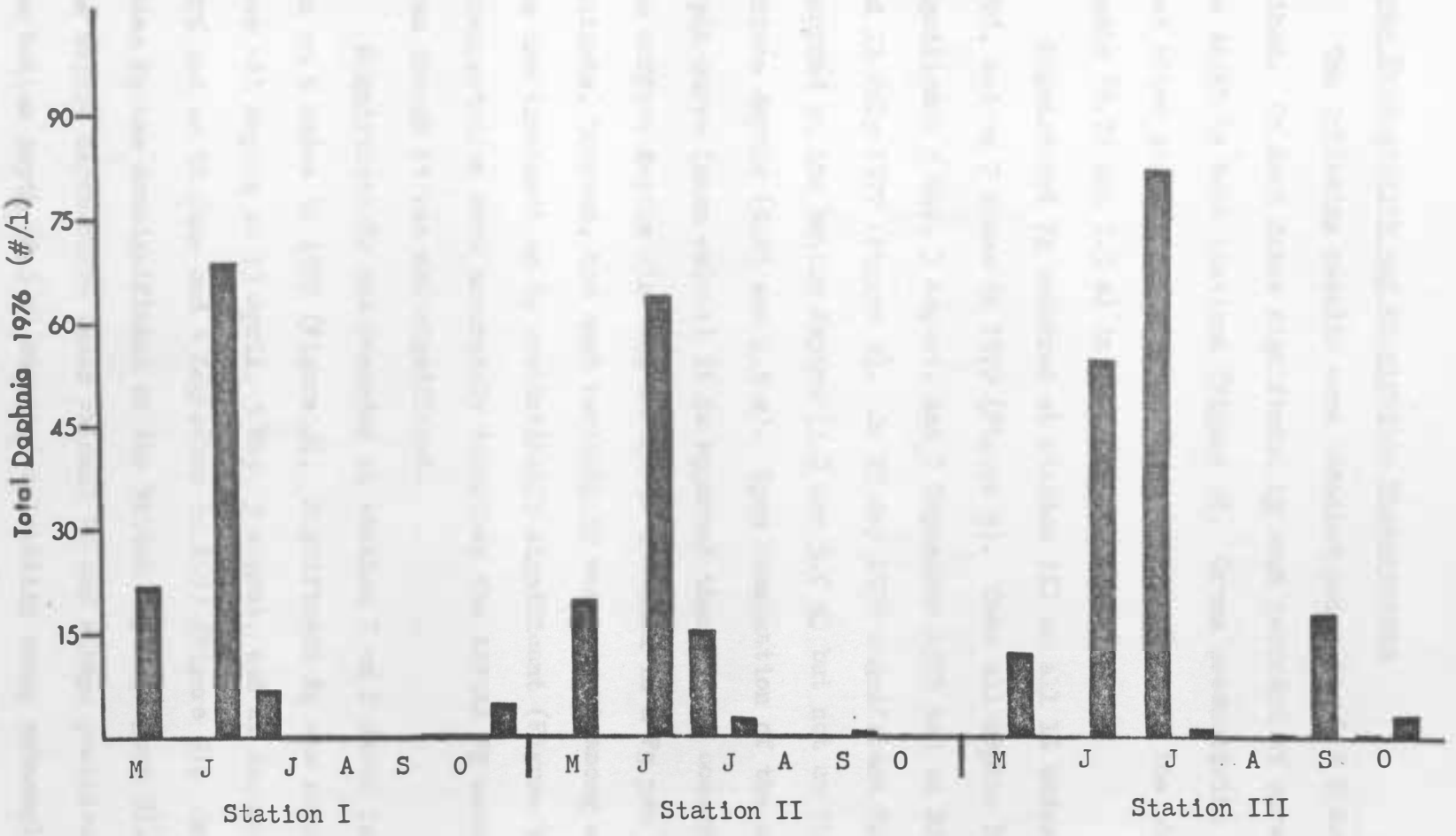



Figure 8. Total Daphnia 1976.

Gross Productivity and Respiration Measurements

The following results were obtained using the L & D bottle method. On most dates significant Pg were recorded at more than one depth in both stations (Figure 9). Gross productivity was most often significant and had the highest values at the shallowest depths (0.25 and 1.5 m) in both stations.

Significant Pg occurred at station III on all 11 dates in 1976, and on 7 dates in 1977 (Figure 9). Over all depths Pg was significant 5 May, 3 August, and 8 September 1976 and on 22 June and 11 July 1977 (Figure 9). On 23 May 1976 significant Pg was recorded at the bottom depths (3.0 and 5.0 m) but not at the surface depths (0.25 and 1.5 m). Upon examination of the oxygen depth-curve (mean values) it is apparent that Pg had occurred at the surface depths also and should be included in a Pg per $m^2$ estimate, however, too much variability was present among subsamples for the treatment to be statistically significant (Figure 9). This interpretation more accurately describes the actual Pg measured even though it was not significant.

Significant Pg was recorded at station I on 8 dates in 1976 and on 6 dates in 1977 (Figure 9). Significant Pg was recorded over all depths on 13 April, 5 May, 3 August, and 21 August in 1976 and on 22 June and 4 September in 1977 (Figure 9). On most dates Pg was nonsignificant at the bottom depth (Figure 9). From the oxygen depth-curve (mean values) Pg was always positive at the bottom depth (2.5 m) but the variability among subsamples

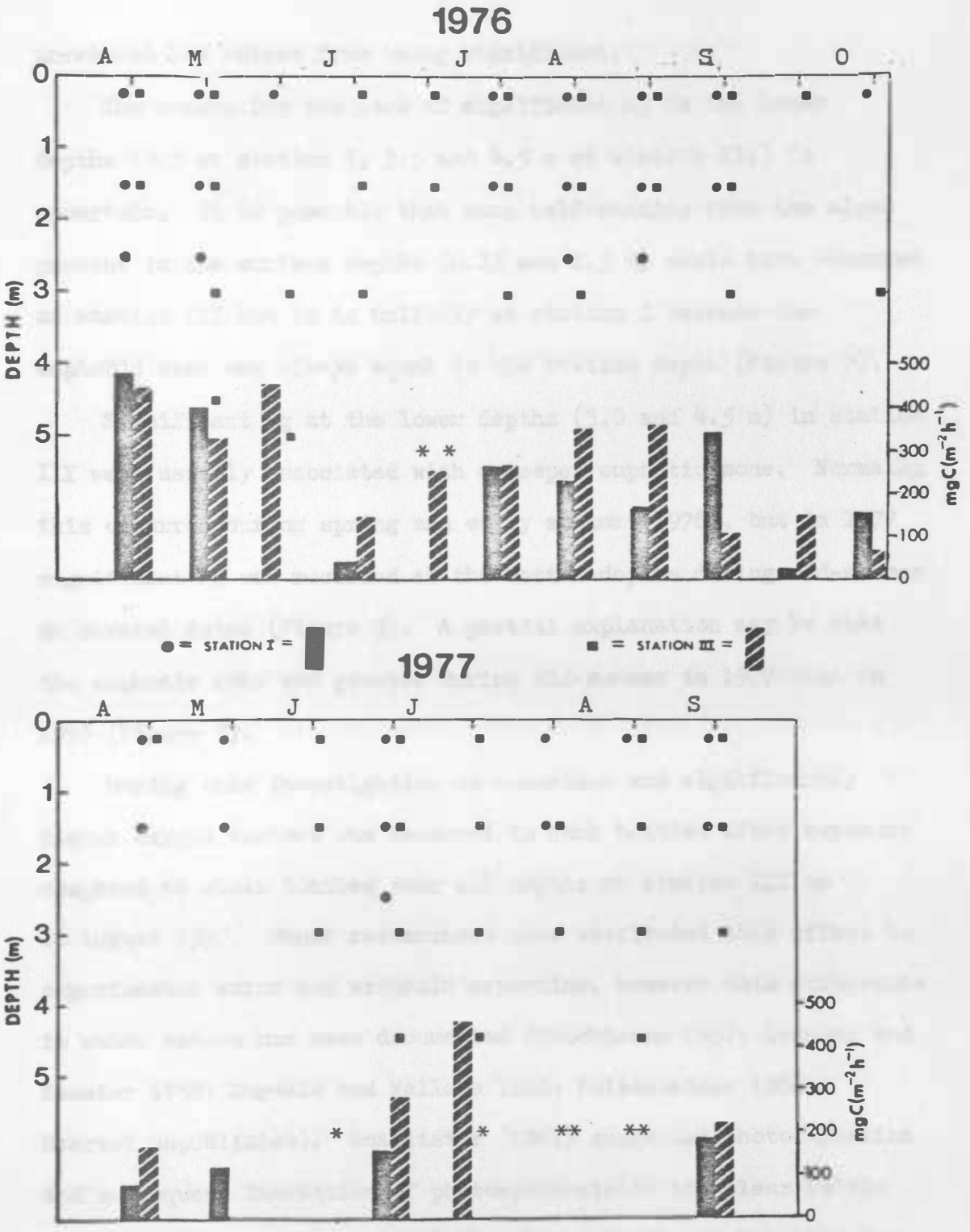



Figure 9. Significant Pg at stations I and III and amount of Pg in $mgC/m^2/hr$. Circle and square represent statistical significance at the 5% level in station I and III respectively.

*"negative respiration" measured

prevented low values from being significant.

The reason for the lack of significant Pg in the lower depths (2.5 at station I, 3.5 and 4.5 m at station III) is uncertain. It is possible that some self-shading from the algae present in the surface depths (0.25 and 1.5 m) could have occurred at station III but it is unlikely at station I because the euphotic zone was always equal to the station depth (Figure 7).

Significant Pg at the lower depths (3.0 and 4.5 m) in station III were usually associated with a deeper euphotic zone. Normally this occurred during spring and early summer (1976), but in 1977 significant Pg was recorded at the bottom depths during mid-summer on several dates (Figure 9). A partial explanation may be that the euphotic zone was greater during mid-summer in 1977 than in 1976 (Figure 7).

During this investigation an anomalous and significantly higher oxygen content was measured in dark bottles after exposure compared to clear bottles over all depths at station III on 16 August 1977. Other researchers have attributed this effect to experimental error and withhold reporting, however this occurrence in other waters has been documented (Hutchinson 1957; Gessner and Pannier 1958; Dugdale and Wallace 1960; Vollenweider 1968; Haertel unpublished). McAllister (1961) suggested photooxidation and subsequent inhibition of photosynthesis in the clear bottle together with possible initial $O_2$ release in the dark bottle due to energy captured before being placed in the dark may be a

possible explanation for the higher values in the dark bottles. Thus, it is entirely possible for calculated gross photosynthetic rates to take on negative values, particularly at low rates of production. Negative respiration (IB - DB is negative) or anomalous production of oxygen in the dark bottle was measured on many dates (Figure 9). On most dates that negative respiration was measured, it was less than net production (LB - IB) and Pg values were positive. However, these dates were removed from the statistical analyses because Pg was probably underestimated. Negative respiration because of loss of oxygen in the IB during time to fixing could have occurred (Hutchinson 1957) but the IB's were always fixed immediately.

In two experiments Pg and Rt were measured for different exposure times. In both cases "negative respiration" occurred in the dark bottles at a greater rate during the shortened exposure times and to a lesser extent in the longer exposure times. It appears that "negative respiration" may occur initially in all of the experiments but does not show up because of the duration of the experiments and the relatively higher oxygen concentration present in the LB in the longer exposures. If so, Pg is underestimated in all cases. In any event, the results of this experiment were inconclusive and no good explanation of the higher oxygen concentration in the dark bottles can be shown.

Spatial Variation. Light and dark bottle estimates of Pg per unit area were greater in station III than station I (Table 6)

Table 6. Comparison of Area-Based and Volume-Based Open Water Means of Phytoplankton Metabolism in Lake Cochrane, 1976.

| Parameters | Station I | Station III |
|---|---|---|
| $\bar{x}$ Pg ($mgC/m^2/hr$) | 201.6 | 323.1 |
| $\bar{x}$ Rt ($mgC/m^2/hr$) | 177.8 | 362.7 |
| $\bar{x}$ Pn ($mgC/m^2/hr$) | 23.8 | -39.6 |
| $\bar{x}$ depth of euphotic zone (m) | 2.7 | 4.4 |
| $\bar{x}$ depth of water (m) | 2.7 | 6.0 |
| $\bar{x}$ Pg ($mgC/m^3/hr$) | 66.3 | 79.1 |
| $\bar{x}$ Rt ($mgC/m^3/hr$) | 63.6 | 66.2 |
| $\bar{x}$ Pn ($mgC/m^3/hr$) | 2.7 | 12.9 |

(Figure 9). Mean values of Pg exceeded Rt at station I giving a Pn value of 23.73 $mgC/m^2/hr$ but Rt exceeded Pg at station III giving a mean Pn of -39.58 $mgC/m^2/hr$. Thus, autotrophic conditions existed at station I and heterotrophic conditions prevailed at station III, probably because the total depth more greatly exceeded the euphotic zone depth at station III than at station I (Table 6).

In deep waters, examination of area-based estimates of Pg and Rt often results in false conclusions about spatial variations in the rate of metabolism. Volume-based summer means of phytoplankton metabolism show a strikingly different spatial variation than area-based estimates (Table 6). The average rates of Pg and Rt per $m^3$ of euphotic zone were only slightly higher at station III than station I (Table 6). Estimates of average Rt per $m^3$ were essentially identical at both stations (Table 6). Increases in area-based rates of Pg at station III primarily were caused by increases in euphotic zone depth and increases in Rt at station III were caused by increases in total water depth.

Temporal Variation. Temporal variation in the magnitude of Pg was large (Figure 9), but Rt is not depicted in the Figure. Patterns of variation at stations I and III were different. Gross productivity (Pg) varied from a minimum of 27 $mgC/m^2/hr$ at station I in September 1976 to a maximum of 1166 $mgC/m^2/hr$ at station III in May 1976 (Figure 9). Rt varied from a minimum of 30 $mgC/m^2/hr$ at station I in June 1976 to a maximum of 1485 $mgC/m^2/hr$ at station III in May 1976.

Patterns of seasonal variation were greatest at both stations in 1976 and were not readily described in 1977 (Figure 9). Maximum values of Pg were recorded in April and May in 1976 at both stations and in June (Station III) and September (Station I) in 1977 (Figure 9). Minimum values of Pg were recorded in June and September 1976 at both stations and in April 1977 at both stations. Increases and decreases in Pg were usually accompanied by similar increases and decreases in Rt but exceptions occurred.

Relations of Productivity and Respiration to Chlorophyll a. The relation of Pg and Rt to chlorophyll a was investigated in an effort to explain spatial and temporal variations in metabolic rates. Variations in solar radiation apparently were not the controlling factor in temporal variations of Pg and Rt (Table 7). Nutrients probably were not limiting and probably did not contribute to variations in Pg and Rt (Table 7). Correlations between Pg and Rt and chlorophyll a concentrations were not significant. Significant correlations between the log of chlorophyll a and specific Rt were recorded at the 5% level (Table 7). Significant correlations between log chlorophyll a and specific Pg were recorded at the 10% level (Table 7).

The relationship between community metabolism and chlorophyll a was investigated using simple multiple regression analyses. The years 1976 and 1977 were analyzed separately and combined. Correlations between specific Pg and log chlorophyll a and between specific Rt and log chlorophyll a were nonsignificant in 1976,

Table 7. CORRELATION MATRIX OF PHYTOPLANKTON STANDING CROP, NUTRIENTS, AND PRODUCTIVITY IN LAKE COCHRANE DURING 1976-77 OPEN-WATER SEASON, N = 22

| | Chloro a | Log Chloro a | Cells | Log cells | N | P | Si | $SiO_3$ | Ca | Mg | Na | Fe | Mn | Zn | Cu | Mo | Temperature |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chloro a | 1.00 | .94*** | .47* | .29 | -.07 | .05 | .30 | -.48* | -.60** | -.18 | .26 | .05 | .33 | -.14 | -.34 | .34 | -.43* | .54** |
| Log Chloro | | 1.00 | .52** | .43* | -.10 | .03 | .26 | -.62*** | -.70*** | -.23 | .07 | .10 | .38 | -.16 | -.34 | .39 | -.52** | .53** |
| Cells | | | 1.00 | .67*** | -.47* | -.43* | .34 | -.43* | -.67*** | -.22 | .11 | -.05 | .37 | -.25 | -.27 | .45* | -.43* | .57** |
| Log cells | | | | 1.00 | -.55** | -.44* | .32 | -.52** | -.47* | -.33 | -.24 | -.11 | .58** | -.45* | -.34 | .55** | -.54** | .44* |
| N | | | | | 1.00 | .92*** | -.57** | .02 | .07 | .21 | .12 | .12 | -.03 | .11 | .41* | .00 | .28 | -.33 |
| P | | | | | | 1.00 | -.59*** | -.05 | -.04 | .25 | .22 | .14 | -.04 | .16 | .36 | -.01 | .27 | -.21 |
| Si | | | | | | | 1.00 | .05 | -.11 | -.52** | .18 | -.15 | .38 | -.33 | -.36 | .31 | -.40* | .39 |
| $SiO_3$ | | | | | | | | 1.00 | .65*** | .04 | .27 | -.13 | -.35 | .13 | .14 | -.46* | .37 | -.29 |
| Ca | | | | | | | | | 1.00 | .05 | .15 | -.16 | -.25 | .02 | .07 | -.41* | .26 | -.49* |
| Mg | | | | | | | | | | 1.00 | .04 | .13 | -.35 | .44* | .26 | -.33 | .40* | -.04 |
| Na | | | | | | | | | | | 1.00 | -.04 | .19 | -.03 | -.07 | .15 | -.68 | .44* |
| Temperature | | | | | | | | | | | | 1.00 | .25 | .58** | -.37 | -.46* | .61** | -.58** |

*, **, and *** denotes statistical significance at the 5, 0.05, 0.01, and 0.001 levels.

however significant relationships existed in 1977 (Table 8). The 1976-77 combined regressions between specific Pg and log chlorophyll a was significant at the 10% level, and the regression between specific Rt and log chlorophyll a was highly significant (Table 8). It appears that an inverse relationship between specific Pg and log chlorophyll a and between specific Rt and log chlorophyll a exists, confirming the hypothesis put forth by Haertel (1977).

Upon examination of the respective regression equations it is apparent that there is a reproducible relationship between log of chlorophyll a and specific Pg (Table 8). All regression equations for Pg (1, 2, and 3) have remarkably similar slopes and y-intercepts (Table 8). The slopes and intercepts are also similar to those obtained for other prairie lakes (Haertel 1977).

Comparisons among $O_2$ curve, 3 point curve and L & D bottle methods. Direct comparisons of the $O_2$ curve method, 3-point curve method, and L & D bottle method were made on 22-23 May, 20-21 August 1976, and 10-11 July 1977 at station III in Lake Cochrane. The average rate of Pg as estimated by the $O_2$ curve method varied from 1.20 to 0.62 of the L & D bottle estimate (Table 9), considerably less than values reported by Talling (1957), Verduin et al (1959), and Eley (1970). A possible explanation for the discrepancies among the values involves the length of exposure time the L & D bottles received. Eley and the other investigators mentioned above maintained the classic 24 hr exposure times. The length of exposure for the L & D bottles in this study was kept

Table 8. SIMPLE REGRESSION ESTIMATES FOR PREDICTION OF SPECIFIC GROSS PRODUCTION AND SPECIFIC RESPIRATION FROM ALGAL DENSITY ESTIMATES FOR LAKE COCHRANE.

| | Years | Regression Equation | R | $R^2$ |
|---|---|---|---|---|
| 1) | 1976-77 (n = 22) | Specific Pg[a] = 10.49 - 5.57 log chlorophyll a[b] | -.34[d] | 11%[d] |
| 2) | 1970-72[c] (n = 15) | Specific Pg = 10.67 - 6.47 log chlorophyll a | -.71** | 51%** |
| 3) | 1970-72 & 1975[c] 1976-77 (n = 48) | Specific Pg = 10.03 - 5.83 log chlorophyll a | -.47** | 23%** |
| 4) | 1976-77 (n = 22) | Specific Rt[a] = 17.31 - 11.7 log chlorophyll a | -.52** | 27%** |

[a]Specific Pg and specific Rt rates in mgC/mg chlorophyll a/hr

[b]Log chlorophyll a in mg chlorophyll a/$m^3$

[c](Haertel 1977, unpublished)

[d]Significant at the 10% level

**Significant at the 1% level

Table 9. COMPARISON OF GROSS PRODUCTIVITY ESTIMATES BETWEEN THE $O_2$ CURVE, 3 POINT CURVE, AND THE LIGHT AND DARK BOTTLE METHODS. (Values in $mgO_2/m^2/day$)

| Date | Lake | $O_2$ Curve | 3 Pt Curve | L & D | Pg:Pg[a] | Pg:Pg[b] | Pg:Pg[c] |
|---|---|---|---|---|---|---|---|
| 22-23 May 1976 | Cochrane | 10.98 | 16.54 | 17.64 | 0.62 | 0.66 | 0.94 |
| 20-21 August 1976 | Cochrane | 16.70 | 11.94 | 13.92 | 1.20 | 1.40 | 0.86 |
| 10-11 July 1977 | Cochrane | 12.40 | 11.50 | 17.78 | 0.70 | 1.08 | 0.65 |
| 20-21 August 1970 | Keystone[d] Reservoir | | | | 1.95 | 1.35 | |
| 1957 | Gebel Aulia[e] Reservoir | | | | 1.90 | | |
| | Victoria | | | | 1.60 | | |
| 1959 | Erie[f] | | | | 2.00 | | |

[a] Pg:Pg ($O_2$ curve: L & D bottle)

[b] Pg:Pg ($O_2$ curve:3 Pt Curve)

[c] Pg:Pg (3 Pt curve:L & D bottle)

[d] (Eley 1970)

[e] (Talling 1957)

[f] (Verduin et al 1959)

constant and less than 6 hours (Vollenweider 1968). The reduction in the length of exposure time from 4 to 6 hrs reduces the risk of encountering the serious errors associated with the longer exposure times caused by buildup of bacteria on the inner surface of bottles (Vollenweider 1968). The shortened exposure time 4 to 6 hours was expanded to obtain day rates which could be compared with the $O_2$ curve estimates. The L & D bottle experiments were conducted during the morning hours to obtain maximum phytoplankton activity (Shalar and Untura 1970; McCaull and Platt 1977).

On 22-23 May 1976 maximum Pg was recorded shortly after sunrise and then it decreased to almost zero. The rate of Rt decreased during the day to a minimum at sunset, Rt remained low through the night, and rapidly increased to a maximum shortly before sunrise. This contradicts the findings of Eley (1970) who showed that the rate of respiration increases during the day to a maximum shortly before sunset.

On 20-21 August 1976 Pg increased in the morning, declined during mid-day, and rose to an afternoon peak rate (Figure 2). Community respiration (Rt) reached a maximum immediately after sunset and then rapidly decreased to minimum levels for the remainder of the evening. This agrees with Eley's (1970) findings and those of other investigators.

On 10-11 July 1977 Pg increased from an early morning low to a maximum at mid-day, and then remained at high levels until sunset. No values were recorded during the night this period

because of extremely adverse weather conditions, and the rate of Rt had to be assumed constant through the evening in order to make Pg and Rt calculations.

Simple Correlation and Stepwise Multiple Regression Analyses

Environmental Data. The results of simple correlation and stepwise multiple regression analyses of the dependent parameters, depth of the euphotic zone (EZ) and secchi depth (SD), for 1976, 1977, and 1976-77 are shown in Tables 10, 11, 12, and 13. The 1977 and 1976-77 EZ analyses were performed on a smaller number of samples than SD because of missing EZ data caused by faulty equipment.

The total amount of observed variation in EZ that could be predicted by multiple regression was 59% in 1976, 86% in 1977, and 52% in 1976-77 (Table 13). The total amount of observed variation in SD that could be predicted by multiple regression was 58% in 1976, 76% in 1977, and 30% in 1976-77 (Table 13).

Highly significant positive correlations between water depth and EZ were recorded for all analyses (Tables 10, 11, and 12). Highly significant negative correlation between temperature and EZ were recorded for all analyses (Tables 10, 11, and 12). Correlations between wind stress and EZ were variable (Tables 10, 11, and 12). Correlations between solar radiation and EZ were nonsignificant in 1976 and 1977, but were highly significant and negative in 1976-77 (Tables 10, 11, and 12). A highly significant correlation between seasons and EZ were recorded in 1976 (Table 10).

Table 10. CORRELATION MATRIX (R) FOR LAKE COCHRANE, MAY THROUGH SEPTEMBER 1976, n = 90

| | Chloro a | Total cells | Ortho $PO_4$-P | Nitrate-N | Silica-Si | Rain-7 day | Secchi Depth | Euphotic Zone | Water Depth | Filtering Rate | Temperature | Light-7 day | Wind-7 day | Seasons |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chlorophyll a ($mg/m^3$) | 1.00 | .21* | .24* | -.32*** | .18 | -.10 | -.53*** | -.31** | -.12 | -.05 | .28** | .11 | .36*** | -.05 |
| Algal cell counts (cells/ml) | | 1.00 | .71*** | -.46*** | .55*** | .25* | -.64*** | -.34** | -.27** | -.48*** | .61*** | -.01 | .11 | .34*** |
| Ortho $PO_4$ | | | 1.00 | -.51*** | .50*** | .28** | -.68*** | -.38*** | -.12 | -.39*** | .66*** | .14 | -.05 | .29** |
| Nitrate-N | | | | 1.00 | -.48*** | -.21 | .24* | .36*** | .05 | .15 | -.73*** | -.08 | -.41*** | -.37*** |
| Silica-Si | | | | | 1.00 | .59*** | -.27* | -.33** | -.21* | -.69*** | .31** | -.64*** | -.02 | .86*** |
| Rain-7 day ave. (cm) | | | | | | 1.00 | -.12 | -.03 | -.03 | -.44*** | .28** | -.19 | -.26* | .64*** |
| Secchi depth (m) | | | | | | | 1.00 | .25* | .14 | .31** | -.46*** | -.27* | -.05 | .06 |
| Euphotic zone (m) | | | | | | | | 1.00 | .51*** | .31** | -.46*** | .05 | -.44*** | -.36*** |
| Water depth (m) | | | | | | | | | 1.00 | .29** | -.06 | .14 | -.02 | -.14 |
| Filtering rate (%) | | | | | | | | | | 1.00 | -.15 | .53*** | .02 | -.68*** |
| Temperature (°C) | | | | | | | | | | | 1.00 | .46*** | .51*** | .25* |
| Light-7 day ave. (ly/d) | | | | | | | | | | | | 1.00 | .20 | -.67*** |
| Wind stress-7 day ave. (g/cm/s) | | | | | | | | | | | | | 1.00 | .11 |
| Seasons | | | | | | | | | | | | | | 1.00 |

Table 11. CORRELATION MATRIX (R) FOR LAKE COCHRANE, MAY THROUGH SEPTEMBER 1977, n = 81[a]

| | Chloro a | Total cells | Ortho $PO_4$-P | Nitrate-N | Silica-Si | Rain-7 day | Secchi depth | Euphotic zone | Water depth | Filtering rate | Temperature | Light-7 day | Wind-7 day | Seasons |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chlorophyll a | 1.00 | .44** | .16 | -.48*** | -.09 | .41** | -.72*** | .12 | -.20 | -.10 | .48*** | -.22 | .45** | --- |
| Algal cell counts | | 1.00 | -.05 | -.44*** | .31** | .44*** | -.60*** | -.17 | -.03 | .45*** | .36*** | -.37*** | -.19 | .36*** |
| Ortho $PO_4$-P | | | 1.00 | -.04 | -.20 | .01 | -.04 | -.16 | -.07 | -.34** | -.04 | .04 | .17 | -.50*** |
| Nitrate-N | | | | 1.00 | -.47*** | -.14 | .63*** | .05 | .24* | -.12 | -.36*** | .55*** | .27* | -.45*** |
| Silica-Si | | | | | 1.00 | -.17 | -.34** | .05 | -.13 | .23* | .18 | -.79*** | -.54*** | .86*** |
| Rain-7 day ave. | | | | | | 1.00 | -.27* | -.25 | -.01 | .18 | .20 | .27* | -.11 | -.11 |
| Secchi depth | | | | | | | 1.00 | .03 | .31** | -.18 | -.45*** | .53*** | .40*** | -.40*** |
| Euphotic zone | | | | | | | | 1.00 | .71*** | -.28 | -.40** | -.15 | .26 | --- |
| Water depth | | | | | | | | | 1.00 | .00 | .01 | .22* | .02 | -.15 |
| Filtering rate | | | | | | | | | | 1.00 | .04 | -.32** | -.11 | .44*** |
| Temperature | | | | | | | | | | | 1.00 | .07 | -.34** | .06 |
| Light-7 day ave. | | | | | | | | | | | | 1.00 | .26* | -.75*** |
| Wind stress-7 day | | | | | | | | | | | | | 1.00 | -.49*** |
| Seasons | | | | | | | | | | | | | | 1.00 |

[a] n = 45 for chlorophyll a and euphotic zone correlations because of incomplete data

Table 12. CORRELATION MATRIX (R) FOR LAKE COCHRANE, MAY THROUGH SEPTEMBER 1976-77, n = 171[a]

| | Chl-a | Total cells | Ortho $PO_4$-P | Nitrate-N | Silica-Si | Rain-7 day | Secchi depth | Euphotic zone | Water depth | Filtering rate | Temperature | Light-7 day | Wind-7 day | Seasons |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chlorophyll a | 1.00 | .12 | .22* | -.31*** | .07 | .24* | -.58*** | -.22* | .17 | -.06 | .33*** | -.05 | .45*** | --- |
| Algal cell counts | | 1.00 | .21** | -.32*** | .32*** | .18* | -.52*** | -.09 | .17 | -.02 | .52*** | -.12 | .07 | .35*** |
| Ortho $PO_4$-P | | | 1.00 | .05 | .14 | .25** | -.06 | -.16 | .06 | -.32*** | .26** | -.12 | -.09 | -.19* |
| Nitrate-N | | | | 1.00 | -.24** | .09 | .59*** | .12 | .19* | -.07 | -.24** | .21** | -.06 | -.34*** |
| Silica-Si | | | | | 1.00 | .20* | -.26** | -.01 | -.11 | -.06 | .21** | -.79*** | -.25** | .73*** |
| Rain-7 day ave | | | | | | 1.00 | -.16* | .07 | .04 | .09 | .12 | -.18* | -.24** | -.04 |
| Secchi depth | | | | | | | 1.00 | .17* | .25** | -.06 | -.36*** | .26** | .07 | -.25** |
| Euphotic zone | | | | | | | | 1.00 | .60*** | .04 | -.43*** | -.22** | -.16 | --- |
| Water depth | | | | | | | | | 1.00 | .13 | -.03 | .13 | -.03 | -.15 |
| Filtering rate | | | | | | | | | | 1.00 | -.06 | -.01 | -.02 | -.07 |
| Temperature | | | | | | | | | | | 1.00 | .22** | .34*** | .17* |
| Light-7 day ave | | | | | | | | | | | | 1.00 | .29** | -.59*** |
| Wind-7 day ave | | | | | | | | | | | | | 1.00 | -.01 |
| Seasons | | | | | | | | | | | | | | 1.00 |

[a] n = 126 for chlorophyll a and euphotic zone correlations

Table 13. MULTIPLE REGRESSION RESULTS FOR LAKE COCHRANE, APRIL THROUGH OCTOBER, 1976-77

| Dependent variable | Year Dates n | 1976 complete 90 | | 1977 complete 81[b] | | 1976-77 complete 171[c] | |
|---|---|---|---|---|---|---|---|
| Chlorophyll a | | | | | | | |
| | Multiple regression Variance ($r^2$) predicted by variables in order of importance[a] | WP | .13** | T | .23** | SD | .33** |
| | | P | .07** | WP | .41** | WP | .18** |
| | | Seasons | .03** | LP | .11** | R | .05* |
| | | Si | .19** | EZ | .01* | FR | .05* |
| | | T | .02* | D | .01* | T | .02* |
| | | LP | .06* | R | .01* | P | .01* |
| | | | | FR | .04* | | |
| | | | .49* | | .81* | | .64* |
| Algal cell counts | | P | .49** | FR | .21** | T | .27** |
| | | Si | .05* | N | .15** | Seasons | .07** |
| | | T | .04* | R | .11** | P | .02* |
| | | Seasons | .03* | LP | .05** | R | .01* |
| | | | .65* | | .58* | | .39* |
| Euphotic zone | | D | .26** | D | .50**[b] | D | .36** |
| | | T | .19** | LP | .09** | T | .12* |
| | | WP | .06* | FR | .20** | LP | .04* |
| | | Seasons | .04* | WP | .04* | | |
| | | R | .03* | A | .03* | | |
| | | | .59* | | .86* | | .52* |

Table 13 (continued)

| Dependent variable | 1976 complete 90 | | 1977 complete 81[b] | | 1976-77 complete 171[c] | |
|---|---|---|---|---|---|---|
| Secchi depth | T | .22** | T | .20** | T | .13** |
| | Fr | .06** | LP | .29** | LP | .12** |
| | Seasons | .22** | R | .06** | D | .04* |
| | WP | .02* | D | .03* | WP | .02* |
| | LP | .03* | Seasons | .02** | | |
| | R | .03* | WP | .16** | | |
| | | .58* | | .76* | | .30* |
| Ortho $PO_4$-P | T | .44** | Seasons | .25** | FR | .10** |
| | WP | .20** | LP | .25** | R | .08** |
| | FR | .06* | WP | .03* | Seasons | .04** |
| | R | .07* | | | LP | .06** |
| | C | .02* | | | T | .16** |
| | Seasons | .02* | | | | |
| | LP | .02* | | | | |
| | | .83* | | .53* | | .45** |
| Nitrate-N | T | .54** | LP | .30** | Seasons | .12** |
| | LP | .07* | T | .16** | A | .10** |
| | FR | .04* | R | .05* | T | .03* |
| | | | FR | .02* | WP | .01* |
| | | | | | R | .02* |
| | | .65* | | .54* | | .27* |

[a] $r^2$ of .75 explains 75% of the variation in the dependent variable.

[b] Chlorophyll a and euphotic zone, n = 45

[c] Chlorophyll a and euphotic zone, n = 125

In the EZ multiple regressions water depth explains 26% in 1976, 50% in 1977, and 36% in 1976-77 of the total variation (Table 13). Temperature accounted for 19% in 1976 and 12% in 1976-77 of the total variation in EZ, but it did not appear significant in the 1977 regression equation (Table 13). Wind stress explains 6% in 1976 and 4% in 1977 of the total variation in EZ but it was nonsignificant in the 1976-77 regression equation (Table 13). Solar radiation accounted for 9% in 1977 and 4% in 1976-77 of the total EZ variation but it was nonsignificant in the 1976 regression (Table 13). Occasionally, prior rainfall, filtering rate, algal cell counts, and seasons were significant in the EZ regression equations but they did not account for a very large fraction of the total predictable variation (Table 13).

Significant positive correlations were recorded between water depth and SD in 1977 and 1976-77; it was nonsignificant but positive in 1976 (Tables 10, 11, and 12). Highly significant negative correlations between temperature and SD were recorded for all analyses (Tables 10, 11, and 12). Correlations between wind stress and SD were variable (Tables 10, 11, and 12). A significant negative correlation between solar radiation and SD was recorded in 1976, but it was highly significant and positive in 1977 and 1976-77 (Tables 10, 11, and 12). Highly significant negative correlations between seasons and SD were recorded for all analyses (Tables 10, 11, and 12).

In the SD multiple regressions, water depth explains 3% in

1977 and 4% in 1976-77 but it was nonsignificant in 1976 (Table 13). Temperature accounted for 22% in 1976, 20% in 1977, and 13% in 1976-77 of the total variation in SD (Table 13). Wind stress explains 2% in 1976, 16% in 1977, and 2% in 1976-77 of the variation in SD (Table 13). Solar radiation predicted 3% in 1976, and 2% in 1977, but it was nonsignificant in the 1976-77 regression equation (Table 13). Occasionally, rain and filter rate appeared significant in the SD regression equations but they did not account for a very large fraction of the predictable variation (Table 13).

Inorganic Plant Nutrients. The results of simple correlation and multiple regression analyses of the dependent variables, ortho $PO_4$-P and $NO_3$-N, are shown in Tables 10, 11, 12, and 13. The total amount of observed variation ortho $PO_4$-P that could be predicted by multiple regression was 83% in 1976, 53% in 1977, and 45% in 1976-77 (Table 13). The total amount of variation in $NO_3$-N that could be explained by multiple regression was 65% in 1976, 54% in 1977, and 27% in 1976-77 (Table 13).

Highly significant positive correlations between temperature and ortho $PO_4$-P were recorded in 1976 and in 1976-77, but it was nonsignificant in 1977 (Tables 10, 11, and 12). Correlations between wind stress and ortho $PO_4$-P were nonsignificant for all years (Tables 10, 11, 12). Highly significant positive correlations between rain and ortho $PO_4$-P were recorded in 1976 and in 1976-77, but it was nonsignificant in 1977 (Tables 10, 11, and 12). Highly significant negative correlations between

zooplankton filtering rate and ortho $PO_4$-P were recorded for all analyses (Tables 10, 11, and 12). Correlations between seasons and ortho $PO_4$-P were highly significant and positive in 1976, highly significant and negative in 1977, and significant and negative in 1976-77 (Tables 10, 11, and 12). Correlations between algal standing crop and ortho $PO_4$-P were usually significant (Tables 10, 11, and 12).

In the ortho $PO_4$-P multiple regressions temperature accounted for 44% in 1976 and 16% in 1976-77 of the total variation but was not significant in 1977 (Table 13). Wind stress explained 20% in 1976 and 3% in 1977 of the variation in ortho $PO_4$-P but was nonsignificant in 1976-77 (Table 13). Rain predicted 7% in 1976 and 8% in 1976-77 of the total variations in ortho $PO_4$-P but was nonsignificant in 1977 (Table 13). Zooplankton filtering rate accounted for 6% in 1976 and 10% in 1976-77 of the variation in ortho $PO_4$-P but was nonsignificant in 1977 (Table 13). Seasons explained 2% in 1976, 25% in 1977, and 4% in 1976-77 of the variation in ortho $PO_4$-P (Table 13). Chlorophyll *a* accounted for 2% of the variation in ortho $PO_4$-P in 1976 but was nonsignificant at other times (Table 13).

Highly significant negative correlations between temperature and $NO_3$-N were recorded for all analyses (Tables 10, 11, and 12). A highly significant negative correlation between wind stress and $NO_3$-N was recorded in 1976 but was significant and positive in 1977, and nonsignificant in 1976-77 (Tables 10, 11, and 12).

Correlations between rain and $NO_3$-N were nonsignificant for all analyses (Tables 10, 11, and 12). Correlations between zooplankton filtering rate and $NO_3$-N were also nonsignificant for all years tested (Tables 10, 11, and 12). Highly significant negative correlations between seasons and $NO_3$-N were recorded for all analyses (Tables 10, 11, and 12). Highly significant negative correlations between both algal cell counts and $NO_3$-N were recorded for all analyses (Tables 10, 11, and 12). Highly significant positive correlations between solar radiation and $NO_3$-N were recorded in 1977 and in 1976-77 but it was nonsignificant in 1976.

In the $NO_3$-N multiple regressions temperature accounted for 54% in 1976, 16% in 1977, and 3% in 1976-77 of the total variations (Table 13). Only 1% of the variations in $NO_3$-N (1976-77) could be predicted by wind stress (Table 13). Rain explained 5% in 1976 and 2% in 1976-77 of the $NO_3$-N variation, but was nonsignificant in the regression equation in 1977 (Table 13). About 12% of the variation in $NO_3$-N (1976-77) could be predicted by seasons (Table 13). Only 10% of the variation in $NO_3$-N (1976-77) could be predicted by algal cell counts (Table 13). Whereas, 7% in 1976 and 30% in 1977 of the $NO_3$-N variation could be predicted by solar radiation (Table 13).

Phytoplankton Standing Crop. The results of simple correlation and multiple regression of the dependent parameters, chlorophyll a and total algal cell counts for 1976, 1977, and 1976-77 appear

in Tables 10, 11, 12, and 13. The 1977 and 1976-77 chlorophyll a analyses were performed on a smaller number of samples than cell counts because of missing chlorophyll a data.

The total amount of variation that could be predicted by multiple regression for chlorophyll a was 49% in 1976, 81% in 1977, and 64% in 1976-77 (Table 13). The total amount of variation in cell counts that could be predicted by multiple regression was 65% in 1976, 58% in 1977, and 39% in 1976-77 (Table 13).

Highly significant positive correlations between wind stress and chlorophyll a was recorded for all analyses (Tables 10, 11, and 12). Highly significant positive correlations between temperature and chlorophyll a were also recorded for all analyses (Tables 10, 11, and 12). Highly significant positive correlations between rain and chlorophyll a were recorded in 1977 and in 1976-77 but in 1976 it was nonsignificant (Tables 10, 11, and 12). Correlations between solar radiation and chlorophyll a were nonsignificant for all analyses (Tables 10, 11, and 12).

In the chlorophyll a regressions wind stress accounted for 13% in 1976, 41% in 1977, and 18% in 1976-77 of the variation (Table 13). Temperature predicted 2% in 1976, 23% in 1977, and 2% in 1976-77 of the total chlorophyll a variation (Table 13). Secchi depth explained 33% of the chlorophyll a variation in 1976-77 but was nonsignificant in 1976 and in 1977 (Table 13). Only 4% in 1977 and 5% in 1976-77 of the variation in chlorophyll

a was predicted by filtering rate (Table 13). About 7% in 1976 and 8% in 1976-77 of the chlorophyll a variation was predicted by ortho $PO_4$-P (Table 13). Occasionally, silicate, seasons, euphotic zone, and water depth were significant in the chlorophyll a regression equations but they did not account for a very large fraction of the predictable variation (Table 13).

Highly significant positive correlations between temperature and cell counts were recorded for all analyses (Tables 10, 11, and 12). Correlations between filtering rate and cell counts were significant for 1976 and 1977 but not in 1976-77 (Tables 10, 11, and 12). Highly significant positive correlations between ortho $PO_4$-P and cell counts were recorded in 1976 and in 1976-77 but not in 1977 alone (Tables 10, 11, and 12). Highly significant negative correlations between $NO_3$-N and cell counts were recorded for all analyses (Tables 10, 11, and 12).

In the cell count multiple regressions temperature accounted for 4% in 1976, 7% in 1977, and 27% in 1976-77 of the total variation (Table 13). Filtering rate explained 4% in 1976 and 21% in 1977 of the cell count variation (Table 13). In multiple regressions ortho $PO_4$-P predicted 49% in 1976 and 2% in 1976-77 of the variations in cell counts (Table 13). Nitrate-N accounted for 15% in 1977 and 2% in 1976-77 of the cell count variation (Table 13). Occasionally, silicate, rain, solar radiation, and seasons appeared significant in the multiple regression equations but they did not account for a very large fraction of the

predictable variation (Table 13).

# DISCUSSION

## Interactions Between Environmental Measurements and Algal Standing Crop

The reduced lake depth during 1976-77 might partially account for the increased turbidity levels. A reduction in lake dpeth would result in an increase in the area of the lake bottom sediments affected by wind action. Direct stirring of the sediments by wind sometimes results in increased nutrient concentrations (Haertel 1976a; Wetzel 1976). However, based on the correlations there is no evidence of wind generated release of ortho $PO_4$-P from the lake sediments. Correlations with $NO_3$-N were extremely variable and the results are inconclusive. Perhaps phosphorus was being regenerated but the phytoplankton assimilated the free phosphorus as it was made available since the turnover time for ortho $PO_4$ is about 20 minutes (Wetzel 1976). This could also partially explain the very low (0.02 mg/l) ortho $PO_4$ values measured on most sample dates in Lake Cochrane.

Increased turbidity may also be attributed to silt and nutrients carried with runoff. Based on the highly significant positive correlations between rain and ortho $PO_4$ in 1976 and 1976-77 it is possible that phosphorus may have been transported into the lake with runoff (Tables 10 and 11). Most likely the phosphorus would be leached from the exposed soil in the sediment control dam construction area. Another source could be fertilized lakeshore lawns (Moss 1972). The leached phosphorus

would probably be complexed as a calcium triphosphate form (White et al 1977). Since rain water is slightly acidic (Wetzel 1976) it is conceivable that some of the complexed phosphorus would be converted to an inorganic form, some of which would be ortho $PO_4$ (White personal communication).

The additional nutrients could stimulate an increase in phytoplankton activity and result in reduced water transparency. The significant positive correlations between rain and cell counts and rain and chlorophyll a indicate that some nutrients may have been entering the lake with runoff water and may have influenced increases in phytoplankton activity (Tables 10, 11, and 12).

The effect of increasing phytoplankton standing crop on water clarity is shown by the highly significant negative correlations between total cells and secchi depth and between chlorophyll a and secchi depth both years (Tables 10, 11, and 12). The data suggests that significant quantities of certain nutrients or silt were entering the lake with runoff water and influenced decreases in secchi depth directly, or indirectly by stimulating phytoplankton activity.

Total kjeldahl nitrogen, $NO_3$-N, total $PO_4$, and ortho $PO_4$ levels were higher in 1976-77 than levels measured in previous years (Haertel 1972, 1977). However, phytoplankton standing crop estimates did not exhibit a parallel increase.

An enigmatic question that remains unsolved involves the lack of a "bloom response" by the phytoplankton community to the

increased nutrient levels. It has been shown that bluegreen algae can reproduce at minute ortho $PO_4$ levels (0.01 mg/l, Wetzel 1976). The levels of ortho $PO_4$ present in Lake Cochrane at all stations exceeded the minimal amount throughout the summer, yet no appreciable bloom occurred. Algal species were most likely nitrogen limited in 1976, as no inorganic nitrogen was measured during most of the summer. Although higher levels of inorganic nitrogen were present in 1977 the N:P elemental ratios were still lower than the required 7.2:1 (N:P) ratios determined for planktonic algae by Redfield (1934) and by Richards and Vaccaro (1956). However, Anacystis cyanea is capable of absorbing sufficient phosphorus and nitrogen from an environment high in these elements and later utilizing these elements when they are deficient (Gerloff and Skoog 1954). Perhaps zooplankton grazing prevented a large build-up of phytoplankton. In any event more work is needed in the area of nutrient cycling and phytoplankton response to environmental stimulii before these questions can be satisfactorily answered.

Unusually low chlorophyll a values recorded on 10 June 1976 may be a reflection of the grazing pressure of the Daphnia (Figure 7). It has recently been shown that zooplankton, especially Daphnia, can exert an influence on the phytoplankton standing crop much in the same way that terrestrial grazers affect grasses in pastures (Porter 1977). Reduced chlorophyll a values at all stations on 10 June 1976 (Figure 7) appear closely aligned with increased

*Daphnia* numbers (Figure 8). Total algal cells also show some inhibition at stations I and III, but it is not as obvious as the chlorophyll *a* measurements (Figure 7). On 28 June 1976 at station I both algal cell counts and chlorophyll *a* showed an increase (Figure 7) and *Daphnia* collapsed (Figure 8). At station III *Daphnia* numbers increased from 65,000 to 80,000 on 28 June 1976. This large increase in *Daphnia* apparently caused algal cell count estimates to remain at their previous levels in station III (Figure 7). No apparent effect was noted in the chlorophyll *a* values (Figure 7). On the following sample date (16 July 1976) *Daphnia* numbers declined to less than 2000 organisms/$m^3$ at all stations (Figure 8). Peak algal cell counts and high chlorophyll *a* values were coincident with the decline in *Daphnia* numbers (Figures 7 and 8). The *Daphnia* remained low throughout the rest of this study, however, a pulse was recorded at stations I and III on 14 October 1976 (Figure 8). The station III phytoplankton standing crop estimates also show some depletion and may be attributed to the grazing pressure of the *Daphnia* (Figure 7). In 1977, *Daphnia* did not attain large numbers and no obvious effect on algal standing crop was apparent from the data (Figure 7).

Increases in secchi depth at both stations were associated with the peak *Daphnia* concentrations and reduced phytoplankton standing crop (Figures 7 and 8). Secchi depth values showed a gradual increase from 5 May to 10 June 1976 (Figure 7). Mean secchi depth values increased from 1.2 on 5 May to 1.3 m on 10 June;

the values decreased to 1.0 m on 28 June, and further declined to 0.65 m on 16 July 1976.

A highly significant negative linear correlation between zooplankton filtering rate and total algal cell counts in 1976 implies that a reduction in algal biomass resulted from the grazing action of the zooplankters (Table 10). The highly significant positive correlations between filtering rate and secchi depth and between filtering rate and euphotic zone in 1976 also implies an increase in water transparency as a result of the grazers (Table 10). The grazing pressure of zooplankton, especially Daphnia, can influence increases in water transparency (Porter 1977, Haertel, M.S. submitted to Ecology).

The importance of temperature in regulating phytoplankton metabolic rates surfaces in the chlorophyll a and cell count linear correlations and multiple regressions (Tables 10, 11, 12, and 13). The highly significant positive correlations between wind stress and chlorophyll a imply a phytoplankton response to the wind action. Possibly, the wind action kept the cells in circulation throughout the water column, thereby reducing the amount of time the cells would remain at the surface. The reduction in the length of time the cells were near the surface would probably lower the risk of encountering light inhibition.

The simple regressions estimates of the log chlorophyll a against specific Pg imply an inverse relationship between the variables (Table 8). High rates of Pg and Rt occur at low

chlorophyll a levels, and low rates of Pg and Rt occur at high chlorophyll a levels. The maximum rates of Pg and Rt were associated with spring and early summer sampling dates; periods when diatoms and unidentified green micro cells were abundant. The lower Pg and Rt values usually occurred during mid- and late summer, periods of abundant, large, macroscopic bluegreen colonies. This agrees with the inverse size metabolism law (Hutchinson 1957). The large colony size lowers the metabolism of the interiorly located cells, possibly by reducing the amount of available nutrients. Lake Cochrane is well-suited to describe this relationship because it normally hosts abundant single-celled diatoms and greens in spring and large concentrations of macroscopic bluegreen colonies in mid- and late summer.

It is difficult to make any definite conclusions concerning the comparison of the $O_2$ curve to the L & D bottle based on only three experiments. Different Pg:Pg ratios were obtained for each experiment. The August 1976 daytime Pg and Rt and nighttime Rt curves agree closely with results of Eley (1970) and his calculated results for eutrophic Kadel Pond, Florida, but slopes indicating a different time of maximum respiration and Pg were found on the other two dates suggesting that diurnal maximums in metabolic rates do not always occur at the same time of the day.

# CONCLUSIONS

The negative effects of the construction of the sediment control dams masked the positive effects of their implementation. The most apparent effect was the reduction in water transparency. Since chlorophyll *a* and cell count values were similar to previous years, the reduction must have been caused by the influx of silt. Based on the significant negative correlations between rain and secchi depth it seems that silt was entering the lake. The source of the silt probably was the exposed soil on the steep slopes of the sediment dam construction site.

The variability recorded among stations in phytoplankton standing crop and zooplankton standing crop necessitates measurement at several locations on different sampling dates. It appears that environmental conditions, especially wind, can have an effect on plankton distribution in prairie lakes. The variability recorded among stations in inorganic nutrients was insignificant. Thus nutrients need be measured at only one location in the lake.

The L & D bottle method successfully measured significant differences between the LB and DB treatments on most sampling dates. The differences between the L & D bottle and the $O_2$ curve method were not as great as those mentioned in the literature. Based on the small number of comparisons between the two methods it appears that either method would suffice. The advantage of the $O_2$ curve method is that it provides an estimate of the 24 hour

Pg and Rt curves, but the L & D bottle does not.

The similarity between regression equations of specific Pg indicates that there is a reproducible inverse relationship with the log of chlorophyll a. As chlorophyll a concentrations increase, Pg decreases. The largest chlorophyll a concentrations were recorded during early summer, periods of abundant macroscopic bluegreen colonies. The fact that lowered Pg values were associated with the larger colonies agrees with the inverse size metabolism law (Hutchinson 1957).

Restriction of silt and dissolved nutrients is critical if eutrophication is expected to be halted (Felderman and Eno 1977). The influx of silt will probably be diminished by the sediment control dams. However, the fertilized lakeshore lawns may be a significant non-point source of inorganic nitrogen and phosphorus. The need for a study of the nutrient and silt loading is apparent.

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