MONTANA STATE UNIVERSITY

An investigation of the general limnology of Georgetown Lake, Montana
by Jonathan Charles Knight

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Botany
Montana State University
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Abstract:
Georgetown Lake, located at an elevation of 1960 m (msl) 17 miles west of Anaconda, Montana, is the most heavily used lake for its size (1479 ha, 4.89 m mean depth, 10 m maximum depth) in Montana. Little information was available to assess its trophic state. Therefore, the primary purpose of this investigation was to provide baseline data to assess the principal limnological factors in Georgetown Lake.

The yearly heating cycle in Georgetown Lake was typical of a temperate, dimictic lake, but, due to the shallow depth, stratification did not develop in the summer. The depth of one percent light penetration averaged 7.2 m during the summer, but the ice-cover reduced penetration 55-82%. Heating and cooling patterns were a function of meteorological conditions during the summer, but, under the ice, water temperatures were a function of heat input from the sediment.

Georgetown Lake was characterized by relatively high dissolved solids (mean conductivity of 212 µmhos cm^-2), principally as calcium-magnesium carbonates. Sodium and chloride concentrations were very low, indicating negligible sewage input, During the summer, dissolved oxygen was at or above saturation levels, carbon dioxide was typically undersaturated, and calcium carbonate percipitation occurred. Under the ice, comparison of the average rate of total inorganic carbon gain to the water column (6.5 to 15.7 mmole m^-2 day^1) and oxygen loss (7 mmole m^-2 day^-1) to mean plankton respiratory rates (0.08 mmole C m^-2 day^-1 and 0.05 mmole O2 m^-2 day^-1) suggest that the sediment was the major site of decomposition. Anaerobic respiration reduced the oxidation-reduction potential at least to a point where sulfate was reduced. Consequently, carbon dioxide, iron, phosphate, nitrite, nitrate, ammonia, bicarbonate, and calcium increased to the yearly maximum observed values.

Total phosphate (mean 26 µg l^-1) and total nitrogen (mean 370 µg l^-1) fluxes could not be attributed to changes in inorganic concentrations nor external nutrient loading, including groundwater. Since the reservoir exhibited a net annual loss of nutrients and external loading models predicted an oligiotrophic classification, the major mechanism controlling phosphate and nitrogen availability appeared to be internal loading and recycling rates. The difference of maximum summer total phosphorus between the two summers (18.5%) was attributed to a difference of lake levels (-7%) suggesting the importance of internal mechanisms.

Georgetown Lake may be classified as eutrophic or mesotrophic based on summer phytoplankton standing crops (17.0 and 2.7 gC m^-2, principally as Anabaena flos-aquae). The total phytoplankton production throughout the summer was 38 gC m^-2 (0.25 gC m^-2 day^-1) indicating an oligotrophia condition. These high standing crops and relatively low production rates imply that most of the phytoplankton production was required for maintenance of the populations.

Phytoplankton were probably of little significance with respect to overall trophic dynamics in Georgetown Lake, since phytoplankton standing crops averaged less than 5% of the total organic

carbon; phytoplankton net production was less than one-fifth the zooplankton production; planktonic respiration rates were consistently greater than phytoplankton gross production; and sport fish yields (32 lbs acre^-1 yr^-1) were very high. These data suggest that the primary organic base in Georgetown lake was the macrophyte-epiphyte associations and subsequent detrital pathways.

Fisheries management of Georgetown Lake should involve the main-tance of the macrophyte populations and attempt to keep water levels high, particularly during the winter to minimize potential fish kills.

High water levels during the summer would tend to reduce the blue-green populations.

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A thesis submitted in partial fulfillment
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ABSTRACT

Georgetown Lake, located at an elevation of 1960 m (msl) 17 miles west of Anaconda, Montana, is the most heavily used lake for its size (1479 ha, 4.89 m mean depth, 10 m maximum depth) in Montana. Little information was available to assess its trophic state. Therefore, the primary purpose of this investigation was to provide baseline data to assess the principal limnological factors in Georgetown Lake.

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Georgetown Lake was characterized by relatively high dissolved solids (mean conductivity of 212 $\mu mhos \cdot cm^{-2}$), principally as calcium-magnesium carbonates. Sodium and chloride concentrations were very low, indicating negligible sewage input. During the summer, dissolved oxygen was at or above saturation levels, carbon dioxide was typically undersaturated, and calcium carbonate percipitation occurred. Under the ice, comparison of the average rate of total inorganic carbon gain to the water column (6.5 to 15.7 $mmole \cdot m^{-2} \cdot day^{-1}$) and oxygen loss (7 $mmole \cdot m^{-2} \cdot day^{-1}$) to mean plankton respiratory rates (0.08 $mmoleC \cdot m^{-2} \cdot day^{-1}$ and 0.05 mmole $O_2 \cdot m^{-2} \cdot day^{-1}$) suggest that the sediment was the major site of decomposition. Anaerobic respiration reduced the oxidation-reduction potential at least to a point where sulfate was reduced. Consequently, carbon dioxide, iron, phosphate, nitrite, nitrate, ammonia, bicarbonate, and calcium increased to the yearly maximum observed values.

Total phosphate (mean 26 $\mu g \cdot l^{-1}$) and total nitrogen (mean 370 $\mu g \cdot l^{-1}$) fluxes could not be attributed to changes in inorganic concentrations nor external nutrient loading, including groundwater. Since the reservoir exhibited a net annual loss of nutrients and external loading models predicted an oligiotrophic classification, the major mechanism controlling phosphate and nitrogen availability appeared to be internal loading and recycling rates. The difference of maximum summer total phosphorus between the two summers (18.5%) was attributed to a difference of lake levels (-7%) suggesting the importance of internal mechanisms.

Georgetown Lake may be classified as eutrophic or mesotrophic based on summer phytoplankton standing crops (17.0 and 2.7 $gC \cdot m^{-2}$, principally as Anabaena flos-aquae). The total phytoplankton production throughout

the summer was 38 $gC \cdot m^{-2}$ (0.25 $gC \cdot m^{-2} \cdot day^{-1}$) indicating an oligotrophic condition. These high standing crops and relatively low production rates imply that most of the phytoplankton production was required for maintenance of the populations.

Phytoplankton were probably of little significance with respect to overall trophic dynamics in Georgetown Lake, since phytoplankton standing crops averaged less than 5% of the total organic carbon; phytoplankton net production was less than one-fifth the zooplankton production; planktonic respiration rates were consistently greater than phytoplankton gross production; and sport fish yields (32 $lbs \cdot acre^{-1} \cdot yr^{-1}$) were very high. These data suggest that the primary organic base in Georgetown lake was the macrophyte-epiphyte associations and subsequent detrital pathways.

Fisheries management of Georgetown Lake should involve the maintance of the macrophyte populations and attempt to keep water levels high, particularly during the winter to minimize potential fish kills. High water levels during the summer would tend to reduce the blue-green populations.

INTRODUCTION

Georgetown Lake, located on the Warm Springs Creek and Flint Creek Divide in the Clark Fork drainage of western Montana, is the most heavily used lake for its size in Montana (Georgetown Lake Pre-Study 1973). The lake, with an average catch rate of 1.5 fish per man-hour in 1973, sustains nearly four percent of the total sport fishing effort in the state of Montana. In addition to fishing, the drainage area provides seasonal and permanent residences, boating, swimming, skiing, horseback riding, camping, and snowmobiling. Also, water is removed from Georgetown Lake for irrigation, hydroelectric power generation, and industrial purposes. Recreational and residential development in the Georgetown watershed was estimated by Lutey et al. (1974) to have an annual growth rate of 18%. Because of the existing and potential developmental trends of the watershed, Deer Lodge and Granite county commissioners and members of conservation districts have become concerned as to the trophic status of the reservoir. Georgetown Lake is considered eutrophic due to periodic blooms of blue-green algae, extensive macrophyte growth, and occasional winter fish kills. In addition, the Montana Department of Fish and Game has estimated that Georgetown Lake is at the limit of eutrophication compatible with a salmonid fishery.

The concepts of oligotrophy and eutrophy, first used by Weber (1907) to describe plant associations in European bogs, were applied to lakes with phytoplankton populations of varying sizes by Naumann (1919). Thiene-

mann (1925) reasoned that continual input of nutrients from the watershed increased biological production, which, in turn, reduced the hypolimnetic oxygen concentrations. Additionally, he hypothesized that the trend from oligotrophy resulted in more organic material being produced than was oxidized. Lindeman (1942) further suggested that the trend of oligotrophy to eutrophy also reduced the efficiency of energy transfer between the 'trophic levels'. However, even though the efficiency of transfer may be reduced, the production of 'higher trophic levels' may increase with increasing eutrophy. For example, fish production was greatly enhanced by artificial fertilization of ponds (Hasler and Einsele 1948; and Hayes 1951). Currently, the term eutrophication is applied to natural or artificial (man-induced) nutrient addition to a body of water (National Academy of Sciences 1969).

The early concepts of eutrophication were challenged by Juday and Birge (1931) who pointed out that in Wisconsin lakes there was no evidence of the loss of phosphorus from the water as algal populations were maintained or even increased. In addition, Pearsall (1932) reported that blue-green algal blooms were observed when nutrients were deficient in the water. Rawson (1939) suggested that a lake's trophic status was the result of climatic conditions, edaphic factors, and the morphometric characteristics of the lake basin, and, under some circumstances, human activities. Rawson's (1939) morphometric hypothesis proposed that the contribution of littoral or shoreline areas to the total productivity of

a lake decreased geometrically as lake volume increases, i.e., as mean depth increases. This geometric relationship becomes increasingly important in shallow lakes with fluctuating water levels, such as small reservoirs. Empirical relationships derived by Northcote and Larkin (1956), Hayes and Anthony (1964), and Ryder (1965) showed good correlation between edaphic factors (e.g., total dissolved solids), and mean depth and plankton standing crops and/or fish yields of various sized lakes.

The importance of edaphic factors and morphometric characteristics has led to the development of models which relate nutrient input and some morphometric characteristic(s) to some index of lake trophic status, e.g., maximum or mean phytoplankton standing crop, phytoplankton production, or oxygen deficits. These models have typically centered on phosphorus since phosphorus was considered to be the major nutrient limiting plant growth. Vollenweider (1968) used external phosphorus and nitrogen loading (usually as $g \cdot m^{-2} \cdot yr^{-1}$) to estimate lake trophic status. Further refinements of such models to include mean depth (Vollenweider 1970), retention time (Vollenweider 1975), fraction of phosphorus retained in the lake (Vollenweider and Dillon 1974) or various other modifications (Schindler, et al. 1978) have been used to assess lake trophic conditions. All of these models assume that lake phosphorus concentrations are a function of phosphorus which is transported into the lake, usually on an annual basis.

Hutchinson (1941) could not attribute the phosphorus fluxes in Lindsley Pond to external loading, but rather attributed the observed concentration

changes to internal mechanisms. These proposed internal mechanisms were involved in transfer rates between the sediments and the overlying water, which resulted from continual decomposition of plankton and littoral vegetation and subsequent 'recycling' of nutrients. Rigler (1956, 1964), using radioactive phosphorus, determined that ionic phosphorus in the epilimnion had turnover times as low as one minute. However, Lean and Charlton (1977) observed that phosphorus exchange rates between algal cells and the free water were a function of phosphorus demand and concentration. In addition, Lean and Charlton (1977) demonstrated that direct phosphorus release from the sediment under aerobic conditions was greater than most external loading values reported by Vollenweider (1968). Additional internal loading via macrophytes has been reported by Carignan and Kalff (1980) and suggested by Lehman and Sandgren (1978) Even though Carignan and Kalff (1980) demonstrated macrophyte uptake at ^{32}P from within the sediments and subsequent release to the water column, the relationships between macrophyte-epiphyte and phytoplankton utilization of phosphorus in the free water are not known. But, the total phosphorus in the water column has been attributed to phytoplankton sinking rates (Hutchinson 1941; Lean and Charlton 1977; Lehman and Sandgren 1978) with subsequent removal of phosphorus. After analysis of phosphorus and phytoplankton grab samples, the U. S. Environmental Protection Agency (1976) concluded that Georgetown Lake was eutrophic. In addition, the E.P.A. utilized the Vollenweider and Dillon (1974) model to estimate the phosphorus loading into Georgetown Lake. However, their data could only account for 18% of the calculated

loading to surface water inputs. The loading model considered the effects of only external factors on the trophic status of the lake. But, since Georgetown Lake is shallow and apparently very productive, both internal and external mechanisms could affect the lake trophic status. However, except for fish creel surveys and periodic dissolved oxygen measurements under the ice, quantitative data on Georgetown Lake were not available. Therefore, the major purpose of this investigation was to provide basic limnological data to assess the primary mechanisms and/or potential mechanisms of nutrient dynamics in Georgetown Lake. Sediment data (Garrison 1976), zooplankton dynamics (Geer 1977), and periphyton collections (Foris 1976), along with this report encompass the overall Georgetown Lake study. The specific objectives of this portion of the overall investigation were to:

1. document the heating and cooling regime of Georgetown Lake,
2. relate oxygen and carbon dioxide concentrations to physical and/or biological activities,
3. provide evidence to establish the major nitrogen and phosphorus inputs to the water column, and,
4. assess the relative importance of phytoplankton to biological activity in Georgetown Lake.

HISTORY AND DESCRIPTION OF THE STUDY AREA

Georgetown Lake, a reservoir formed by the impoundment of Flint Creek, is located at latitude 46°10'16" N, longitude 113°10'42" W, in the Clark Fork drainage 17 miles west of Anaconda, Montana (Fig. 1). Patented mining claims in the Georgetown area were established as early as 1862. Cattle were first grazed on the Georgetown meadow ten years later. In 1885, a small earthen dam was built across Flint Creek by the Montana Water Electric and Power Company to provide power for the Bi-Metallic Mining Company at Phillipsburg. The Anaconda Copper Mining Company purchased the dam in 1901 and constructed a masonry dam to an elevation 1958.1 m above mean sea level. At that time, the Montana Power Company installed a power house. In 1919, the Anaconda Company raised the dam to the present level of 1959.7 m. The Montana Power Company acquired the entire project in 1925 and in 1966 strengthened the structure and constructed a two-lane highway across the dam (Beal 1953; Georgetown Lake Pre-Study 1973). Currently, rights to the water in Georgetown Lake are shared by the Montana Power Company, the Anaconda Mining Company, and irrigation concerns in the Phillipsburg valley.

At maximum pool elevation, the lake is 7.05 km long with a maximum and mean breadth of 3.64 km and 1.72 km, respectively, and a surface area of 1479.2 ha. The mean depth is 4.89 m with a maximum depth of 10.67 m. Table 1 presents the ranges of morphometric data observed during the study. Figure 2 illustrates the area and water volumes associated with lake elevations.

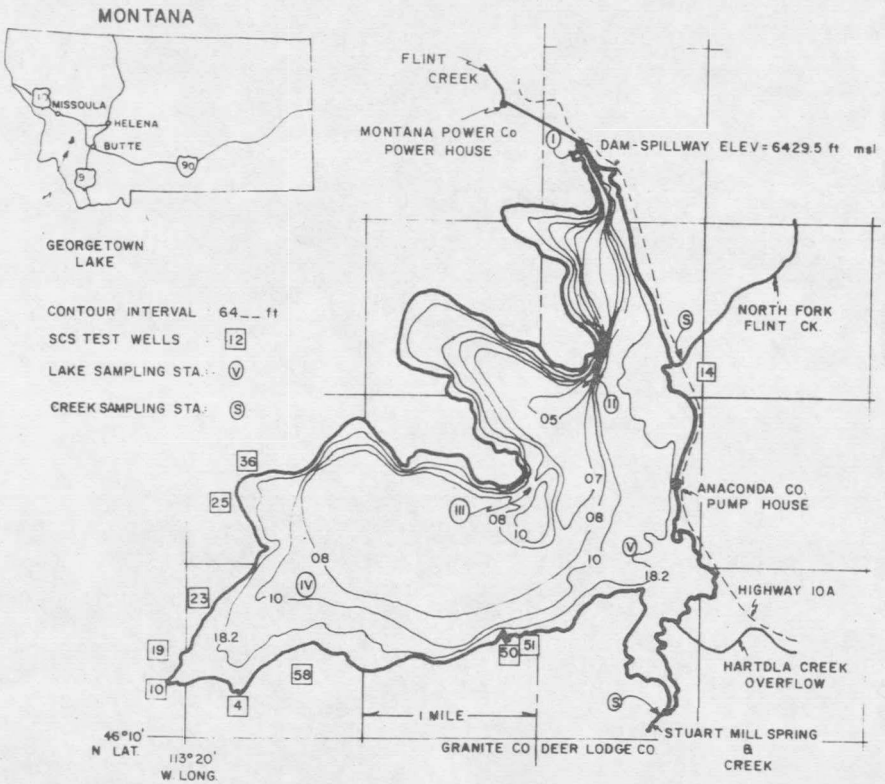


Figure 1. Sampling Locations on Georgetown Lake, Montana.

Table 1. Morphometric Data of Georgetown Lake, Montana, from 10 July, 1973 through 16 June, 1975.

	Full Pool	Range
Surface Elevation[1]	1959.7 m	1958.3-1959.3 m
Maximum Depth[1]	10.67 m	9.27-10.27 m
Mean Depth[2]	4.89 m	3.9-4.6 m
Maximum Length	7.05 km	7.00-7.03 km
Maximum Breadth	3.64 km	3.56-3.60 km
Mean Breadth[2]	1.72 km	1.56-1.67 km
Length of Shoreline	26.87 km	24.6-26.2 km
Shoreline Development[2]	2.18	2.11-2.16
Surface Area[1]	1219.2 Ha	1100-1200 Ha
Mean Retention Time		
summer	804 days	337-6112 days
winter	493 days	

[1]Supplied by Anaconda Co., Anaconda, MT.

[2]Definition of these parameters in Reid (1961)

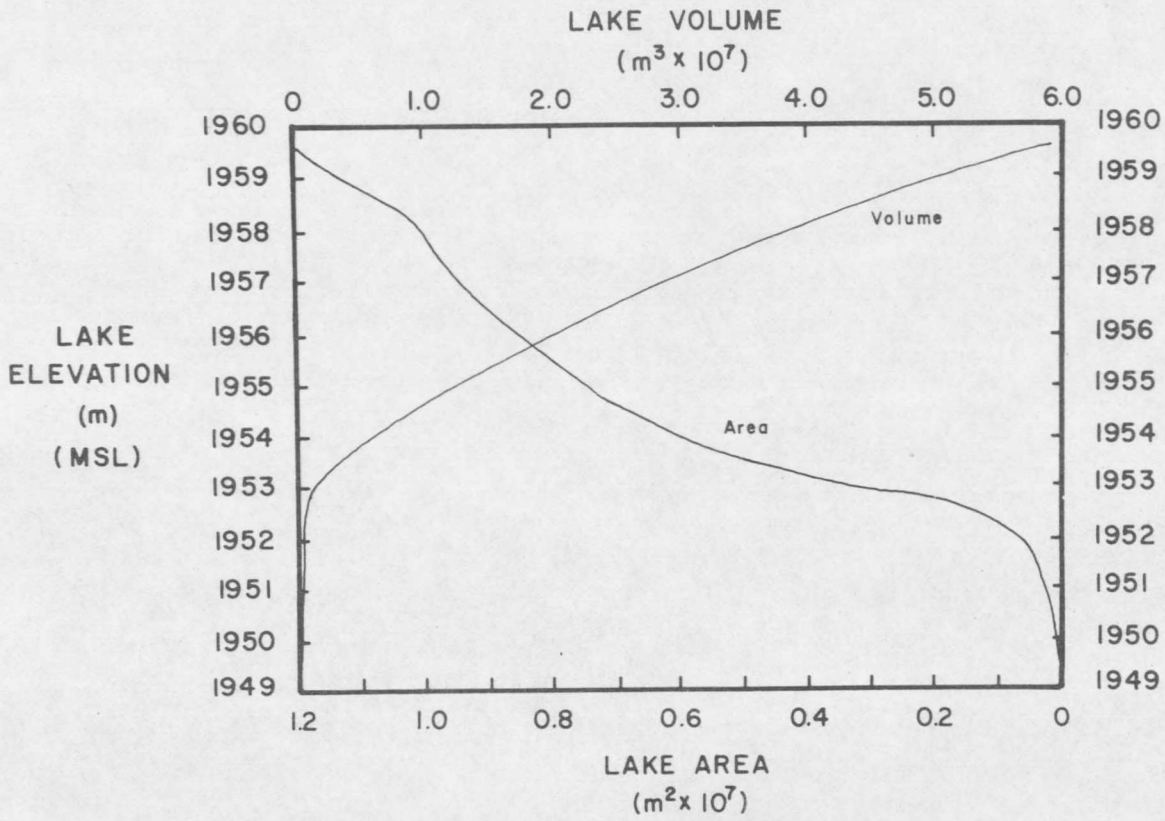


Figure 2. Relationship of the Volume and Area of Georgetown Lake, Montana, to the Lake Elevation.

The structures associated with outflows from the lake are summarized in Knight et al. (1976). Throughout the study period, however, the Montana Power Company's hydroelectric facility and Anaconda Company's pumping to Silver Lake were the only water withdrawals from the lake.

The lake receives surface water from several principal sources, and, presumably groundwater originating within its 13,728 ha drainage. The North Fork of Flint Creek discharges surface water into the lake from a drainage area of approximately 4895 ha. Flint Creek originates in the area of Fred Burr Pass, and flows past old mines and the most developed section of the lake watershed. Stewart Mill Creek originates from a spring 200 m from the lake. The spring receives its flow from a drainage area of approximately 4222 ha. Hardtla Creek, a return flume from Silver Lake controlled by the Anaconda Mining Company, has a capacity of 1.13 $m^3 \cdot sec^{-1}$. The remaining area of 4611 ha, excluding Flint Creek and Stewart Mill watersheds, presumably discharges groundwater to the lake.

A complete geologic history of the Georgetown Lake drainage can be found in Alt and Hyndman (1972). Briefly, the area is characterized by deposition in shallow sea, uplift, and subsequent erosion leaving a fretted upland of maximum elevation of 3004 m. Non-metallic resources such as limestone, clay, and gravel are abundant in the area.

METHODS AND MATERIALS

Biological, chemical, and physical data were collected at biweekly, triweekly, or monthly intervals from 10 July, 1973, to 16 June, 1975. Five sampling stations were established within the lake (Fig. 1). Station I was located in the main channel in the vicinity of the dam. Stations II and III were adjacent to Rainbow Point and Piney Point, respectively. Station IV was in Jericho Bay and Station V was located at the mouth of Stewart Mill Bay (Fig. 1).

Sampling points were also established on the creeks: the North Fork of Flint Creek was sampled at the bridge on Highway 10A; Stewart Mill Creek samples were taken at the bridge on the road to the south of the lake; and Flint Creek was sampled below the lake at the power house outflow. During the winter months, ice and snow cover usually limited sampling to only Station I and the creeks. In addition, at the request of the Soil Conservation Service, Phillipsburg, Montana, ten test wells were sampled on 24 July, 1975.

Light

Instantaneous solar radiation incident upon the reservoir surface was measured with either a Kipp and Zonen Model CM-3 or a Kahl Scientific pyranometer, and was continuously recorded with an Esterline Angus, Model 80-M recorder. These instruments were installed at Montana Fish and Game Department cabins located on the North Fork of Flint Creek. Integration

of the corrected instantaneous readings with respect to time yielded Langley·hr^{-1} or Langley·day^{-1}.

A vertical profile of light penetration was obtained by taking readings at one meter intervals with a Kahl Scientific submarine photometer containing a Weston Model B56 selenium photocell. Extinction coefficients per meter were calculated by the equation of Hutchinson (1957).

Temperature and Conductivity

Temperature was recorded at all lake sampling locations at one meter intervals using a Yellow Springs Oxygen Meter equipped with an electronic thermistor. Conductivity, corrected to μmhos·cm^{-2} at 25°C, was measured in the laboratory at a frequency of 1 KH_z with a Yellow Springs AC Conductivity Bridge, Model 31.

Meteorology

Hourly air and dew point temperatures, wind speed and barometric pressure data from the Butte, Montana, airport were provided by the National Climatological Center, Asheville, North Carolina. The hourly values were averaged to estimate daily averages, which, in turn, were averaged for mean meteorological conditions between sampling dates. All values were corrected for altitude differences and subsequent adiabatic effects according to Blair (1942).

Water Chemistry

All lake water samples, with the exception of those for oxygen determinations, were collected with a 3 liter polyvinylchloride Van Dorn type water bottle. Oxygen concentrations were measured either *in situ* with a Yellow Springs Oxygen Meter or by the Winkler technique as modified by Strickland and Parsons (1972) following collection with a sewage sampler. All samples at Station I were collected at two-meter intervals. Collections at other lake stations were made at three-meter intervals. The influent and effluent waters were collected directly into reagent bottles.

Immediately after collection, one liter of water was filtered through a Gelman Type A glass fiber filter. The filter was then immersed in a darkened centrifuge tube containing five ml of 90% acetone. Also, 500 ml of the filtrate was saved in an acid-washed glass reagent bottle for inorganic nutrient analysis. A 300-ml glass reagent bottle was filled with unfiltered water for alkalinity, chloride, and conductivity determinations.

Concentrations of Na, K, Ca, and Mg were determined by atomic emission-absorption spectroscopy using an Instrumentation Laboratory AA/AE Model 131 spectrophotometer. Alkalinity and chloride were determined titrimetrically as described by APHA (1971). Sulfate was determined turbidimetrically as described by APHA (1971) but utilizing Hach

Chemical Co. Sulfate Ver(R) III. The pH was determined with a Beckman Expanded Scale pH meter, Model 76. Inorganic carbon species were calculated from pH, total alkalinity, and temperature, using the equations of Rainwater and Thatcher (1960).

Concentrations of nitrogen and phosphorus species (filtered and unfiltered water) were determined colorimetrically with a Klett-Summerson spectrophotometer using the following tests: NH_3-N by the hypochlorite oxidation method of Strickland and Parsons (1972); NO_3-N by the reduction method of Mullin and Riley (in Barnes 1962); NO_2-N using Hach Chemical Co. reagents and procedures; total Kjeldahl nitrogen using sulfuric acid and potassium sulfate digestion and the hypochlorite oxidation method of Strickland and Parsons (1972); ortho-PO_4-P by the combined reagent method in Strickland and Parsons (1972); total phosphorus using acid and persulfate digestion and the combined reagent method in Strickland and Parsons (1972).

Iron and silica were determined colorimetrically with a Klett-Summerson spectrophotometer using the following tests: Iron using Hach Chemical Co. Ferro Zine(R); silica using the molybdosilicate complex method in APHA (1971).

Floride was analyzed colorimetrically using Hach Chemical Co. SPANS reagent.

Total organic carbon was measured with a Beckman Laboratory Carbonaceous Analyzer.

Phytoplankton Standing Crop

A 125-ml whole water phytoplankton sample, collected simultaneously with the water chemistry sample, was preserved with Lugol's solution. Later in the laboratory, discrete (Station I) and composite (Stations II, III, IV, V) samples were uniformly resuspended, and an appropriate volume was concentrated according to the membrane filter technique (APHA 1971). The phytoplankton cells were counted at two magnifications (150X and 1500X) until 100 individuals of at least one taxon were enumerated at each power. Taxa recorded under one magnification were not counted under the other power.

Phytoplankton cells were measured to obtain mean cell volume and mean cell surface area per taxon, by assuming appropriate geometric formulae. Standing crop estimates were expressed as cell density, cell volume, and cell surface area per cubic meter ($No.\cdot m^{-3}$, $mm^3\cdot m^{-3}$, and $mm^{-2}\cdot m^{-3}$, respectively).

Phytoplankton organisms were identified to the lowest practical taxonomic division. Prescott (1962), Smith (1950), and Drouet (1959) were used for identification of all taxa except the Bacillariophyceae. The diatoms were identified by use of FWPCA Bulletin (1966), Patrick and and Reimer (1966), and Hustedt (1930).

The standing crop of phytoplankton was also estimated from pigment concentrations. The 90% acetone extract was analyzed with a Beckman DU-2 spectrophotometer for chlorophylls a, b, and c, phaeo-pigments, and carotenoids according to Strickland and Parsons (1972).

Community Metabolism

Samples used to measure carbon metabolism were collected simultaneously with the chemical samples, while samples used for oxygen metabolism were collected in a 'sewage sampler'. All samples were collected from two-meter intervals at Station I. The unfiltered water was collected in 300-ml BOD bottles which were previously treated as described by the USEPA (1969), wrapped in aluminum foil to minimize light exposure, and autoclaved. The clear (aluminum foil was removed immediately prior to the lowering of samples) and opaque BOD bottles were incubated three to six hours *in situ* at the depth from which they were collected. The BOD bottles were suspended from plexiglass bottle holders similar to those described by Schindler and Holmgren (1971).

Oxygen metabolism was measured by changes in the dissolved oxygen concentration between an initial sample and the samples incubated in the light and opaque bottles. Dissolved oxygen was determined by titration with a microburet using the modified Winkler reagents for high concentractions of organic matter (APHA 1971; Strickland and Parsons 1972). This technique could detect an oxygen change of $\geq$ 35 mg $O_2 \cdot m^{-3}$.

Carbon metabolism based on pH changes was determined by calculating the change of inorganic carbon concentration (Rainwater and Thatcher 1960) between an initial sample and the incubated water samples. The pH was measured in the field using a Beckman Expanded Scale pH meter, Model 76. Alkalinity was determined by constructing titration curves (meq. acid vs pH) and interpolating the meq acid titrate at the inflection point (consistently at pH 4.5). The use of an expanded-scale pH meter and titration curves provided optimium sensitivity to detect a change of inorganic carbon concentration. Carbon metabolism based on radioactive carbon labelling was measured as the rate of accumulation of radioactive carbon into the particulate ($\geq$ 0.45 µm) and dissolved fractions collected in the clear and opaque bottles. Immediately prior to incubation, the samples were inoculated with 10 µCi of sterile $NaH^{14}CO_3$ solution (specific activity of 1.0 µCi·10µg $NaHCO_3$) obtained from New England Nuclear. The mean recoverable activity from the 10µCi inoculation into 300 ml lake water was 9.5 µCi $\pm$ 0.25 µCi. Immediately after the incubation period, the spiked samples were preserved with one ml of one percent merthiolate solution and stored on ice. Upon return to the laboratory, two ten ml and two twenty-five ml aliquots were filtered through separate 25-mm, 0.45 µm Millipore(R) HAWP membrane filters. The remaining portion was filtered through a 47-mm, 0.45 HAWP filter. One hundred ml of 0.002 N HCl was passed through each filter to remove the inorganic carbon contamination reported by Arthur and Rigler (1967). The entire filtrate was

combined, acidified with one meq HCl, and purged 20 minutes with compressed nitrogen. After purging, one meq NaOH was added to neutralize the filtrate. The filtrate was concentrated to approximately five ml by vacuum distillation at 30°C. Each 25 mm filter and 0.2 ml of the concentrated filtrate was placed in separate Beckman polyethylene scintillation vials. Absolute methanol (4 ml) was added as a secondary solvent and 12 ml of Toluene-PPO-POPOP was added as the scintillation cocktail. All samples were counted on a Packard Tri-Carb Liquid Scintillation spectrophotometer and corrected to dpm by the sample channels ratio method. All radiocarbon data, expressed as carbon assimilated per cubic meter were calculated from the equation of Strickland and Parsons (1972).

RESULTS AND DISCUSSION

PHYSICAL PARAMETERS

Optical Properties

The monthly mean daily incident solar radiation (Q_s) ranged from 78 Langley·day^{-1} in December to 712 in June (Table 2, Fig. 3). The total annual incident radiation received at Georgetown Lake was 149,000 Langley, with 80,000 Langley received during the heating period (from 1 April to 31 July, as defined by Hutchinson (1957)). The latter value agrees well with Steinhawser's (1939, cited in Hutchinson 1957) estimate of 83,000 Langley received in middle Europe at a similar latitude and altitude as Georgetown.

The net radiation (Q_s'), i.e., incident radiaton (Q_s) minus that reflected and/or absorbed by ice cover, ranged from 9 to 676 Langley·day^{-1}. Reflected radiation, measured by difference with a submarine photometer, averaged 5% during the ice-free period and ranged from 55-83% during ice cover. The albedo was not well defined with respect to ice thickness, but, as Bauer and Dulton (1960) have indicated, the crystalline structure of ice and snow greatly influence the albedo and ice absorptivity.

Photosynthetically active radiation (PAR) was calculated according to Vollenweider's (1974) estimate of 47% the value recorded by a pyranometer. PAR entering the water column at Georgetown ranged from a low of 9 Langley·day^{-1} in January to a high of 318 in June (Table 2, Fig. 3).

Table 2. Summary of the Monthly Mean Light Intensities and Extinction Coefficients, Georgetown Lake, Montana.

Month	Q_S Monthly Mean Daily Solar Radiation ($Ly \cdot day^{-1}$)	Q_S' Monthly Mean Daily Incident Radiation Entering ($Ly \cdot day^{-1}$)	Q_{PAR} Photosynthetically Active Radiation Entering The Water Column ($Ly \cdot day^{-1}$)	Mean Extinction Coefficient (m^{-1})
January*	97	9	9	0.71
February*	227	18	18	0.60
March*	404	37	37	0.73
April*	654	57	57	0.85
May*	585	126	126	0.93
June	712	676	318	0.61
July	658	625	294	0.71
August	593	563	265	0.75
September	462	439	206	0.67
October	327	311	146	0.45
November*	97	21	21	0.43
December*	78	13	13	0.59

*Months of ice cover

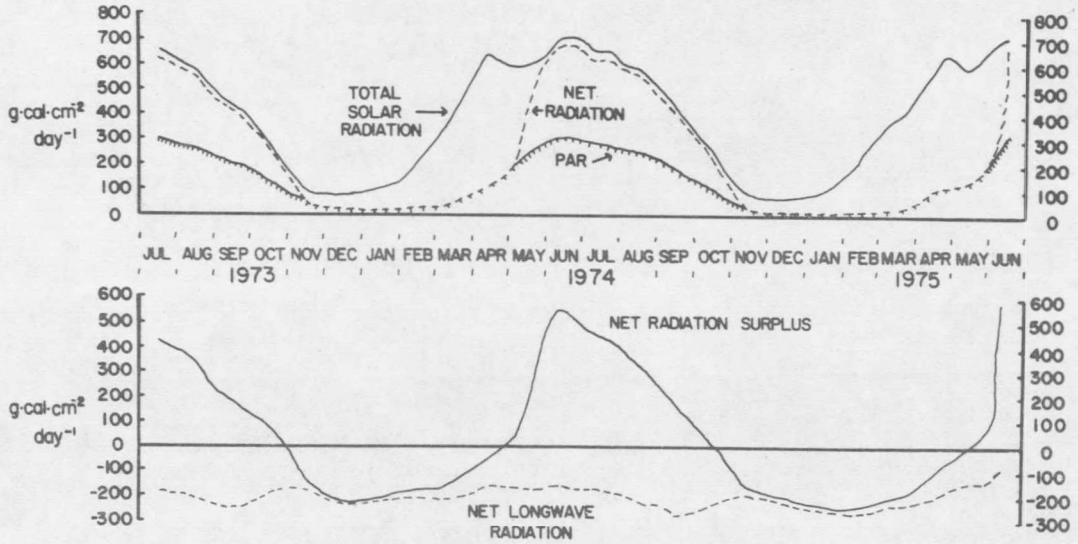


Figure 3. Seasonal Distribution of Total Radiation, Net Radiation, Photosynthetically Active Radiation, Net Longwave Radiation, and Net Radiation Surplus Incident to Georgetown Lake, Montana, 1973-75.

The difference between the net radiation (Q_s') and PAR (Q_{PAR}) represents the ultraviolet and infrared radiation absorbed within the first few centimeters of water (Hutchinson, 1957). However, according to Pivorarov (1972), ice and snow transmitted light only from 400 to 700 μm. Hence, the net radiation and PAR were equal during the period of ice cover.

From the air temperature and cloud cover data, Swinbank's formula (in Ryan and Harleman 1973) was used to calculate the atmospheric longwave radiation (Q_A). Ryan and Harleman's (1973) equation was used to calculate longwave radiation from the water surface (Q_w). The resultant net longwave radiation (Q_A-Q_W) ranged from -271 to -91 Langley·day^{-1} (Fig. 3). The lowest values occurred during the autumn cooling period when atmospheric temperatures were lowest relative to the water temperatures. Conversely, the highest net longwave values occurred immediately after ice melt when air temperatures were highest relative to water temperatures.

The net radiation surplus (Q_B=Q_S'+Q_A-Q_W), as defined by Hutchinson (1957), generally paralleled Q_S during the ice-free season and the net longwave radiation during the ice-covered period. The seasonal trends (Fig. 3) followed the observations reported in Hutchinson (1957) and Dutton and Bryson (1962), with the absolute differences dependent upon the incident solar radiation and climatic conditions.

The light attenuation in the water column (Fig. 4) indicated a

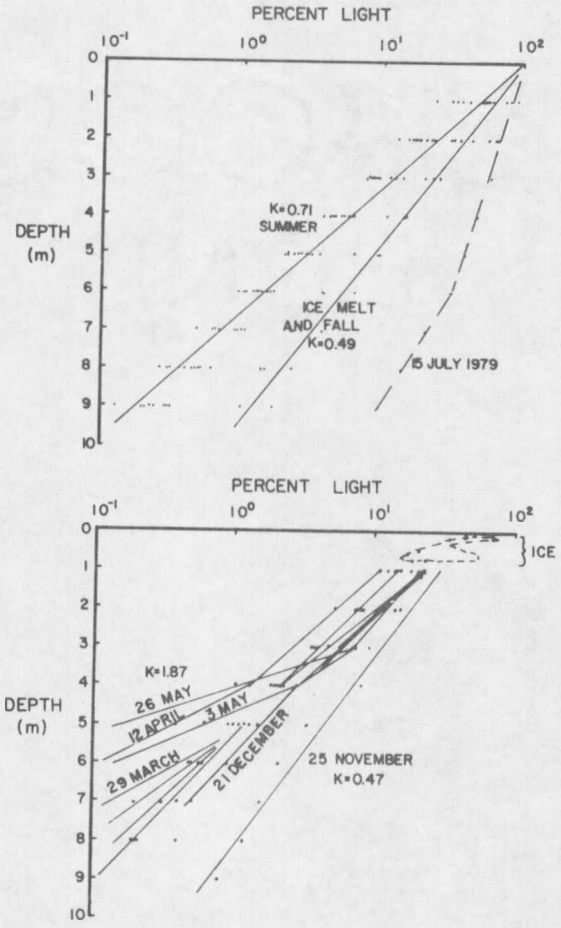


Figure 4. Percent Light Penetration in Georgetown Lake, Montana, as a Function of Depth during 1973-75.

relatively homogeneously mixed water column during the ice free period, while two distinct water strata were indicated throughout the duration of ice cover. The lower extinction coefficients (k=0.49) found prior to the formation of ice cover and shortly after the ice melted and by fairly constant values (k=0.71) throughout the summer indicate increased dissolved or particulate matter followed by fairly uniform concentrations throughout the summer with a decrease of matter prior to ice formation. Conversely, progressively higher extinction coefficients (k_{max}=1.87) observed throughout the ice-covered period in the lower layers indicate an accumulation of material below 3 to 4 meters. As mentioned previously, light transmittance through the snow and ice cover varies with thickness and crystalline structure, but the extinction coefficients (Fig. 4) in the upper 3 to 4 m remain fairly constant throughout the winter, indicating relatively constant concentrations of matter in the upper layer.

Thermal Properties

Lake and Equilibrium Temperatures

Georgetown Lake may be classified as a temperate lake (Hutchinson 1957) since summer temperatures were above 4°C while winter temperatures were below 4°C. Although chemical stratification and inverse thermal stratification were observed under the ice (Fig. 5), the lake cannot be strictly classified as dimictic since lake morphometry (specifically, a shallow mean depth (4.3 m) and significant wind fetch) prevented the development of a thermocline during the ice-free period.

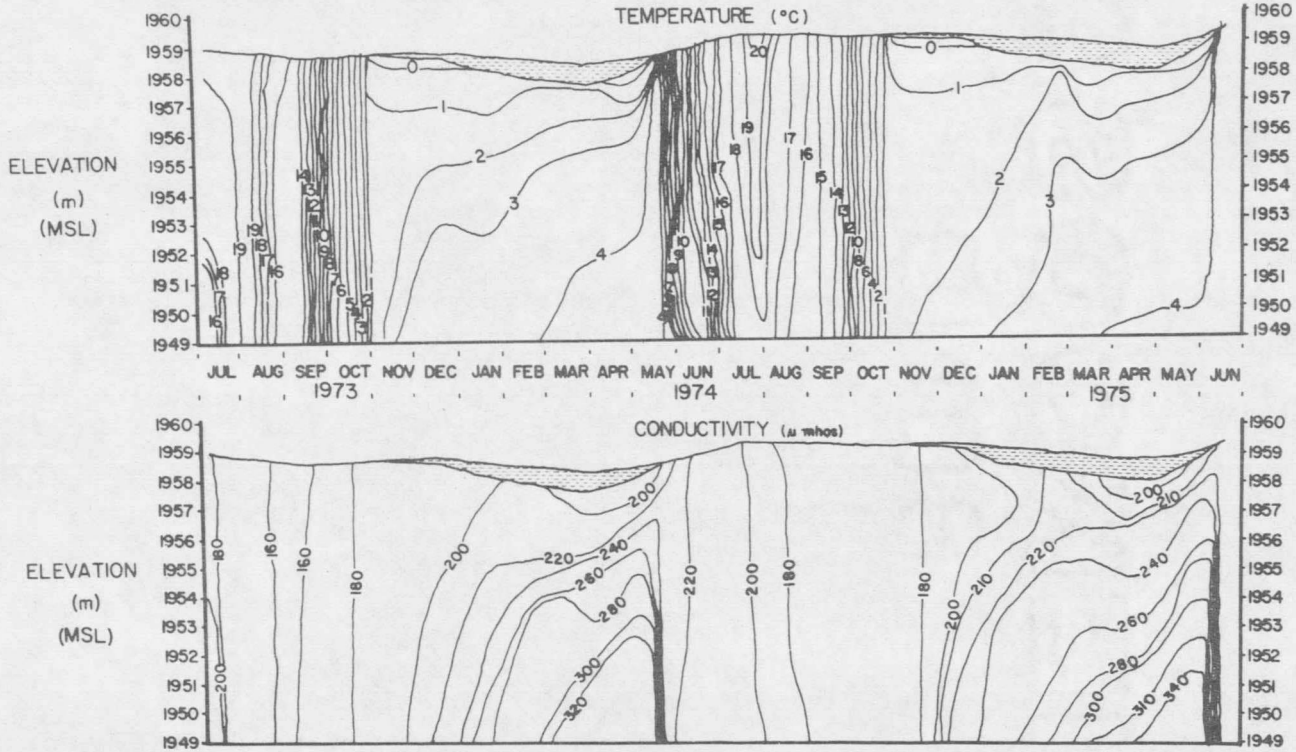


Figure 5. Seasonal and Vertical Distribution of Temperature and Conductivity in Georgetown Lake, Montana, 1973-75.

After ice melt, a period of rapid warming occurred which resulted in lake temperatures between 16 and 20°C throughout July and August of each year (Fig. 5). The lake cooled substantially during September and October until ice cover formed on or about the first of November each year (Anaconda Co. records). As suggested from the lower temperatures throughout the water column in November and December of 1974, wind-distributed heat was more pronounced prior to ice formation compared to 1973. Even though temperatures gradually increased throughout the water column during the 1974-75 period of ice cover, temperatures lagged behind those observed in 1973-74. Assuming relatively equal heating rates under the ice, this lag effect probably resulted from the greater loss of heat prior to ice formation in 1974. Slight depressions of isotherms in March 1975, and late April 1974, indicate some degree of ice melt. However, in May 1975, a depression of the isotherms did not accompany ice melt which indicated a high rate of heating of melt water. Schindler et al. (1974) attributed similar temperature increases directly under the ice in arctic lakes to high incident solar radiation.

Heating and cooling of lakes as a function of meteorological conditions may be examined by comparison of lake temperatures with the equilibrium temperature (Ryan and Harleman 1973). The equilibrium temperature, defined as the theoretical temperature the water would attain at a given set of meteorological conditions, is given by:

$$Q_S + Q_A = 4x10^{-8}(T_E+460)^4+f_{(W)}[(e_E-e_a)+0.255(T_E-T_a)]$$

where,

$Q_S + Q_A$ = net incoming radiation ($BTU \cdot ft^{-2} \cdot day^{-1}$)

T_E = equilibrium temperature (°F)

T_a = air temperature (°F)

$f_{(W)}$ = wind speed function

e_E = saturated vapor pressure (monthly) at T_E

e_a = vapor pressure (monthly) at T_a

During the ice-free season, the mean lake temperature ($\overline{T}_w$) followed the equilibrium temperature (Fig. 6), indicating that lake temperatures were a function primarily of meteorological conditions. [T_E was greater than $\overline{T}_w$ during the heating period, indicating a net transfer of heat from the atmosphere to the water through the lake surface. During the fall cooling period, $\overline{T}_w$ was greater than T_E, indicating a net transfer of heat from the lake to the atmosphere.] Even though meteorological conditions had little influence on lake water temperatures under the ice, the formation and duration of ice was greatly influenced by meteorological conditions. The formation of ice on or about the first of November each year coincided with T_E falling below 0°C. The rate of ice accumulation peaked on the first of January each year, which corresponded to the time of maximum negative equilibrium temperatures. Also, the duration of equilibrium temperatures below 0°C was 18 days longer in 1975 than in 1974; this period agrees well with the 23 days longer ice cover observed

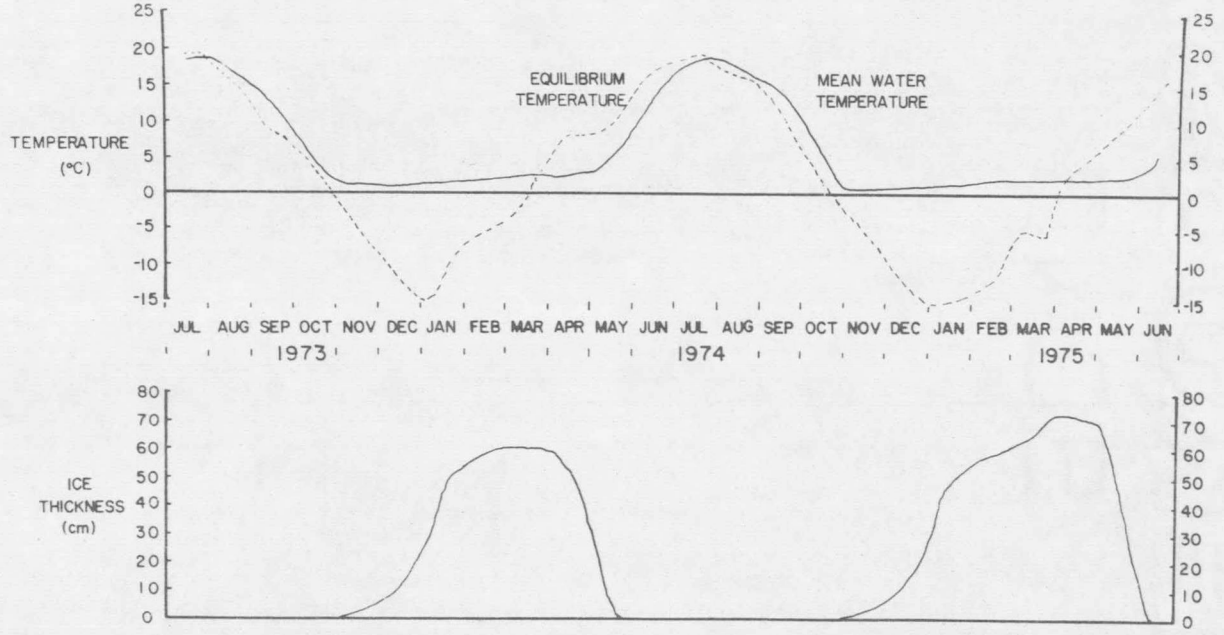


Figure 6. Seasonal Distribution of Mean Water Temperature, Equilibrium Temperature, and Ice Thickness of Georgetown Lake, Montana, 1973-75.

in 1975. In addition, the equilibrium temperature degree days (calculated from 0°C as $\Sigma T_E \cdot$day) during the 1975 ice thaw was 23% greater than during the period of ice melt in 1974. Again, this value agrees well with the 20% greater number of ice days (calculated as Σcm·day from $T_E>0$) in 1975 as compared to 1974. The seasonal patterns of T_E, $\overline{T}_w$, and ice thickness indicate that meteorological conditions were the primary factors influencing lake temperatures during the periods of open water, ice formation, and the duration of ice cover. Meteorological conditions did not contribute substantially to the gradual water temperature increase throughout the period of ice cover.

Analytical Heat Budget

Specific rates of heat gain and loss to Georgetown Lakewere calculated using the general energy equation presented by Hutchinson (1957),

$$Q_\Theta = Q_s' + Q_A - Q_w - Q_E - Q_e + Q_c + Q_m + Q_p - Q_I + Q_i$$

where all values are expressed as $g \cdot cal \cdot cm^{-2} \cdot day^{-1}$,

Q_Θ = rate of storage of heat in lake

Q_s' = net incoming shortwave radiation

Q_A = atmospheric longwave radiation

Q_w = longwave radiation from water surface

Q_E = latent heat of evaporation

Q_e = energy lost in heating evaporated water

Q_c = energy gain (or loss) from conduction
e.g., sensible heat during ice-free period,
ice conduction during ice-covered period,

Q_m = heat gain (or loss) from lake sediments

Q_p = heat gain (or loss) from precipitation

Q_I = energy loss in heating frozen water (not latent heat of fusion)

Q_i = net energy flux by advection (including ground water)

Hutchinson's (1957) general energy equation was not applied to heat exchange rates within and above the ice cover, but rather heat exchange rates of only the liquid water.

The Q_A and Q_w terms were significant only during the ice-free period, since the black body emmissivity values of liquid water and ice were equal (Kothandaraman and Suramanyan 1977). Hence, the net exchange of longwave radiation between the two water phases was equal to zero. Also, as described by Pivovarov (1972), only shortwave radiation (400 to 700 μm) penetrates the ice cover. Therefore, the $Q_s'+Q_A-Q_w$ term 'net radiation surplus' was equal to a fraction (0.47 Q_s') of the net radiation during ice cover. The term 'effective radiation' (Fig. 7) accounts for the radiation available to the liquid water phase for heating.

The method described by Likens and Johnson (1969) was used to calculate the heat flux due to sediment heat exchange. The mean annual sediment heat budget (H_{ba_m}) of Georgetown Lake was calculated to be 3300 $g \cdot cal \cdot cm^{-2} \cdot yr^{-1}$. This value is extremely high compared to other mean estimates (Hutchinson 1957; Likens and Johnson 1969). One of the

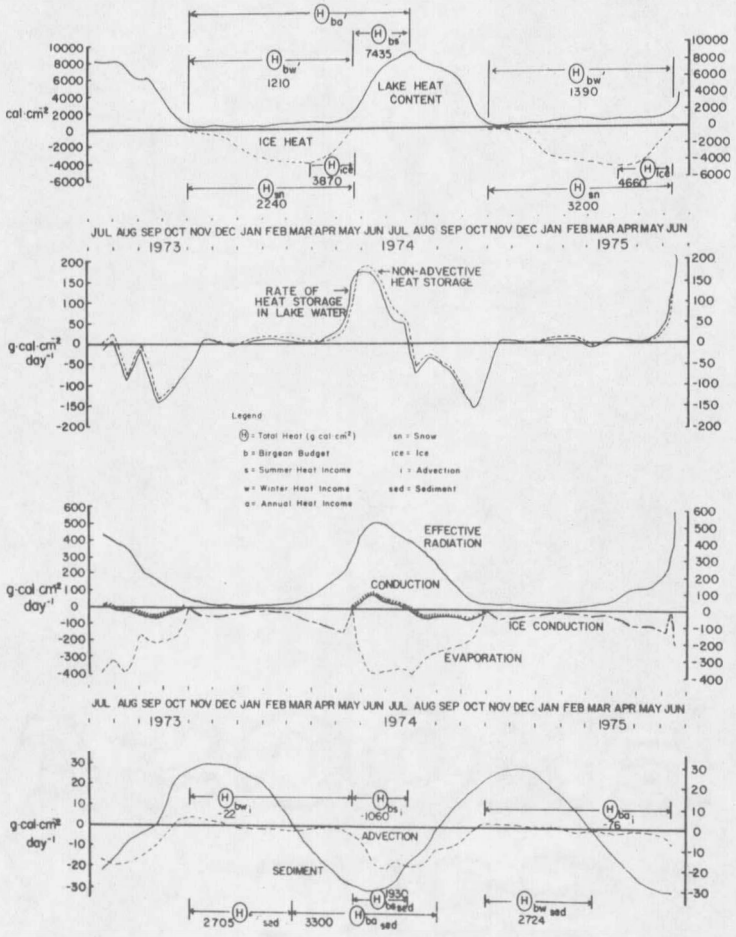


Figure 7. Seasonal Distribution of the Analytical Heat Budget of Georgetown Lake, Montana, 1973-75.

largest was reported by Birge, et al. (1928) for Lake Mendota, with an annual sediment heat budget in the 0 to 8 m depth zone to be 3000 $g \cdot cal \cdot cm^{-2} \cdot yr^{-1}$. The high sediment heat budget for Georgetown Lake resulted from the 13°C amplitude of the seasonal temperature change (maximum lake temperature minus the annual mean temperature (Likens and Johnson 1969)) in contact with the entire lake sediment, since the lake did not stratify during the summer. Utilizing an ideal sinusoidal annual temperature variation (Likens and Johnson 1969) and the calculated mean annual sediment budget, the daily sediment heat flux (Q_m) was estimated throughout the study period (Fig. 7). The calculated annual variation of sediment heat gain and loss in Georgetown agrees well with results presented by Hutchinson (1957). Heat gain to the sediment (negative values) occurred during the heating period, while heat loss from the sediments to the overlying water (positive values) occurred during the fall cooling period and after the ice formed. The water column received 2725 $g \cdot cal \cdot cm^{-2}$ during the period of ice cover. However, since the water column gained only 1200 to 1390 $cal \cdot cm^{-2}$ throughout the period of ice cover, much of the sediment heat input was lost by conduction through the ice and/or advected from the reservoir. Apparent deviations from the idealized sinusoidal response were most obvious prior to ice breakup, since the calculated values suggest rapid heat gain to the sediments during March, April, and May, while the overlying water temperatures did not change appreciably. This suspected deviation contributed very little error to the overall spring heat budget.

Heat loss via conduction through the ice (calculated by setting Q_A, Q_w, Q_E, Q_e and Q_p equal to zero) was considerably less than heat loss calculated by using the method presented by Knauss (1978). The conductive heat flux as calculated by the method of Knauss is inversely proportional to the ice thickness and directly proportional to freezing degree days, but ignores snow cover. This, comparison of the two techniques indicated that the snow cover on Georgetown reduced heat loss by at least 50%. Nonetheless, heat loss by conduction through the ice was the major loss of heat from the water during the winter (Fig. 7).

Evaporation (Q_E and Q_e), conduction (Q_c), and advection (Q_i) were calculated by solving the conservation of energy equation (heat budget) and the conservation of mass equation (water budget, in Knight, et al. 1976) simultaneously to within 1.0 $g \cdot cal \cdot cm^{-2} \cdot day^{-1}$. Groundwater (and/or direct runoff) contributions and evaporative losses were the two unknowns in the water budget and, in addition to sensible heat exchange (conduction), were also the unknowns in the heat budget equation. Sensible heat exchange and evaporation rates were assumed proportional to the Bowen Ratio (Hutchinson 1957; Knauss 1978; Lerman 1978; Ryan and Harleman 1973; Wright and Horral 1969). Sensible heat exchange contributed to the heat gain during the ice-free heating period and to the heat loss during the period of fall cooling. Evaporation rates accounted for the majority of lake cooling during the ice-free season. As indicated by the equilibrium temperature data, and reported by the above authors, net radiation, evaporation, and

sensible heat exchange (all considered meteorological factors) contributed the most to the observed heat content during the ice-free season. The mean evaporation rate (287 $g \cdot cal \cdot cm^{-2} \cdot day^{-1}$) during the ice-free season from Georgetown Lake was 59% of the 486 $g \cdot cal \cdot cm^{-2} \cdot day^{-1}$ calculated from Wright and Horral's (1969) data from the geothermally heated upper Madison River. The Georgetown estimate is 50% greater than the mean annual lake evaporation estimate for Western Montana provided by the U. S. Environmental Data Service (1968), but the Georgetown estimate was within the reported 95% confidence interval. Wright and Horral's data, as compared to the Data Service and the Georgetown estimates, indicate substantial additional heat loss imposed by heat inputs from the geyser basins.

Net advected heat flux indicated that Georgetown Lake served as a heat trap, as suggested for most reservoirs by Wright (1967). The inflowing water required a mean summer heat flux of 15 $g \cdot cal \cdot cm^{-2} \cdot day^{-1}$ to warm inflowing water to ambient conditions, estimated to be 2010 $g \cdot cal \cdot cm^{-2} \cdot yr^{-1}$ (10% total annual heat budget of the lake, Table 3). In contrast, the advected water tended to add heat to the reservoir at the rate of 2 $g \cdot cal \cdot cm^{-2} \cdot day^{-1}$ (Fig. 7) from late October through January. The net advected heat flux was about 10% of the sediment heat flux during the same time period. Since a majority of advected heat originated from underground sources, principally groundwater and spring-fed Stewart Mill Creek, the annual trend of advected heat flux should represent the transport of heat stored underground. By comparison with the annual trend of

Table 3. Summary of the Seasonal Heat and Water Budgets of Georgetown Lake, Montana, 1973-1975.

		BIRGEAN HEAT BUDGET				WATER BUDGET		
			1973-74		1974-75		1973-74	1974-75
			g·cal·cm^{-2}	%	g·cal·cm^{-2}	%	cm	cm
Winter Budget	ΔHeat Storage	(H_{bw_t})	1210	(12.1)	1390	(11.6)	ΔLake Storage -7	0
	Ice	(H_{bw_I})	3870	(38.6	4660	(38.9)	Ice +59	+70
	Snow	(H_{bw_s})	2240	(22.3)	3200	(26.7)	Snow 22	38
	Sediment	(H_{bw_m})	2705	(27.0)	2725	(22.7)	Advected inflow 113	126
							Advected Outflow 146	162
	Total	(H_{bw})	10025		11975			
Summer Budget	ΔHeat Storage	(H_{bs_t})	7435	(87.5			ΔLake Storage 65	
	Advected Heat	(H_{bs_i})	1060	(12.5)			Advected Inflow 140	
							Advected Outflow 40	
	Total	(H_{bs})	8495				Evaporation Loss 41	
							Precipitation 9	
Annual Budget (including Fall Cooling Period)	ΔHeat Storage	(H_{ba_t})	8645	(43.1)			ΔLake Storage 48	
	Ice	(H_{ba_I})	3870	(19.2)			Advected Inflow 315	
	Snow	(H_{ba_s})	2240	(11.2)			Advected Outflow 230	
	Advected Heat	(H_{ba_i})	2010	(10.0)			Ice +59	
	Sediment	(H_{ba_m})	3300	(16.4)			Total Precipitation 41	
							Evaporation Loss 78	
	Total	(H_{ba})	20065					

daily sediment heat flux (Fig. 7), the advected heat lagged behind the estimated sediment heat flux. This difference indicates that the sediment heat input was not an ideal sinusoidal relationship, but rather a function of the time of occurrence of the spring thaw. However, the advected heat and sediment heat flux were out of phase with the lake heat content indicating that both were functions of underground heat transfer and storage.

The annual heat budget of Georgetown Lake (Table 3) was of intermediate magnitude compared to the data calculated from other lakes (Hutchinson 1957). However, unlike most temperate lakes, Georgetown's winter budget exceeded the summer heat income, comprising 50% and 42% of the total respectively. The remaining 8% was accounted for by additional sediment heat income and net advected heat. Factors affecting the winter heat income are principally the ice formation. As was discussed previously, all are functions of meteorological conditions. The large contribution to the heat budget from the sediments, and the relatively small winter and summer storage terms were probably the result of the shallow mean depth of the reservoir.

Summaries of the heat and water budgets (Table 3) indicate contrasts between heat and water exchange rates. Generally, advected water was a major factor controlling the seasonal lake level, although it contributed little to the overall heat budget. Based upon the seasonal pattern of

lake level and stream discharge presented in Knight, et al. (1976), immediately after ice formed, the outflow of water was minimal, but the major influent was of groundwater origin. This source tended to add heat to the reservoir. The decrease in lake level from January through April was primarily the result of the pumping activities of Anaconda Mining Company; however, heat loss from the reservoir was minimal. The increase of lake volume from April through June was principally due to runoff from snowmelt. The heat required to warm this water amounted to 12.5% of the total summer heat income. Generally, throughout the summer and fall, the lake level remained fairly constant (i.e., influent approximately equaled effluent plus evaporation). Evaporation accounted for 25% of the total annual water loss (50% during the summer heating period), but the latent heat of evaporation cooled the reservoir by 45,000 $cal \cdot cm^{-2}$, or greater than twice the total annual heat budget. Precipitation was minimal in both budgets during the summer, but contributed substantially to the winter heat budget due to the high latent heat of melting of the snow.

Dutton and Bryson (1962), Hutchinson (1941 and 1957), Likens and Johnson (1969), Ragotzkie and Likens (1964), Schindler, et al. (1974), and Quay (1977) have discussed the importance of density currents in relation to sediment exchange of heat and dissolved solids to the overlying water. Since wind-induced turbulence typically masks these effects, density currents in Georgetown Lake were investigated during the ice-covered period utilizing the method of Hutchinson (1941). Georgetown appeared to

exhibit Hutchinson's criteria for investigating the significance of density currents, namely the lake:

1. was well stratified (during ice cover),
2. was small enough for the mud to have an appreciable influence on the free water (evidenced from the heat budget),
3. had a bottom contour permitting recognition of conspicuous morphometric features, and,
4. had no hydrological disturbance.

Under such conditions, heat and dissolved solids originating from the sediments should be distributed in the water column as a function of the morphometric curve ($\delta A/\delta V$), estimated by $\Delta A/\Delta V$. However, since the influent and effluent flows were substantial during the winter but net advected heat was minimal (Table 3), the assumption of no hydrological disturbance was investigated by comparing the profiles before (25 Nov) and during (21 Dec to 12 Apr) the Anaconda Co. pumping operations (all other flows were relatively constant (Knight, et al. 1976)).

Throughout the winter, the vertical distributions of temperature, conductivity, and subsequent water density did not coincide with the morphometric curve (Fig. 8). The 25 November profiles resembled those of temperate, dimictic lakes reported by Hutchinson (1957). The water density and temperature gradients indicated three distinct regions within the water column. The first region was the upper meter, characterized by a rapid change of temperature and density, persumably due to

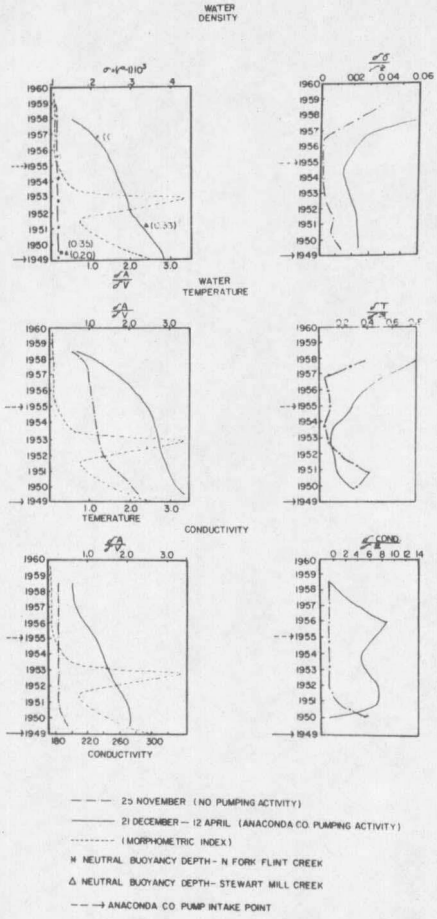


Figure 8. Vertical Distribution of Water Density, Temperature, and Conductivity under the Ice Compared to the Morphometric Index of Georgetown Lake, Montana, 1974-75.

a loss of heat by conduction to the ice cover. The middle region was characterized by steady gradients of water temperature (0.05°C per meter) and density. The conductivity values were equal in the upper two regions. The lower region, below the 1952 m elevation, was distinguished by an increasing density, temperature, and conductivity gradient. The maximum gradients of all three parameters were located below the depth of a maximum value of the morphometric curve. These data suggest three explanations:

1. density currents transported heat and dissolved solids originating from one sediment depth to a greater depth,
2. since the densities of the groundwater and Stewart Mill Creek influents were greater than the maximum density of the lake water, density currents originating from these influents transported heat and dissolved solids to the deeper portions of the reservoir, or
3. selective withdrawal of the denser, bottom water by Montana Power hydroelectric operations produced density flows towards the bottom discharge.

Comparison of the mean profiles below the 1955 m elevation during Anaconda Co. pumping activities suggests that all three explanations may be valid. The increase of temperature and dissolved solids was probably due to inputs from the sediment, as evidenced by increased gradients at the depth of the maximum morphometric value. However, the substantial

decrease of the conductivity gradient at the depth of neutral density of Stewart Mill Creek and groundwater indicates the presence of a density current of the influent water and selective water removal from the hydroelectric discharge.

Differences between the profiles above the 1955 m elevation (elevation of the Anaconda Co. pump intake) were observed between the two time periods. In general, the pumping activity increased the temperature and density gradient 2 m above the pump intake. The temperature gradient directly under the ice increased slightly (conductive heat loss). The effect of inputs from the N. Fork of Flint Creek during the winter appeared to be negligible due to very low flows. The increase of the conductivity gradients indicates that dissolved solids diffused upwards towards the lower concentrations, but were removed from the reservoir by the Anaconda Co. discharge.

In summary, the increased heat and dissolved solids during the ice-covered period originated from the sediments, but density currents imposed by diffusion from the sediments appeared to be substantially altered by the concentrations of influent solids. The Anaconda Co. operation appeared to affect only the water mass above the 1955 intake depth, while Montana Power's hydroelectric facility continued to remove the heat and dissolved solids accumulated in the lower depths.

CHEMICAL PARAMETERS

Georgetown Lake may be classified as a calcium carbonate, moderately hard water lake (Table 4). The mean salinity of 184 $mg \cdot l^{-1}$ is higher than the worldwide lake average of 146 $mg \cdot l^{-1}$ presented in Hutchinson (1957). Enriched calcium, magnesium, carbonate, and sulfate ions, relative to sodium and chloride, are typical of waters draining from calcareous, sedimentary rock formations. The very low sodium and chloride concentrations observed in Georgetown Lake indicate negligible contributions of dissolved material from human activities.

The conductivity isoclines, representing dissolved solid concentractions, illustrated stratification patterns similar to those observed for temperature (Fig. 5). Conductivity values were generally decreased from the time of ice melt to the end of September. Conductivity values generally increased from October through the ice-covered period, with some dilution occurring directly under the ice from dilute influent water and/or ice-snow melt. Chemical stratification began to occur about a month after the onset of ice cover, and became more pronounced until the ice melted, at which time a very rapid decline of conductivity values occurred.

Seasonal changes in the distribution and concentrations of dissolved compounds in open systems have typically been related to hydrological contributions (dilution or concentration effects) and changing equilibrium conditions (Hutchinson 1957; Stumm and Morgan 1970). Seasonal changes in

Table 4. Ranges and Means, in parenthesis, of the Chemical Parameters Measured in Georgetown Lake, Montana, from 10 July 1973 through 16 June, 1975.

Analysis	Georgetown Lake	Stewart Hill Creek (Inflow)	North Fork Flint Creek (Inflow)	Flint Creek (Outflow)
Temperature (°C)	0 - 20.6 (8.9)	4.8 - 10.0 (6.4)	0.3 - 18.1 (7.5)	2.5 - 19.0 (9.6)
Conductivity (umhos·cm^{-2})	140 - 348 (212)	175 - 317 (268)	134 - 275 (217)	168 - 335 (245)
pH	7.20 - 9.28 (8.61)	7.57 - 8.50 (7.90)	7.74 - 8.52 (7.96)	7.59 - 9.13 (7.92)
Dissolved gases:				
Oxygen (mg·l^{-1})	0 - 13.26 (5.60)	7.65 - 11.6 (9.93)	5.87 - 10.94 (9.22)	5.75 - 11.16 (8.96)
Carbon Dioxide (mg·l^{-1})	0.09 - 25.2 (0.67)	1.95 - 9.65 (4.50)	0.75 - 7.20 (2.32)	0.15 - 18.1 (3.15)
Cations:				
Calcium (mg·l^{-1})	18.2 - 47.0 (28.4)	34.9 - 42.0 (37.6)	21.0 - 37.0 (31.0)	18.4 - 45.2 (33.5)
Magnesium (mg·l^{-1})	8.8 - 17.0 (10.6)	9.6 - 14.8 (12.4)	5.6 - 11.1 (7.6)	6.8 - 16.5 (10.6)
Sodium (mg·l^{-1})	1.1 - 1.9 (1.6)	0.8 - 1.8 (1.4)	1.0 - 1.7 (1.2)	1.3 - 1.9 (1.7)
Potassium (mg·l^{-1})	0.7 - 2.2 (1.4)	1.1 - 2.0 (1.6)	0.7 - 2.4 (1.4)	1.0 - 2.1 (1.8)
Iron (ug·l^{-1})	1 - 850 (35.6)	0 - 10 (2.0)	5 - 120 (53)	18 - 830 (170)
Total Cations (meq·l^{-1})	(2.4)	(3.0)	(2.3)	(2.7)
Anions:				
Bicarbonate (mg·l^{-1})	85.2 - 225 (126)	126 - 181 (164)	80.6 - 176 (121)	92.8 - 236 (140)
Carbonate (mg·l^{-1})	0.09 - 6.41 (1.57)	0.17 - 0.93 (0.5)	0.15 - 1.71 (0.26)	0.21 - 4.30 (0.32)
Sulfate (mg·l^{-1})	2.5 - 10.2 (6.3)	4.8 - 10.2 (7.9)	3.8 - 7.9 (5.2)	1.0 - 9.0 (6.3)
Chloride (mg·l^{-1})	0.1 - 1.0 (0.6)	0.1 - 0.4 (0.2)	0.1 - 0.5 (0.2)	0.1 - 0.9 (0.5)
Fluoride (mg·l^{-1})	0 - 0.3 (0.10)	0 - 0.3 (0.1)	0 - 0.3 (0.1)	0 - 0.3 (0.1)
Silica (mg·l^{-1})	0.2 - 18.2 (6.1)	3.7 - 14.4 (8.7)	6.7 - 14.5 (11.2)	3.2 - 18.2 (7.4)
Total Anions (meq·l^{-1})	(2.4)	(3.0)	(2.4)	(2.6)
Nutrients:				
Total Phosphorus (ug·l^{-1})	12 - 165 (28.7)	3 - 32 (13.5)	4 - 38 (18.3)	17 - 134 (46.8)
Ortho-Phosphorus (ug·l^{-1})	0 - 114 (5.2)	1 - 23 (5.2)	0 -13 (5.2)	0 - 97 (18.8)
Total Nitrogen (ug·l^{-1})	30 - 1560 (370)	0 - 350 (145)	0 - 355 (163)	100 - 1015 (493)
Nitrate-Nitrogen (ug·l^{-1})	0 - 95 (9.8)	16 - 63 (48)	0 - 36 (7.0)	0 - 46 (10.2)
Nitrite-Nitrogen (ug·l^{-1})	0 - 19 (2.3)	0 (0.0)	0 (0.0)	0 (0.0)
Ammonia-Nitrogen (ug·l^{-1})	0 - 208 (19.3)	0 - 9.0 (3.6)	0 - 16 (2.9)	0 - 410 (54.4)
Organic Carbon (ug·l^{-1})	1.9 - 14.3 (5.9)	0 - 4.3 (1.2)	0.5 - 6.9 (3.7)	2.0 - 15.5 (4.1)

the concentrations of dissolved ions in Georgetown Lake have been related to the high plant production and subsequent microbial decomposition (Knight et al. 1976) and to the oxidation - reduction of the sediment mud-water interface (Garrison 1976). However, as discussed in the previous section, hydrological considerations substantially affected the distribution of dissolved material within the water column during the stratified period.

Oxygen and Carbon Dioxide

Dissolved oxygen concentrations were relatively high during the ice-free months (Figs. 9, 10). Throughout the summer, oxygen concentrations within the water column fluctuated around the 100% saturation level (Fig. 10), while surface concentrations were consistently higher than those observed at lower depths. Carbon dioxide concentrations were gradually reduced throughout the summer months; concentrations of CO_2 in August and September of both years were consistently undersaturated with respect to atmospheric levels. Concentrations of CO_2 at lower depths were usually slightly greater than those recorded at the surface. These data suggest that plant production during the summer was the major factor influencing dissolved O_2 and CO_2 concentrations. However, as Schindler (1975) and Schindler and Fee (1973) have discussed, atmospheric exchange rates of CO_2 and O_2 are primarily a function of partial pressure differences between the water and atmosphere, and turbulent mixing within the water column. The shallow mean depth of Georgetown Lake, coupled with the high

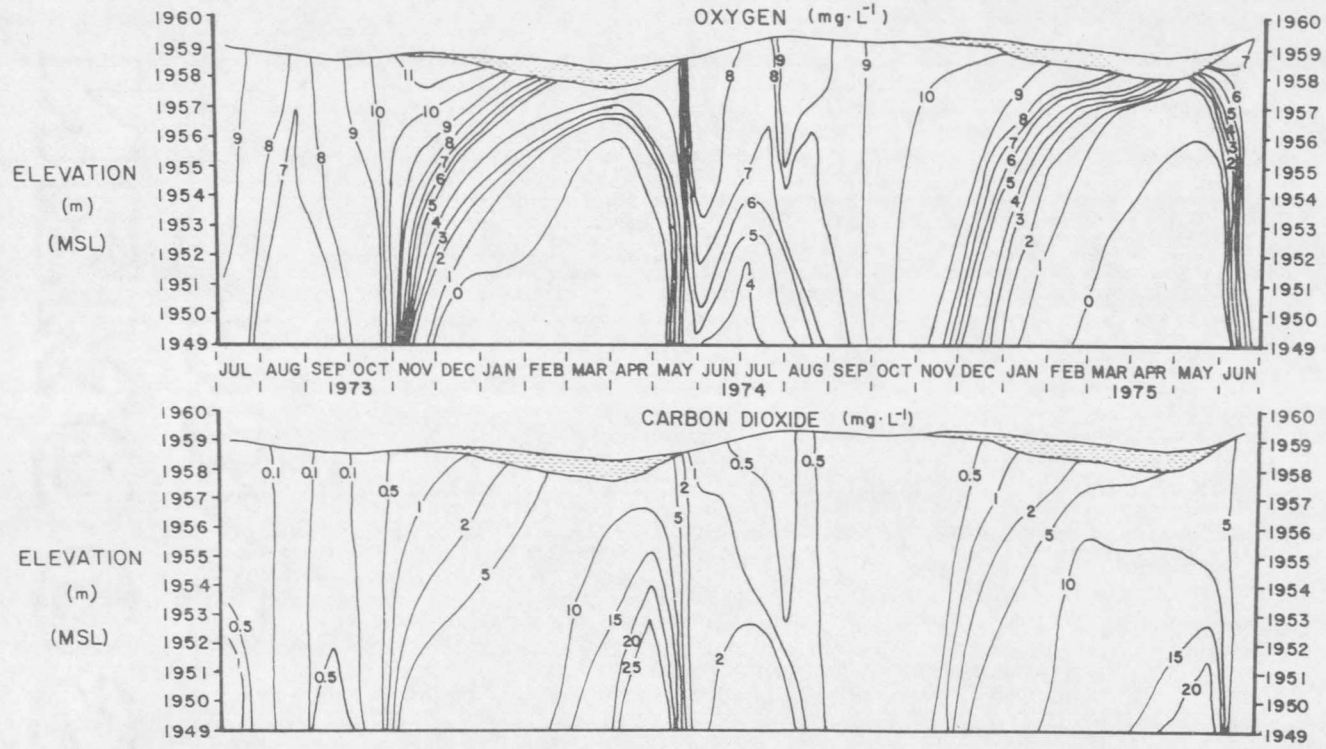


Figure 9. Seasonal and Vertical Distribution of Oxygen and Carbon Dioxide in Georgetown Lake, Montana, 1973-75.

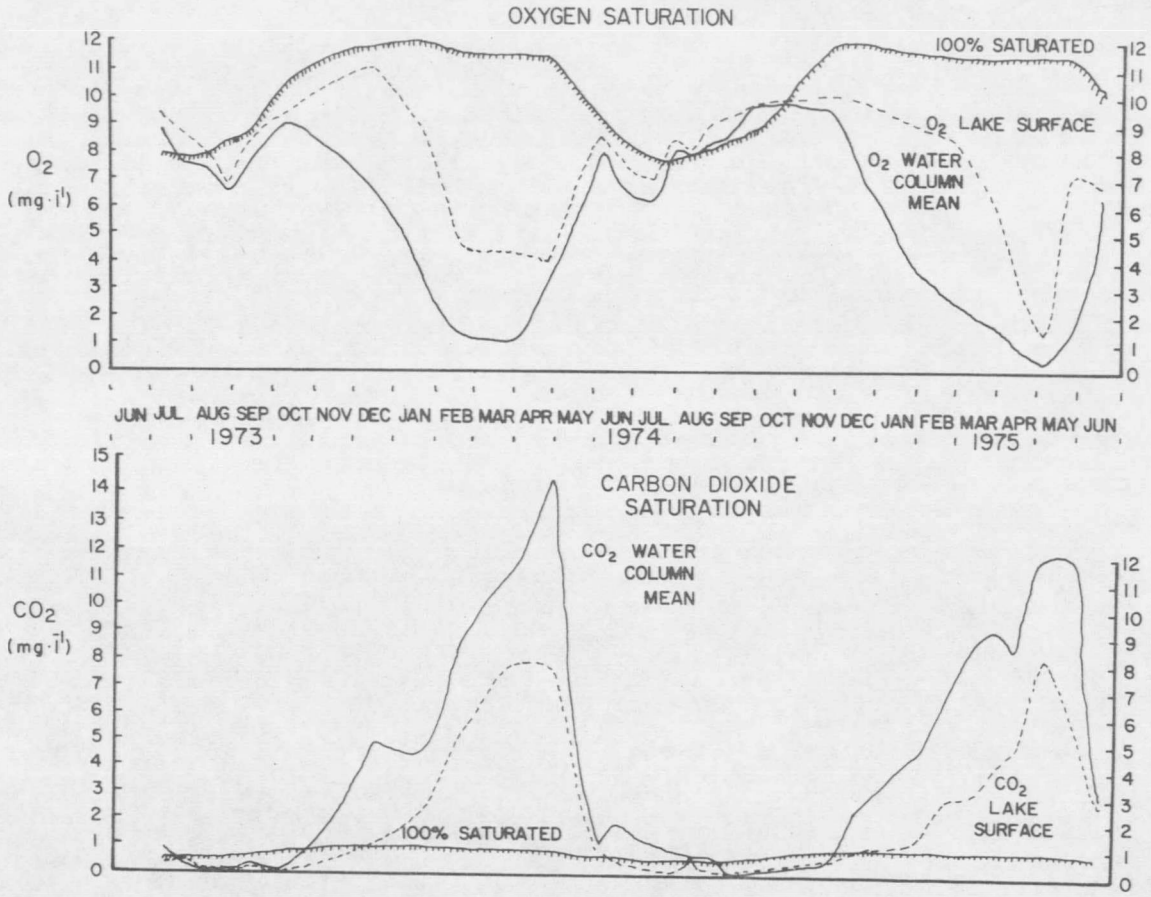


Figure 10. Seasonal Distribution of Mean and Surface Concentrations of Oxygen and Carbon Dioxide Compared to Saturated Concentrations in Georgetown Lake, Montana, 1973-75.

plant production, would favor high rates of CO_2 invasion from the atmosphere and a net loss of oxygen to the atmosphere.

With the onset of ice cover, dissolved oxygen throughout the water column decreased. Anoxic conditions were first observed in December 1973, and February 1975, of each winter, respectively (Fig. 9). Total dissolved oxygen in the water column continued to decrease until the ice began to melt. At maximum anoxic conditions of each winter, oxygen was not detected in the lower seven meters of the water column. During the period of ice melt, the oxygen concentrations rapidly increased to saturated levels (Fig. 10). In contrast to oxygen, CO_2 concentrations increased under the ice cover (Fig. 9), until peak concentrations were observed to be 15 times the saturated level (Fig. 10). The maximum CO_2 concentrations coincided with minimum oxygen values. Also, CO_2 concentrations increased in the anoxic zone (Fig. 9), indicating substantial anaerobic respiration. As with oxygen, the onset of ice melt produced rapid equilibration of carbon dioxide levels to saturated conditions.

The general decrease of oxygen concentrations to well below saturated levels and supersaturated carbon dioxide under the ice, suggest that atmospheric exchange rates were minimal. Hence, during the period of ice cover, the predominant influence on O_2 and CO_2 concentrations was aerobic and anaerobic respiration. However, with the onset of ice melt, the rapid oxygen increase and subsequent loss of CO_2 illustrate the high exchange rates with the atmosphere.

Since most chemical and/or adsorption reactions are functions of pH and reduction-oxidation potential (Stumm and Morgan 1970), the biologically mediated production or consumption of oxygen and carbon dioxide basically determined the chemical regime in Georgetown Lake. Throughout the ice-free months, plant production and atmospheric exchange tend to favor highly oxidative reactions while maintaining pH values ranging from 8.1 to 9.3. In contrast, during the winter, minimal atmospheric exchange and net biological consumption of oxygen produced an environment which favored reduction reactions. Anaerobic metabolism continued to decrease the oxidation-reduction potential. The carbon dioxide released through respiration lowered the pH to a minimum observed value of 7.2. However, the pH range was probably limited due to precipitation and redissolution of calcium carbonate.

Calcium Carbonate

As stated in the introduction to the chemical section, Georgetown Lake may be classified as a calcium carbonate system. However, significant amounts of magnesium and sulfate ions were also present. Based upon the principal solubility products of most freshwater reactions (Table 5), throughout the course of a year calcium concentrations were supersaturated or undersaturated with respect to both calcite and dolomite. Magnesium solubility with solid dolomite exhibited similar fluctuations throughout an annual cycle. The observed concentrations of hydroxide and sulfate ions were not great enough to affect calcium or magensium solubility.

Table 5. Solubility Products of Major Ions in Georgetown Lake, 1973-1975.

Compound	Equilibrium Reaction	Annual Range of Activity Products of The Reactants in Georgetown Lake	Equilibrium Condition
Calcium Hydroxide	$[Ca]\cdot[OH]^2 = 10^{-5.43}$	$\log_a Ca + 2\cdot\log_a OH < -8.3$	Calcium was not in equilibrium with Calcium Hydroxide
Magnesium Hydroxide	$[Mg]\cdot[OH]^2 = 10^{-11.5}$	$\log_a Mg + 2\cdot\log_a OH < -13.3$	Magnesium was not in equilibrium with Magnesium Hydroxide
Gypsum	$[Ca]\cdot[SO_4] = 10^{-4.63}$	$\log_a Ca + \log_a SO_4 < -7.4$	Calcium was not in equilibrium with Gypsum
Calcite	$\frac{[Ca]\cdot[HCO_3]}{[H]} = 10^{1.99}$	$1.5 < \log_a Ca + \log_a HCO_3 + pH < 2.7$	Calcium was in equilibrium with Calcite; supersaturated and undersaturated conditions existed throughout the year.
Dolomite	$[Mg]\cdot[Ca]\cdot\left(\frac{[HCO_3]}{[H]}\right)^2 = 10^{3.96}$	$2.8 < \log_a Ca + \log_a Mg + 2\cdot\log_a HCO_3 + 2\cdot pH < 5.5$	Calcium and Magnesium were in equilibrium with Dolomite; supersaturated and undersaturated conditions existed throughout the year.

Selected removal of calcium was indicated by the annual mean influent calcium-magnesium ratios of 1.84 and 2.47 for Stewart Mill Creek and North Fork Flint Creek respectively, and the annual mean Ca:Mg ratio of 1.62 for lake water. Also, the molar calcium to magnesium ratios throughout the year were primarily a function of the calcium concentration (Fig. 11). As Stumm and Morgan (1970) point out, for an unknown reason dolomite does not precipitate even though the water may be supersaturated. Therefore, the calcite equilibrium was the predominant reacton influencing the solubility of calcium. However, small variations of magnesium concentrations may be the result of hydrological effects and, as Stumm and Morgan (1970) suggest, co-precipitation of a magnesium-calcium complex.

Concentrations of bicarbonate and calcium followed the same seasonal trend as conductivity (Fig. 12), since they were the major ionic species and both were influenced by the calcite equilibrium. Bicarbonate and calcium concentrations decreased throughout the ice-free season due to carbon utilization by aquatic plants and subsequent precipitation of calcite. The trend was reversed during the period of ice cover, when respiratory addition of CO_2 favored redissolution of calcite. Even though metabolic activities greatly influenced the $CaCO_3$ equilibrium, seasonal trends in areal concentrations of inorganic carbon and calcium (Fig. 13) illustrate that total carbon concentrations (principally CO_2 and HCO_3^-) changed more rapidly than calcium. The actual rates of change for carbon and calcium content, corrected by mass balance effects of

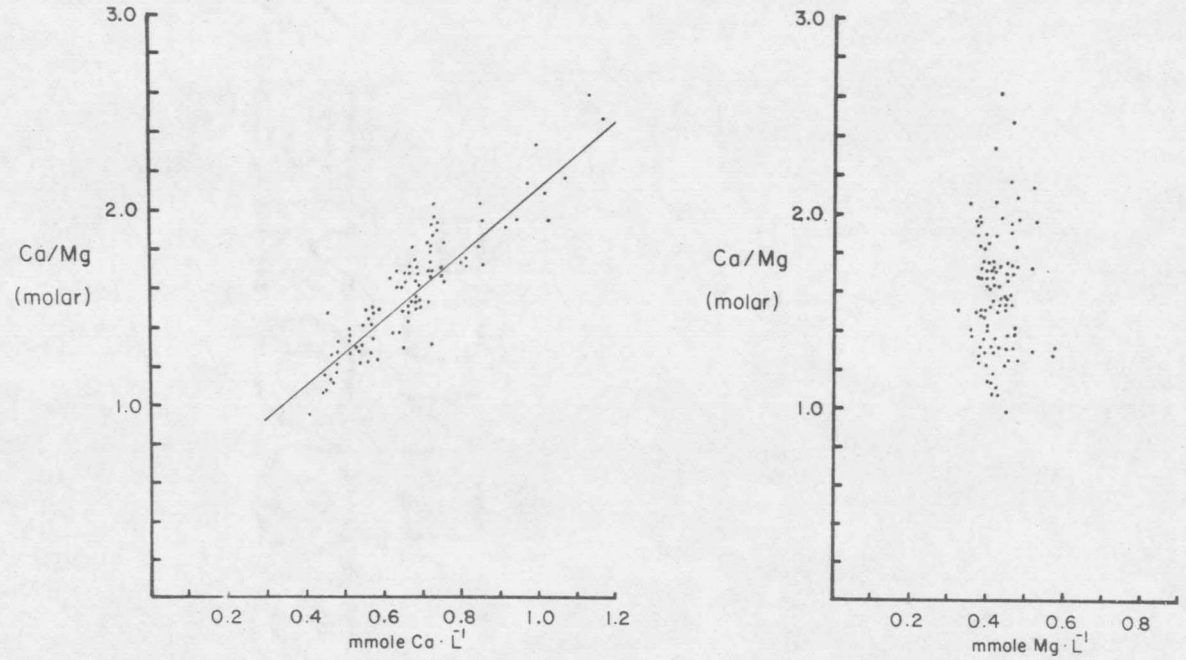


Figure 11. Molar Ratios of Calcium to Magnesium as a Function of the Respective Concentrations of Each in Georgetown Lake, Montana, 1973-75.

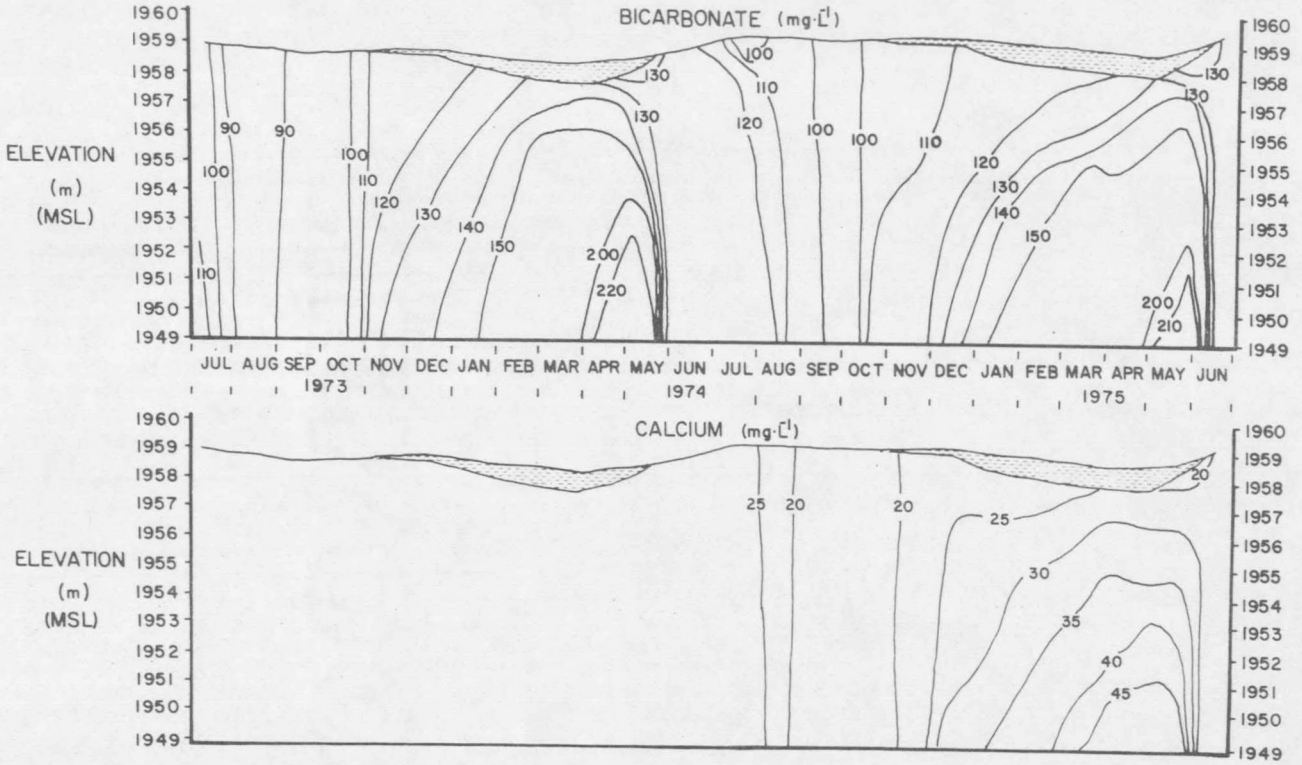


Figure 12. Seasonal and Vertical Distribution of Bicarbonate and Calcium Concentrations in Georgetown Lake, Montana, 1973-75.

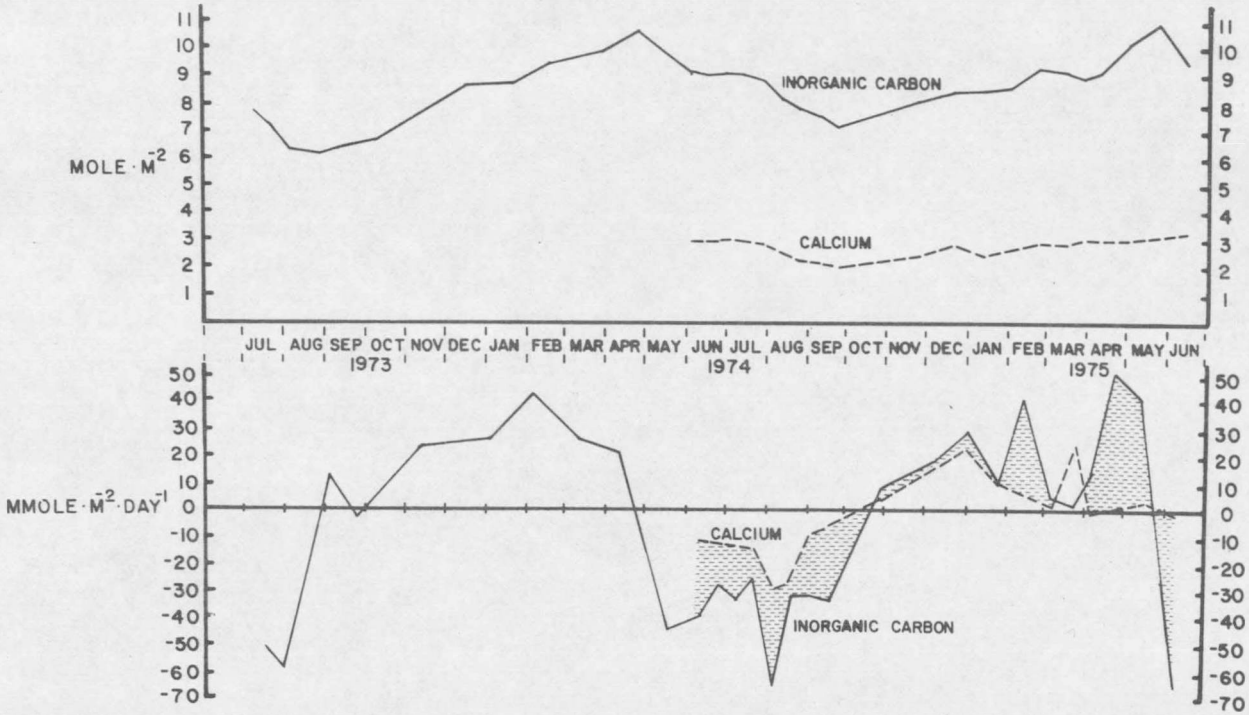


Figure 13. Seasonal Distribution of Total Inorganic Carbon and Calcium within the Water Column and the Respective Rates of Change in Georgetown Lake, Montana, 1973-75.

influents and effluents, illustrate the general trend for sediment content described by Garrison (1976). Exchangeable calcium (presumably $CaCO_3$) increased in the sediments during the ice-free period which coincided with calcium loss from the water column. Conversely, Garrison (1976) reported a decrease in the exchangeable calcium content of the sediments with the onset of ice cover. This trend corresponds with an increased exchange rate of calcium to the water column during the winter. However, the significantly increased release of calcium to the water observed in March (Fig. 13) was not accompanied by a corresponding rate of increase of carbon. This may be due to adsorption characteristics of the sediment since Garrison (1976) observed a noticeable increase of exchangeable calcium preceeding anoxic conditions, followed by a rapid decline of exchangeable calcium.

Typically, the rates of inorganic carbon exchange within the water column exceeded those of calcium (Fig. 13). The carbon exchange rates, in excess of $CaCO_3$ (Fig. 13 - shaded area), represent CO_2 and HCO_3^- uptake or release by metabolism and/or atmospheric contributions. Since the rates of inorganic carbon loss in excess of $CaCO_3$ from the water column during the ice-free period averaged 0.2 g $C \cdot m^{-2} \cdot day^{-1}$ and the net planktonic primary production estimate of Knight et al. (1976) averaged 0.6 g $C \cdot m^{-2} \cdot day^{-1}$ for the same time, at least 0.4 g $C \cdot m^{-2} \cdot day^{-1}$ must have entered the water column from the atmosphere and/or from sediment respiration. Additional CO_2 (or HCO_3) presumably entered the water column if

macrophtic production was included. The mean input of 0.4 g $C \cdot m^{-2} \cdot day^{-1}$ was less than one-half the atmospheric flux reported by Megard and Smith (1974). In addition, Schindler (1975) pointed out that the annual average CO_2 flux in the oceans ranges from 0.33 to 1.08 g $C \cdot m^{-2} \cdot day^{-1}$. Based upon these values, the 0.4 g $C \cdot m^{-2} \cdot day^{-1}$ CO_2 flux estimation for Georgetown Lake could well represent net atmospheric CO_2 invasion to the water column.

Since ice cover prevented significant atmospheric influence, the extent to which changes in carbon dioxide and bicarbonate exceeded changes in calcium would be indicative of metabolism within the lake. However, the more rapid increase of bicarbonate with respect to calcium ions indicates a corresponding increase of some other cation, probably ammonium ions, to preserve the electrical neutrality. Two major periods of inorganic carbon accumulation under the ice were observed in 1974-75. These coincided with oxic and anoxic conditions (Fig. 13). When average rates of carbon dioxide accumulation were compared to oxygen consumption (corrected for hydrological mass balance) (Fig. 14), the resultant CO_2/O_2 molar quotient of 0.76 was less than the conventional respiratory quotient range of 0.85 to 1.0 presented by Hutchinson (1957) and Wetzel (1975). However, during the period preceeding anoxia, the total inorganic carbon (CO_2 plus bicarbonate) to oxygen quotient of 0.93 indicates that aerobic respiration could account for the observed rate of change. The difference of 1.2 mmole$C \cdot m^{-2} \cdot day^{-1}$ between carbon dioxide and total inorganic carbon

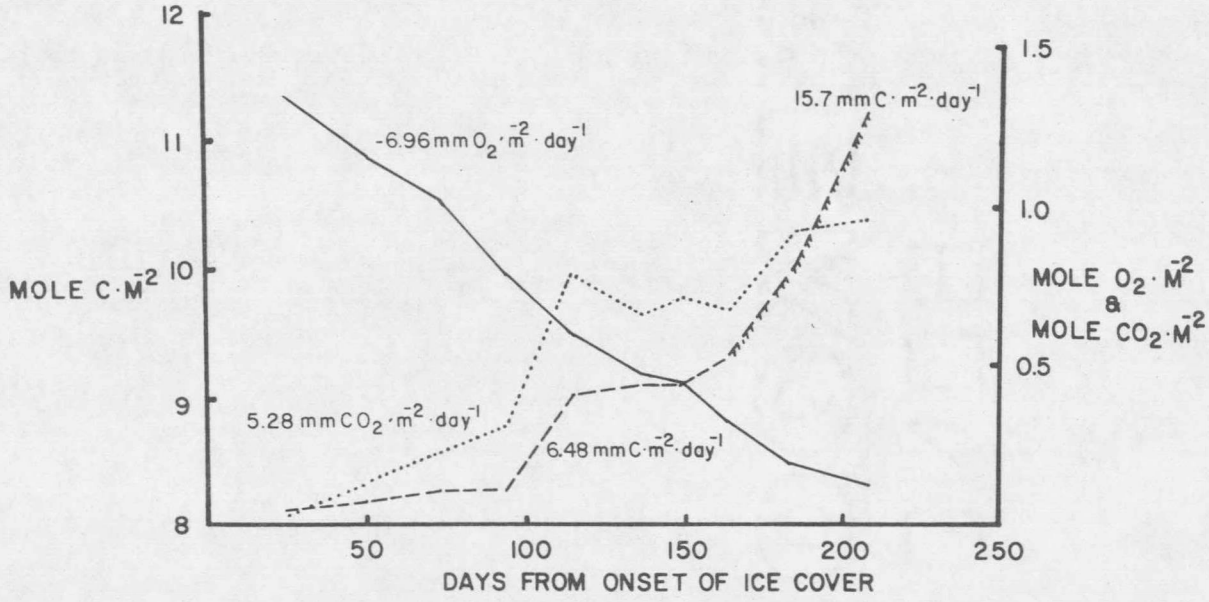


Figure 14. Total Oxygen, Dioxide, and Inorganic Carbon in the Water Column Under the Ice in Georgetown Lake, Montana, 1974-75.

probably represented bicarbonate which originated from the disassociation of calcium carbonate to maintain equilibrium conditions. As oxygen depletion continued at a constant rate in the upper depths, the rate of accumulation of inorganic carbon increased throughout the water column (Fig. 14-hatched line). The onset of rapid carbon accumulation occurred simultaneously with the occurrence of anoxic conditions above the 1954 m contour, the depth of the maximum morphometric index (Fig. 8). This pattern suggests that as anoxic conditions developed, density currents became significant with respect to the accumulation of bicarbonate at the deep sampling location. The total inorganic carbon accumulation, corrected for aerobic and anaerobic respiration rates (Table 6), yielded a probable value of 4.6 mmoleC$\cdot m^{-2}\cdot day^{-1}$ transported via density currents to the deeper region of the lake. This estimate compared favorably with Hutchinson's (1941) value of ≈5 mmole $HCO_3^-\cdot m^{-2}\cdot day^{-1}$ accumulation due to density currents in the hypolimnion of Linsley Pond. The average aerobic and anaerobic respiration rates in Georgetown Lake, 6.48 and 4.6 mmole $C\cdot m^{-2}\cdot day^{-1}$, respectively, were very similar to the rates measured by Rich (1979) in Dunham Pond. Also, oxygen depletion rates in Georgetown were slightly less than the mean depletion rate of 9 mmole $O_2\cdot m^{-2}\cdot day^{-1}$ of ten prairie lakes reported by Barica and Mathias (1979).

Nitrogen and Phosphorus

The seasonal trend of inorganic concentrations of phosphorus and nitrogen, primarily nitrate and ammonia, were very similar to the seasonal

Table 6. Partition of the Total Inorganic Carbon Accumulation During the Anoxic Period in Georgetown Lake, 1974-75.

Total inorganic carbon accumulation		=	15.7 mmole $C \cdot m^{-2} \cdot day^{-1}$
minus			
Aerobic Respiration:			
Respiratory Quotient	x Oxygen Depletion		
0.93	x 6.96 mmole $O_2 \cdot m^{-2} \cdot day^{-1}$	=	6.5 mmole $C \cdot m^{-2} \cdot day^{-1}$
Carbon Accumulation corrected for Aerobic Respiration			9.2 mmole $C \cdot m^{-2} \cdot day^{-1}$
minus			
Anaerobic Respiration:			
$\left(\frac{\text{Anaerobic Rate}}{\text{Aerobic Rate}}\right)^{*}$	x Aerobic Respiration		
0.7	x 6.5 mmole $C \cdot m^{-2} \cdot day^{-1}$	=	4.6 mmole $C \cdot m^{-2} \cdot day^{-1}$
Unaccounted for (presumably due to density currents)			4.6 mmole $C \cdot m^{-2} \cdot day^{-1}$

* From Rich (1979)

distribution of carbon dioxide (Figs. 15, 16, and 9, respectively). Throughout the ice-free period, orthophosphate, nitrate, and ammonia concentrations were very low, often below detectable levels (Figs. 15 and 16). Conversely, under the ice, inorganic nitrogen and phosphorus concentrations increased. Generally, as was postulated with respect to carbon dioxide, high plant production during the ice-free period depleted inorganic nutrient concentrations; under the ice, decomposition predominated and subsequent mineralization tended to accumulate inorganic phosphorus and nitrogen.

Organic phosphorus concentrations averaged 26 μg $P \cdot l^{-1}$ throughout the year. Even though the summer and winter orthophosphate concentrations varied by two orders of magnitude, organic phosphorus concentrations were observed to vary threefold without a well defined distribution within the water column (Fig. 15). Organic nitrogen concentrations (Fig. 17) varied much more than phosphorus. Generally, the highest concentrations of organic nitrogen were observed in late July to early August, but the organic nitrogen distribution within the water column was very patchy and poorly defined with respect to season.

Total nitrogen and phosphorus ($mmole \cdot m^{-2}$) within the water column exhibited wider fluctuations during the ice-free period than during the season of ice cover (Fig. 18). Total nitrogen exhibited a major peak in August of each year, which coincided with the peak abundance of Anabaena

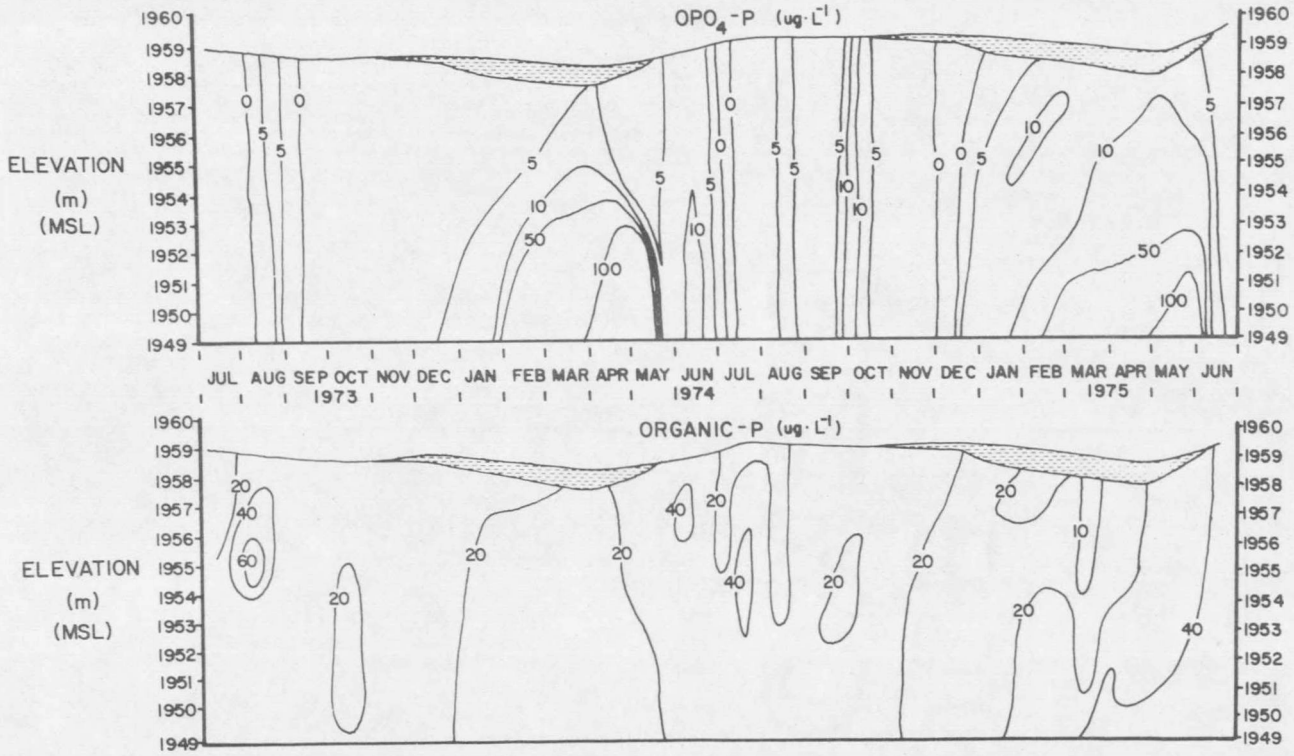


Figure 15. Seasonal and Vertical Distribution of Orthophosphate and Organic Phosphate in Georgetown Lake, Montana, 1973-75.

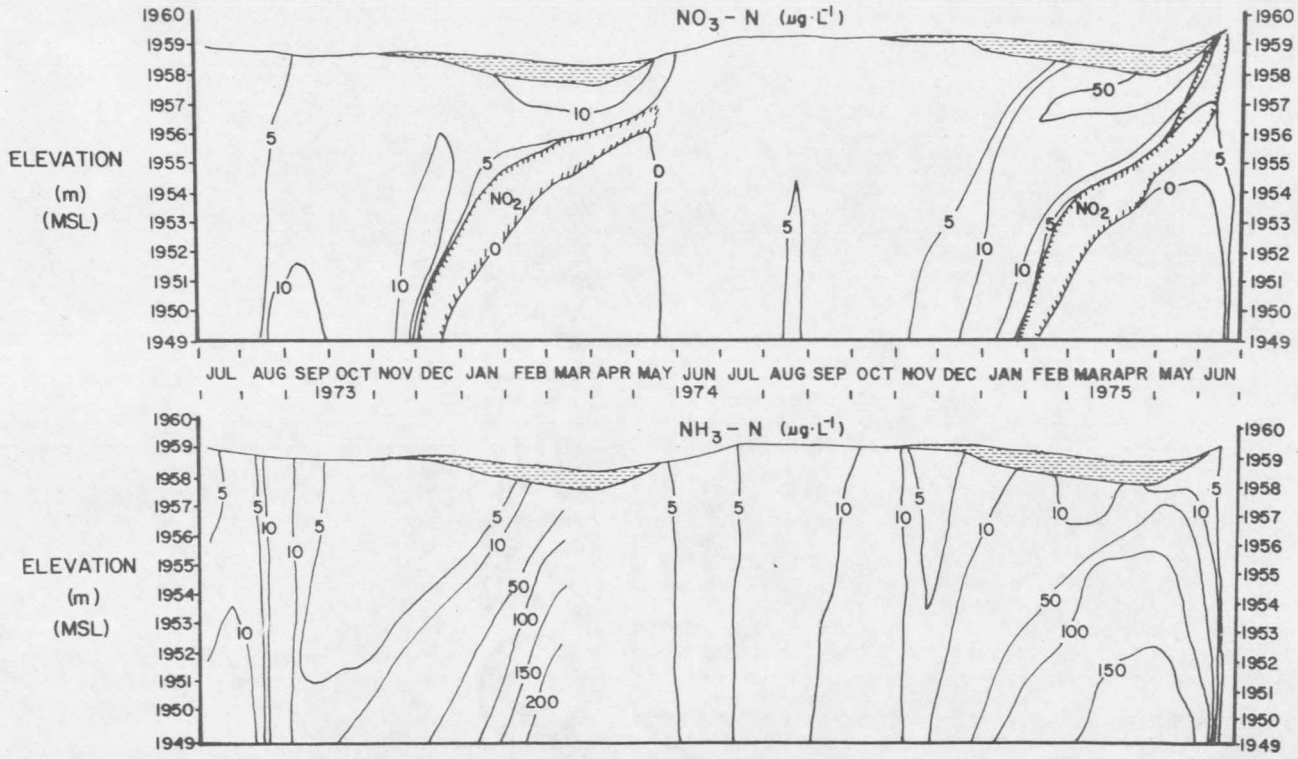


Figure 16. Seasonal and Vertical Distribution of Nitrate and Ammonia in Georgetown Lake, Montana, 1973-75.

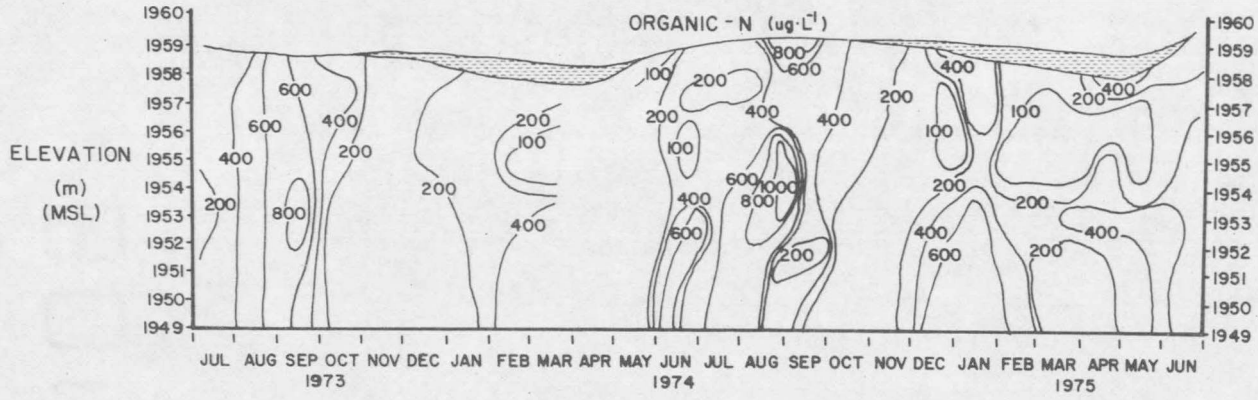


Figure 17. Seasonal and Vertical Distribution of Organic Nitrogen in Georgetown Lake, Montana, 1973-75.

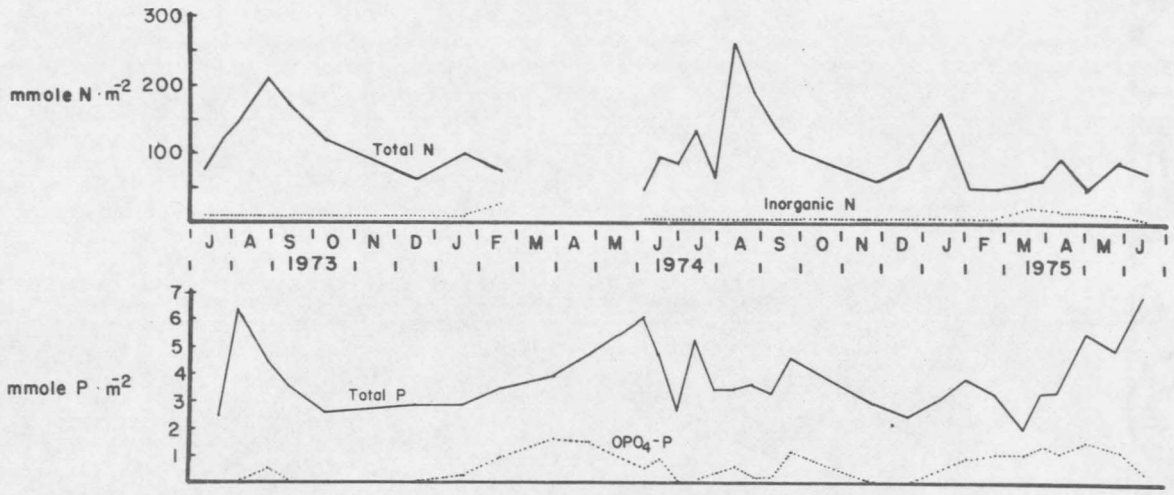


Figure 18. Seasonal Distribution of the Total and Inorganic Nitrogen and Phosphorus in the Water Column of Georgetown Lake, Montana, 1973-75.

flos-aquae. A minor peak of nitrogen was observed in January of both years. Total phosphorus concentrations were highest after the ice melted. A secondary phosphorus peak was observed both summers prior to the summer maximum of total nitrogen. However, a phosphorus increase was not observed to precede the winter maximum of nitrogen. Even though inorganic forms of nitrogen and phosphorus contributed to the total concentrations, particularly during the winter, the large fluctuations of total nitrogen and phosphorus could not be accounted for by corresponding changes of the inorganic species. Hutchinson (1941) noted similar fluctuations of total phosphorus in Linsley Pond. He suggested that phosphorus fluxes were controlled by either the gain or loss through the inlets and outlets, or by purely internal processes, such as exchange with the sediment (or macrophytes) and loss via sedimentation.

External Nutrient Loading

The average daily import and export of total nitrogen and phosphorus were calculated according to the mass balance equation:

$$mM \cdot m^{-2} \cdot day^{-1} = \frac{\sum_{i=n}^{n} n_i V_i}{A}$$

where,

n_i = total nutrient concentration of the i^{th} inlet or outlet ($mM \cdot m^{-3}$)

v_i = average daily discharge of the i^{th} inlet or outlet ($m^{-3} \cdot day^{-1}$)

A = average lake area (m^2)

Groundwater volumes were obtained from the mass-energy balance calculations presented in the heat budget section. Since mean phosphorus concentrations measured from test wells (Table 7) were slightly greater (by 10 $\mu g \cdot \ell^{-1}$) than concentrations measured in Stewart Mill Creek, and, since Stewart Mill Creek originates as a spring 200 m from the lake, the seasonal concentrations from Stewart Mill Creek were used in the above equation for the estimate of the groundwater contribution.

Total phosphorus loading averaged 0.003 $mM \cdot m^{-2} \cdot day^{-1}$. However, 67% of the total annual influent of 1.64 mM $P \cdot m^{-2} \cdot yr^{-1}$ ($0.05 gP \cdot m^{-2} \cdot yr^{-1}$) entered the lake during the spring runoff period (Fig. 19). Total nitrogen loading averaged 0.1 $mM \cdot m^{-2} \cdot day^{-1}$, with 45% of the nitrogen input associated with the spring snowmelt period. Nitrogen and phosphorus were released from the lake at an average rate of 0.15 and 0.007 $mM \cdot m^{-2} \cdot day^{-1}$, respectively. The annual loss was estimated to be 57.9 mM nitrogen and 2.3 mM phosphorus $\cdot m^{-2}$. These calculations tend to illustrate that the daily rates of input or release of nutrients were approximately one order of magnitude less than rates which would be required to account for the observed fluctuations of the total nitrogen and phosphorus content in the lake. In addition, Georgetown Lake lost more nutrients both years than it received from the inflowing water.

Because of the limitations of the very simplistic mass balance approach, Tapp (1978) recommends either complex reservoir models that approximate the interactions that occur within a water body or, a more

Table 7. Chemical Analysis of Soil Conservation Service Test Wells, Collected 29 July, 1975, Georgetown Lake, Montana.

Well No.*	Total Dissolved Solids ($mg \cdot l^{-1}$)	$O\text{-}PO_4\text{-}P$ ($\mu g \cdot l^{-1}$)	$NO_3\text{-}N$ ($\mu g \cdot l^{-1}$)	$NH_3\text{-}N$ ($\mu g \cdot l^{-1}$)
14	346	69	127	94
50	436	50	254	51
51	431	10	86	16
58	439	25	145	14
4	399	23	114	16
10	175	16	225	15
19	125	33	17	61
23	78	38	5	90
25	89	22	45	11
36	89	17	23	11
Mean	261	30	104	38
(Stewart Mill) Spring	303	20	38	14

*See Figure 1 for well locations.

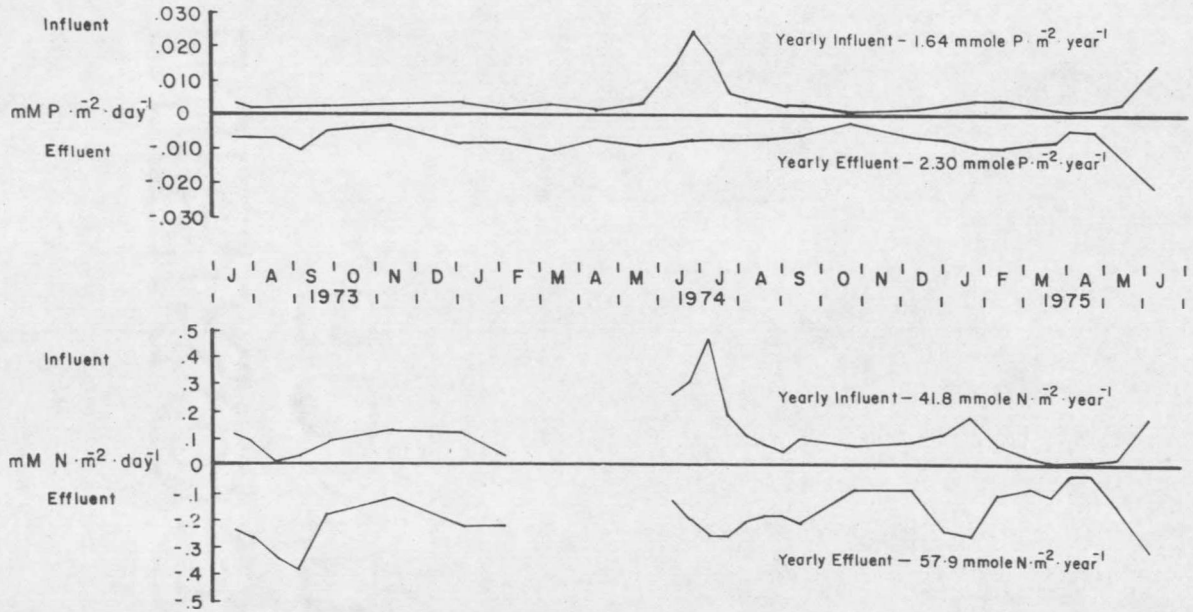


Figure 19. Seasonal Distribution of Nitrogen and Phosphorus Loading and Export Rates of Georgetown Lake, Montana, 1973-75.

simplistic approach that relates the input or the concentration of phosphorus in a water body to the physical properties of that water body, i.e., the Vollenweider approach.

The most commonly used expressions by the U. S. Environmental Protection Agency to assess limitations of phosphorus and nitrogen (Tapp, 1978) are those of Vollenweider (1975), Vollenweider and Dillon (1974), and Larsen and Mercier (1975). Georgetown Lake data used in all the above expressions (Fig. 20) indicated that Georgetown Lake was oligotrophic in the Vollenweider (1975) and Dillon (1974) models, and off the scale (i.e., oligotrophic due to the negative fraction of phosphorus retained) in the Larsen-Mercier (1975) model. In addition, using Georgetown Lake phosphorus loading in the regression equations derived by Oglesby (1977) and Schindler, et al. (1978), the calculated dependent values (chlorophyll, phytoplankton standing crop, and primary production) were underestimated for Georgetown Lake (Table 8).

Utilizing the 'trophic status' of Georgetown Lake and the Vollenweider-Dillon model, the U.S.E.P.A. (1976) as part of the National Eutrophication Survey, has suggested that actual phosphorus loading into Georgetown Lake should equal 4250 $kgP \cdot yr^{-1}$. Since the U.S.E.P.A. data could attribute only 18% of the loading to measurable sources, presumably surface inflows, the remainder was accounted for by 'submarine springs'. However, based upon the calculated yearly groundwater flow and the U.S.E.P.A. phosphorus

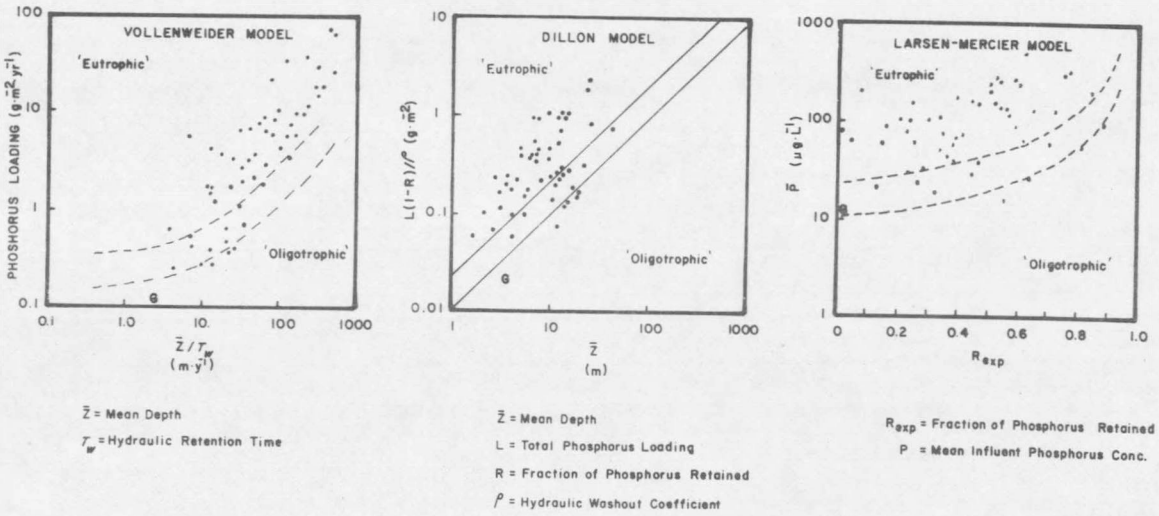


Figure 20. Comparison of Phosphorus Loading into Georgetown Lake, Montana, to Three Models Used by the U. S. Environmental Protection Agency. The mean point for Georgetown Lake is indicated by G.

Table 8. Comparison of Ice Free Season Predictions of Total Phosphorus (ΣP), Chlorophyll (CHL), Algal Standing Crop (S), and Primary Production (PP) Utilizing the Equation of Schindler, et al. (1978) and Oglesby (1977) to Measured Values in Georgetown Lake, Mt. 1973-75.

	DEPENDENT VARIABLE			
	ΣP ($mg \cdot m^{-3}$)	CHL ($mg \cdot m^{-3}$)	S (wet $mg \cdot m^{-3}$)	PP ($gC \cdot m^{-2} \cdot yr^{-1}$)
MEASURED VALUES	26	9	14000	130
Independent Variables of Schindler et al.				
ΣP	-	24	6600	63
L_p	9	3	1600	18
$L_p z^{-1}$	10	4	1700	21
$I_p V_o^{-1}$	12	4	1400	19
$\frac{I_p + M_p}{V_L + V_o}$	13	6	1700	25
$\frac{I_p V_o^{-1}}{1+\sqrt{T_w}}$	11	3	1500	20
Independent Variable of Oglesby				
Λ'_{mp}		3		

L_p = annual input of phosphorus ($mg \cdot m^{-2} \cdot yr^{-1}$) [50.]

$L_p z^{-1}$ = annual loading per unit volume ($mg \cdot m^{-3} \cdot yr^{-1}$) [10.2]

$I_p V_o^{-1}$ = annual average concentration of phosphorus in the inflow ($mg \cdot m^{-3}$) [32.3]
I_p = Total quantity of phosphorus received by the lake (mg) [7.4×10^8]
V_o = Volume of outflow (m^{-3}) [2.29×10^7]

$\frac{I_p + M_p}{V_L + V_o}$ = means of accounting for nonequilibrium conditions due to changes in I_p [27.8]
M_p = total mass of phosphorus in the lake the previous year (mg) [1.37×10^9]
V_L = lake volume (m^3) [5.28×10^7]

$\frac{I_p V_o^-}{1+\sqrt{T_w}}$ = the expression of Vollenweider (1976) [12.8]
T_w = water renewal time, $V_L \div V_o$ [2.3]

Λ'_{mp} = annual input of biologically available phosphorus (assumed to be total phosphorus for Georgetown Lake) calculated as being to a volume equivalent to that of the August mixed zone. [10.2]

NOTE: Values in brackets are those calculated from Georgetown Lake Data.

loading estimate, the mean groundwater concentration of phosphorus would have to be 35 to 82 times greater (Table 9) than those concentrations measured in test wells around Georgetown Lake (Table 7).

All of the measured values for Georgetown Lake indicate that Georgetown should be classified as meso-to-eutrophic, while the models predict an oligotrophic condition. This discrepancy is probably because of internal loading. The models were developed for lakes depending upon phosphorus added to the system and phosphorus concentrations at spring overturn.

Internal Nutrient Loading

Since this investigation was concerned with general limnological aspects of Georgetown Lake, detailed experimentation with respect to nutrient dynamics was not pursued. However, general facets of internal phosphorus and nitrogen exchange may be considered for Georgetown Lake with respect to available data and published information.

The total nutrient change within the water column, expressed as $mM \cdot m^{-2}$ in Figure 18, has typically been related to the transfer of material to or from the sediment. Nutrient loss from the water column has been attributed to sedimentation processes (Hutchinson 1941; Lean and Charlton 1977; Lee 1969; and Lehman and Sandgren 1978), while nutrient gain to the water column has been correlated to physical, chemical, or biological processes within the sediments and/or water column (Lee 1969). Since Georgetown Lake exhibited a shallow mean depth,

Table 9. Calculated Groundwater Phosphorus Concentration for Georgetown Lake, Montana, Based on USEPA (1976) Loading Estimate.

Calculated Yearly	
Mean Groundwater Volume	= $1.5 \times 10^6 m^3 \cdot yr^{-1}$
Mean Lake Area	= $1.14 \times 10^7 m^2$
Calculated Loading	= $52.5\ mgP \cdot m^{-2} \cdot yr^{-1}$
minus Calculated Groundwater Loading	= $1.8\ mgP \cdot m^{-2} \cdot yr^{-1}$
Annual Surface Loading	$50.7\ mgP \cdot m^{-2} \cdot yr^{-1}$
EPA (1976) Estimated Loading	= $4250\ kg \cdot yr^{-1} \cdot (10^6 mg \cdot kg^{-1} \div 1.14 \times 10^7 m^2)$
	= $372.8\ mgP \cdot m^{-2} \cdot yr^{-1}$
Surface Loading	= 50.7 (67.1 U.S.E.P.A. estimate)
Estimated Groundwater Loading	= $322.1\ mgP \cdot m^{-2} \cdot yr^{-1}$
Calculated Mean Groundwater Phosphorus Concentration Based on EPA Loading Estimate	= $\frac{322.1\ mgP \cdot m^{-2} \cdot yr^{-1} \cdot 1.14 \times 10^7 m^2}{1.5 \times 10^6 m^3 \cdot yr^{-1}}$
	= $2.448 \times 10^3 mg \cdot m^{-3}$ OR $2.45\ mg \cdot \ell^{-1}$
* Maximum Measured Groundwater Phosphorus Concentration	= $69 \mu g \cdot \ell^{-1}$ (or 35 times less than estimate)
* Mean Measured Groundwater Phosphorus Concentration	= $30\ \mu g \cdot \ell^{-1}$ (or 82 times less than estimate)

* See Table 7 for Analysis of SCS Test Well Survey

high biological activity, a calcium carbonate dominated system, prolonged ice cover, and large fluctuations in oxygen and carbon concentrations, nutrient fluxes and availability were a function of many interactions.

According to Stumm and Morgan (1970), a steady state between plant production and subsequent decomposition is a prerequisite for the maintenance of a constant chemical composition of the water (chemostasis). Most reported lakes have a spatial separation of production and decomposition, i.e., epilimnion and hypolimnion. However, as has been discussed previously with respect to oxygen and carbon dioxide, Georgetown Lake has an apparent seasonal separation of net production and net decomposition. On an annual basis, the relationships of Georgetown's mean total phosphorus to mean total carbon and mean total nitrogen concentrations are within the range presented by Schindler (1977, Fig. 21). This comparison of Georgetown Lake data indicates that the phosphorus to carbon to nitrogen ratio on a yearly average, was similar to conventional nutrient ratios for freshwater, which, coupled with Schindler's (1977) 'evolution of nutrient ratio' hypothesis, implies chemostatis on an annual basis. This appears to be contradictory with a net loss of phosphorus and nitrogen from the system (Fig. 19), but in terms of absolute numbers, the net phosphorus loss via surface waters amounted to less than 0.01% of the total phosphorus flux within the reservoir. As mentioned previously, however, chemostatis did not exist within seasons, but only on an annual basis.

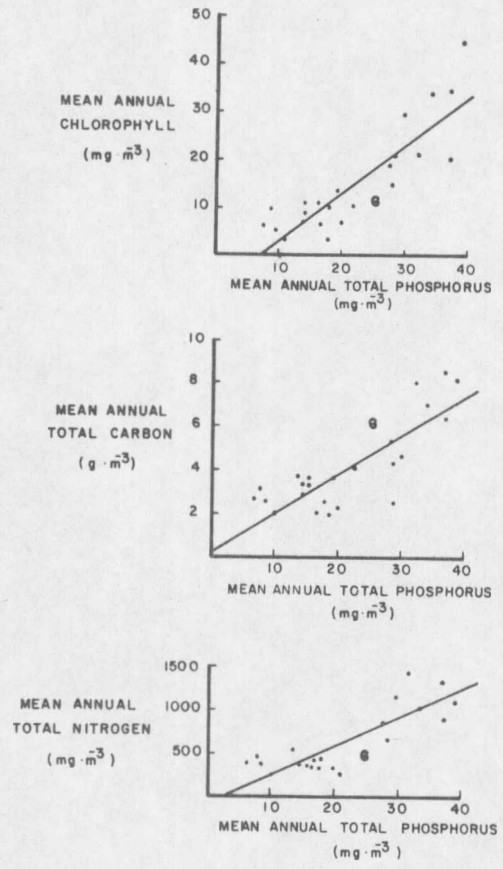


Figure 21. Comparison of the Annual Mean Total Phosphorus, Total Nitrogen, Total Carbon, and Chlorophyll Calculated from Georgetown Lake, Montana, to the Relationship Presented by Schindler (1977). The mean value for Georgetown Lake is indicated by G.

During the ice-free season, inorganic nutrients remained very low, often undetectable, while total nutrient concentrations fluctuated. Garrison (1976) observed similar fluctuations of total nutrients in Georgetown sediments during the same period. However, with the available data on Georgetown Lake, specific mechanisms with respect to the sediments and/or the macrophytes acting as a source or sink for nutrients cannot be ascertained. Usually, nutrient loss to the sediments is primarily in the form of organic matter, (principally as plankton or, as Lehman and Sandren (1978) reported, continual contributions from macrophytes) that settles on the sediment-water interface. The decomposition and subsequent mineralization rates of organic matter within the Georgetown sediments was probably very high during the summer since Garrison (1976) observed lower organic fractions relative to inorganic nutrient extractions during the summer. This conclusion agrees with Tilson, et al. (1980), who observed that decomposition rates were directly related to temperature. In addition, Hill (1979) determined that 20-60% of macrophyte biomass was mineralized within eight days. However, Lee (1969) and Mortimer (1971) reported that mineralization was not complete, and residual organics tended to accumulate and contribute to the sediment composition.

Mineralized nutrients are considered to be retained by the oxidized microzone that forms during the period of oxygenation (Hutchinson 1941; Lee 1969; Stumm and Morgan 1970; Mortimer 1971; and Golterman 1973). Additonal water column nutrient loss based upon chemical equilibria,

(e.g., ferric hydroxide-phosphate complexes (Lee 1969; Mortimer 1971), calcium phosphate (Stumm and Morgan 1970; Golterman 1973), and ion exchange with hydroxides (Lee 1969; Stumm and Morgan 1970; Gelin and Ripl 1978; Ripl and Lindmark 1978)) were all favored under the oxygenated-high pH conditions in Georgetown Lake during the ice free period. These forms of phosphorus are generally considered to be insoluble under oxidized conditions. There have, however, been a number of instances in which these phosphorus sources have become available to the phytoplankton. Traditionally, phosphorus has been considered to be transported to the water column by turbulent mixing (wind-induced turbulence, density currents, or macroinvertebrate movement, Lee 1969). Additionally, Lean and Charlton (1977) have reported input of phosphorus to the water column from the sediment in the absence of such processes at rates equal to or greater than 0.25 mM $P \cdot m^{-2} \cdot day^{-1}$. This rate is greater than most loading values reported by Vollenweider (1968) for eutrophic lakes. Lean and Charlton (1977) attributed these high sediment release rates to the formation of an anoxic zone after the deposition of organic matter. The August release of phosphorus reported by Lean and Charlton (1977) could be analogous to the increase of phosphorus in July-August of each year in Georgetown. Gelin and Ripl (1978) also reported that high phosphate exchange rates with the sediment during oxygenated periods in a shallow, Swedish Lake. Additional inputs of phosphorus have been attributed to macrophyte release (Carignan and Kalff, 1980). Lehman and Sandgren (1978)

could not find evidence of turbulent processes influencing nutrient input and also suggested that phosphorus release from macrophytes was the major source to the water column. However, they maintained that the total phosphate in the water column was controlled by the rate of algal sinking.

As mentioned previously, direct evidence for any of the mechanisms for Georgetown Lake is lacking. However, the morphometry, biological activity, and chemistry of the system were very similar to the conditions reported by the above authors. The lowest observed inorganic nitrogen to phosphorus ratios of 16:1 during 1973 (Fig. 22) indicate that phosphorus was in high demand the first summer. However, during the second summer, inorganic phosphorus was more available relative to inorganic nitrogen (observed ratios ranged from 1:1 to 50:1). The organic ratios (particulate plus dissolved fractions) generally ranged between 30:1 and 16:1, the former value reported by Schindler (1977) and the latter by Stumm and Morgan (1970) for 'mean' algal protoplasm. Higher ratios, possibly indicating high phosphorus demand, are associated with periods of nitrogen fixation (July-August-September). Also, the high ratios of organic fractions could be indicative of lower turnover times of nitrogen and/or more residual compounds relative to phosphorus (Hutchinson 1941; Lean and Charlton 1977; Liao and Lean 1978; Ripl and Lindmark 1978). The iron to inorganic phosphorus ratios ranged from 0.5:1 to 50:1 with the three major peaks associated with very low phosphorus concentrations (Fig. 22). However,

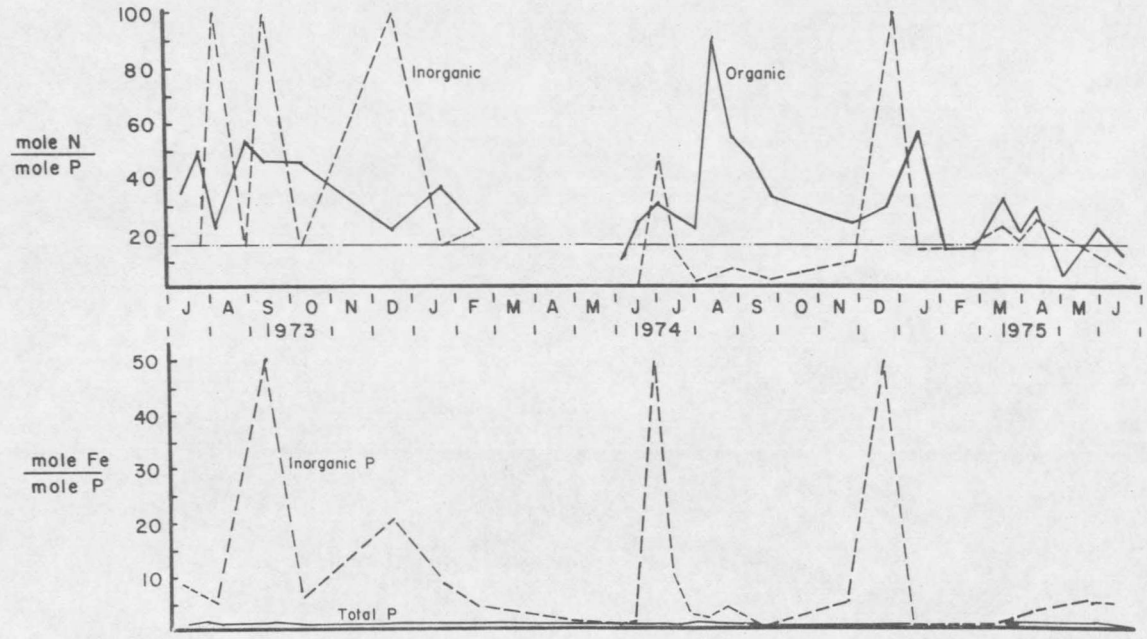


Figure 22. Seasonal Distribution of Molar Nitrogen to Phosphorus and Iron to Phosphorus Ratios in Georgetown Lake, Montana, 1973-75.

the total iron to total phosphorus ratios were consistently between 0.1 and 1.0. This data indicates that iron-phosphate complexes were the major forms of phosphates that were available, even though rapid phosphate uptake occurred during the summer. The iron-phosphate ratios again support the important role of internal nutrient cycling within the lake.

The period of ice cover exhibited gradual increases in inorganic phosphate and inorganic nitrogen, principally ammonia (Fig. 15 and 16). Since water temperatures were reduced, biological decomposition rates were probably also lower than during the ice-free season. This again was evidenced by Garrison's (1976) observation of increased organics in the sediment relative to the inorganic fraction during this period. Even with decreased decomposition rates, inorganic nutrients accumulated as low light levels and temperatures restricted plankton growth and mineral uptake rates. Also, accumulation of inorganic nutrients undobutedly occurred from sediment release due to reduced pH (see section on oxygen and carbon dioxide) and lowered oxidation-reduction potential. A chemically reduced environment was evidenced by an accumulation of ferrous iron, and a decrease in sulfate (Fig. 23), presumably through a reduction to sulfide. Sediment adsorptive properties were decreased and chemical solubilities were altered under the reducing conditions, allowing mineralized nutrients to diffuse from the sediment (Hutchinson 1941; Lee 1969; Mortimer 1971; Golterman 1973: Lean and Charlton 1977; and Ripl and Lindmark 1978).

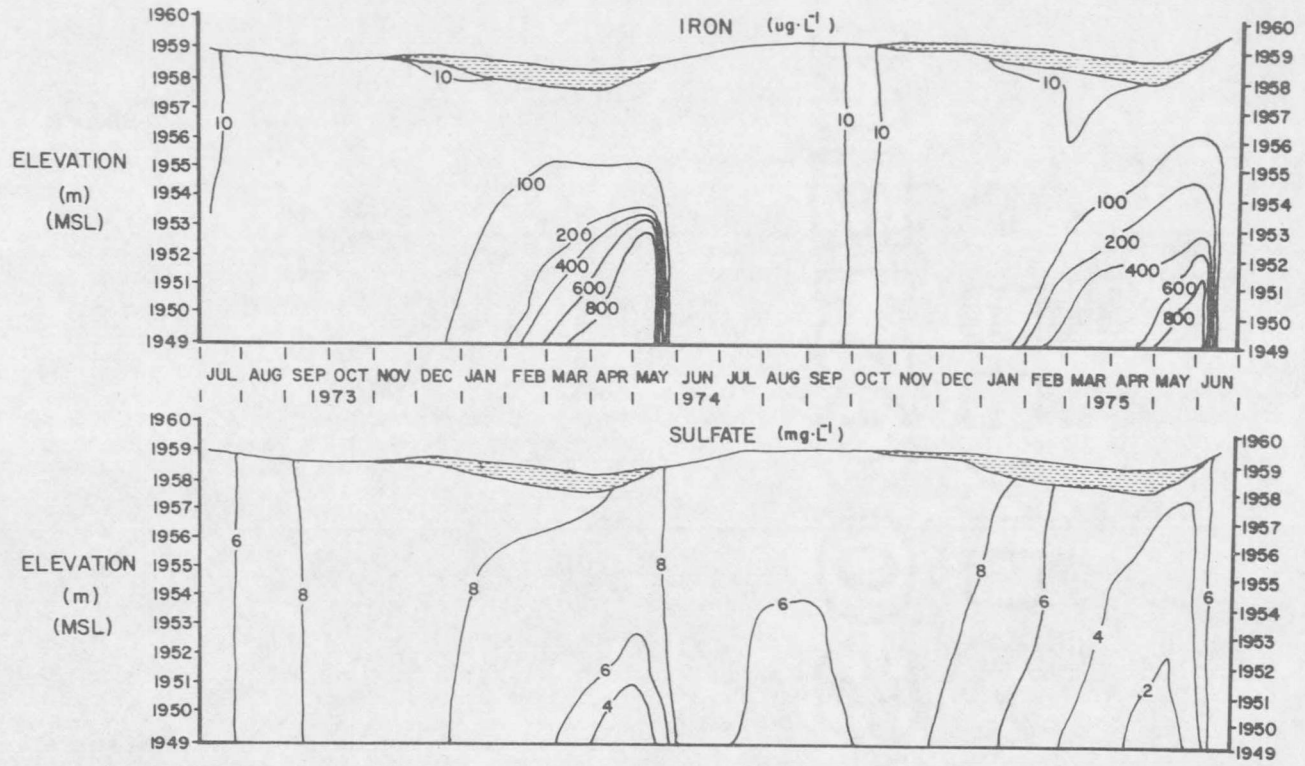


Figure 23. Seasonal and Vertical Distribution of Concentrations of Iron and Sulfate in Georgetown Lake, Montana, 1973-75.

PHYTOPLANKTON

Taxonomic Composition and Seasonal Change

The phytoplankton collections yielded 110 identified taxa (Table 10), with most taxa encountered infrequently. Undoubtedly, the taxa list is incomplete, since the occurrence of rare species is a function of the collection and enumeration technique, and the sample size (Hurlbert 1971).

The Chlorophyta (green algae) were represented by at least 22 genera and species. Phacus, the only observed Euglenophyte, was found in one sample. The Chrysophyta were the most diverse division and were represented by three classes, 22 genera, and 61 species. The majority of the Chrysophyte biomass was accounted for by Dinobryon sertularia, Cyclotella bodanica, Stephanodiseus astrea, Asterionella formosa, Fragillaria crotenensis, and Synedra sp. The four species of dinoflagellates, although in low numbers, made a noticeable contribution to the total biomass due to their large cell size. The Cyanophyta (blue-green algae) were represented by five genera and seven species, with Anabaena flos-aquae observed to exhibit the largest standing crop of any phytoplankton taxon. The Cryptophyceae, principally Cryptomonas ovata, made a substantial contribution to the total biomass in every sample.

Seasonal changes of phytoplankton taxa have been considered to be primarily a function of physical factors (e.g., temperature, light, and turbulence), chemical factors (e.g., nutrient concentration and organic

Table 10. List of Phytoplankton Taxa Collected From Georgetown Lake, Montana, 1973-1975.

Taxa	Mean Cell Volume $u^3 \cdot m^{-3}$
Division Chlorophyta	
Class Chlorophyceae	
Order Volvocales	
Family Chlamyomonadaceae	
Chlamydomonas° sp. Ehrenberg	35
Carteria° sp. Diesing	440
Family Volvocaceae	
Eudorina unicocca° Smith	900
Pandorina morum° Bory	525
Order Tetrasporales	
Family Palmellaceae	
Gleocystis gigas (Kuetz) Lagerheim	2150
Sphaerocystis schroeteri Chodat	900
Order Ulotrichales	
Family Ulotrichaceae	
Ulothrix variabilis° Kuetzing	300
Family Protococcaceae	
Protococcus° sp. Agardh	30
Order Chlorococcales	
Family Micractiniaceae	
Golenkinia radiata* (Chodat) Wille	4200
Family Dictyosphaeriaceae	
Dictyosphaerium pulchellum° Wood	310
Family Hydrodictyaceae	
Pediastrum duplex[4] Meyer	3000
Sorastrum americanum* (Bohlin) Schmidle	30
Family Oocystaceae	
Ankistrodesmus falcatus (Corda) Ralfs	100
A. spiralis° (Turner) Lemmermann	70
Chlorella° sp. Beijerinek	40
Chodatella longiseta° Lemm.	1000
Oocystis gloeocystiformis Borge	40
O. pusilla° Hansgirg	2450
Planktosphaeria gelatinosa Smith	65
Tetraedron minimum (A. Braun) Hansgirg	50
T. trigonum (Naeg.) Hansgirg	1750
Family Scenedesmaceae	
Scenedesmus bijuga (Turp.) Lagerheim	4300
S. quadricauda (Turp.) de Brebisson	60
Order Zygnematales	
Family Zygnemataceae	
Mougeotiopsis calospora° Palla	226,200
Family Desmidiaceae	
Cosmarium tumidum° Wolle	202,700
Stauratrum aspinosum Wolle	3225
S. eustephanum° (Ehrb.) Ralfs	268,000
Unidentified Chlorophyta	
microplankton$_a$	35
microplankton$_b$	65
microplankton$_c$	525
microplankton$_d$	85
microplankton$_e$	12
Division Euglenophyta	
Class Euglenophyceae	
Order Euglenales	
Family Euglenaceae	
Phacus° sp. Dujardin	4400
Division Chrysophyta	
Class Xanthophyceae	
Botryococcus brauntii* Kutzing[1,4]	3550
Class Chrysophyceae	
Order Chrysomonadales	
Family Ochromonadaceae	
Dinobryon sertularia Ehrenberg°	580
Class Bacillariophyceae[2]	
Order Centrales	
Family Coscinodiseaceae	
Cyclotella antiqua* W.Sm.	5300
C. comta (Ehr.) Kutz	1950
C. bodanica Eulenst	6870
C. glomerata Bachmann	150
C. meneghiniana* Kutz	3150
Melosira distans (Ehr.) Kutz	950
M. granulata* (Ehr.) Ralfs	570
Stephanodiscus astrea (Ehr.) Grun	760
Order Pennales	
Suborder Fragilarineae	
Family Diatomaceae	
Diatoma hiemale* (Roth)	2750
Family Fragilariaceae	
Asterionella formosa Hass	235
Fragilaria brevistriata* (Pat.) Hust	90
F. capucina Desm	450
F. construens (Ehr.) Grun	135
F. crotenensis Kitton	565
Synedra capitata* Ehr.	35,350
S. parasitica* (W.Sm.) Hust	135
S. ulna (Nitz.) Ehr	3050
S. sp.	80

Table 10. (Continued) List of Phytoplankton Taxa Collected from Georgetown Lake, Montana, 1973-1975.

Taxa	Mean Cell Volume $u^3 \cdot m^{-3}$
Family Achnanthaceae	
Achnanthes hungarica* (Grun.) Grun	170
A. lancolata (Breb.) Grun	625
A. minutissima Kutz	70
Cocconeis diminuta* Pant	450
C. placentula Ehr.	8600
Rhoicosphenia curvata* (Kutz.) Grun	650
Family Tabellariaceae	
Tabellaria fenestrata* (Lyrgb.) Kutz	5450
Suborder Naviculineae	
Family Naviculaceae	
Navicula bacillum* Ehr.	2350
N. cryptocephala Kutz	150
N. cuspidata* (Kutz.) Kutz	12,500
N. pupula* Kutz	200
N. radiosa* Kutz	2050
N. rhynchocephala Kutz	875
N. salinarum* Grun	450
N. tripunctata (O.F. Mull) Bory	2000
Pinnularia biceps* Greg	6200
P. nodosa* (Ehr.) W.Sm.	4400
Family Gomphonemataceae	
Gomphonema acuminatum Ehr.	1450
G. constrictum Ehr.	1450
G. olivaceum (Lyngbye) Kutz	500
G. parvulum* (Kutz.) Grunow	400
G. sphaerophorum Ehr.	1650
G. subtile* Ehr.	900
Family Cymbellaceae	
Amphora ovalis* Jutz	14,500
Cymbella affinis Kutz	1800
C. microcephala Grun.	100
C. prostrata (Berkeley) Cleve	2750
C. turgida* (Greg.) Cleve	17,700
C. ventroicosa Kutz	1400
Epithemia sorex Kutz	3150
E. turgida (Ehr.) Kutz	35,600
E. zebra (Ehr.) Kutz	35,000
Rhopalodia gibba (Ehr.) O. Mull.	31,500
Suborder Surirellineae	
Family Nitzschiaceae	
Nitzschia filiformis* (W. Smith) Hust	700
N. fonticola Grun	160
N. hantzschiana* Rabh.	650
N. linearis W. Smith	3050
N. palea (Kutz.) Smith	550
N. sigmoida* (Ehr.) W. Smith	17,800
N. sublinearis Hust.	2275
Family Surirellaceae	
Cymatopleura solea* (Breb.) W. Smith	290,300
Division Pyrrophyta	
Class Dinophyceae	
Order Gymnodiniales	
Family Gymnodiniaceae	
Gymnodinium pulustre Schilling	88,400
Order Peridiniales	
Family Glenodiniaceae	
Glenodinium pulvisculus (Ehr.) Stein	5500
Family Peridiniaceae	
Peridinium gatunense Nygaard	130,900
Family Ceratiaceae	
Ceratium hirundinella* (O.F.Muell.) Dujardin	73,800
Division Cyanophyta[3]	
Class Myxophyceae	
Order Chroococcales[4]	
Family Chroococcaceae	
Anacystis cyanea* (Kutz.) Drouet and Daily	413,100
A. incerta* (Lemm.) Drouet and Daily	
A. marina (Hansgirg) Drouet and Daily	225
Gomphosphaeria lacustris Chodat	365
Order Oscillatoriales[5]	
Suborder Oscillatorineae	
Family Oscillatoriaceae	
Oscillatoria rubescens° de Candolle	5025
Suborder Nostochineae	
Family Nostocaceae	
Anabaena flos-aquae (Lyngbye) Debrebisson	1350
Family Scytonemataceae	
Fremyella diplosiphon° (Gomont) Drouet	6350
Unidentified Cyanophyta[5]	210
Division Uncertain	
Class Cryptophyceae[6]	
Order Cryptomonadales	
Family Cryptochrysidaceae	
Rhodomonas lacustris Pascher, Ruttner	100
Family Cryptomonadaceae	
Cryptomonas erosa Ehrenberg	575
C. ovata Ehrenberg	5500

[1] There is disagreement as to the classification of Botryococcus, for discussion, see Smith (1950) and Prescott (1962).
[2] Patrick and Reimer (1966) consider the Bacillariophyta as a division, with a class Bacillariophceae, the orders not being the Centrales and Pennales, but rather what Smith (1950) defines as suborders.
[3] The taxonomy of the Cyanophyta is based on revisions made by Drouet and Daily, in Edmondson.
[4] Mean cell volume was based on the average number of cells per colony.
[5] Mean cell volume was based on a trichome length of 100 um
* Taxa were encountered in only a few samples.
° Identification and/or the presence of taxa were based on living samples.
[6] Prescott (1962) considers this class belonging to the division Pyrrophyta, however, Rhodomonas is not mentioned by Prescott (1962).

materials), and biological factors (e.g., predation and competition) (Hutchinson 1967), The same criteria are usually applied to total phytoplankton abundance. However, since detailed knowledge of the physiology of individual species is lacking, inferences on dominant or indicator species are typically based upon relative abundance and/or presence or absence in relationship to physical and chemical data. Riley et al. (1949), Smayda (1974), Hulburt (1970), and Titman and Kilhan (1976) maintained that cells with higher sinking rates may have an advantage in turbulent water due to higher nutrient uptake at lower depths. Recently, however, Schindler (1977) has advocated the use of nitrogen to phosphorus ratios as a determinant of the abundance of species capable of nitrogen fixation. Furthermore, Porter (1977), has stressed the potential importance of grazing to the observed relative abundance phytoplankton. In addition, Laws (1975) and Harris (1978) suggested that certain algae may be favored based upon their surface to volume ratios as related to metabolic activity (respiration and photosynthesis) and/or nutrient uptake rates.

Seasonal change of the relative abundance of the dominant phytoplankton taxa in Georgetown Lake (Fig. 24) appeared related to phosphorus availability, relative to nitrogen, and zooplankton grazing. Immediately after the ice melted, the phytoplankton were dominated by small cryptomonads and green algae. However, as the phosphorus was depleted to very low levels, especially relative to nitrogen, Dinobryon sertularia increased.

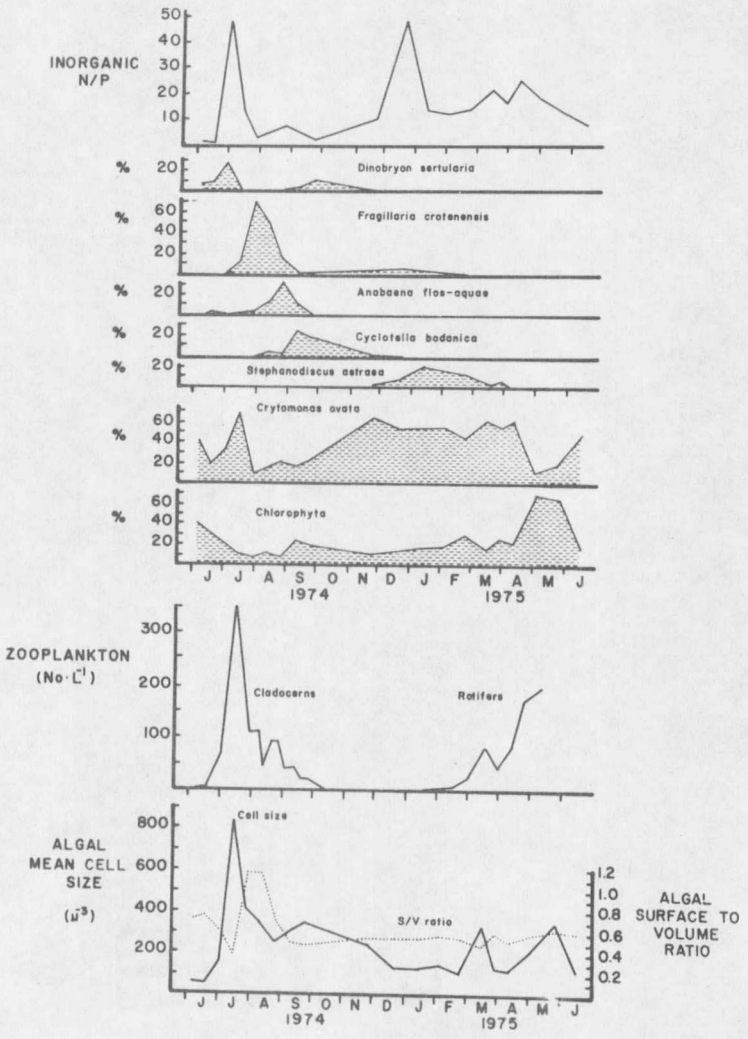


Figure 24. Seasonal Distribution of the Relative Abundance of the Major Phytoplankton Taxa Compared to Inorganic N/P Ratios, Zooplankton Concentration, and Algae Size in Georgetown Lake, Montana, 1974-75.

Hutchinson (1967) reported an increase of Dinobryon under similar conditions. At the same time, the percentage of small Chlorophytes was decreasing as the filter feeding zooplankton, principally Bosmina, Ceriodaphnia quadrangula and Chydorus sphaericus (Geer 1977) increased. The preference for small cells and the extent of grazing pressure by these zooplankton is reflected in the rapid change to a phytoplankton assemblage of larger cells with smaller surface to volume ratio, as suggested by Porter (1977).

At the time of maximum zooplankton concentration, the inorganic nitrogen to phosphorus ratio decreased as Fragillaria crotonensis began increasing. Immediately after the zooplankton maximum, F. crotonensis reached its maximum relative abundance. The mean cell size decreased, perhaps reflecting reduced grazing pressure, and the mean phytoplankton surface to volume ratio increased to the maximum observed value. These events suggest that F. crotonensis preferentially used more nitrogen relative to phosphorus, but that nutrient demand was high as evidenced by the shift to higher surface to volume ratios (Harris 1978). As F. cortonensis declined, Anabaena flos-aquae increased. Hutchinson's (1967) review described this species shift as related to nitrogen depletion by F. crotonensis to such low levels as to favor the growth of a species capable of nitrogen fixation, in this case Anabaena flos-aquae. Geer (1977) attributed a decrease of Daphnia to inhibited reproduction, growth, and survival due to the poor food source of Anabaena flos-aquae.

As Anabaena decreased in August and September, Chlorophytes and Cyclotella bodanica increased, probably reflecting less grazing pressure and more nutrient availability. This was evidenced by a reduced phytoplankton surface to volume ratio at this time (Fig. 24). Hutchinson (1967) reported that C. bodanica was typically found in the autumn phytoplankton of many temperate lakes.

With the onset of ice cover, Cryptomonas ovata, Rhodomonas lacustris, and Glenodinium pulvisculus were the dominant taxa observed. All of these organisms were motile and capable of both autotrophic and heterotrophic growth and all appeared to have a distinct advantage due to diversified habits and low light requirements. Stephanodiscus astrea, a cold water form (Hutchinson 1967), also appeared to be adapted to low light conditions. The constant algal surface to volume ratio throughout the period of ice cover indicates that nutrient availability had little effect on the relative abundance of taxa. However, as light intensity increased under the ice (Fig. 3), the small Chlorophytes also increased rapidly and appeared to reverse the trend of increasing nitrogen to phosphorus ratios. These data indicate that nitrogen was preferentially utilized by the green algae as compared to phosphorus. Rotifer grazing, as evidenced by a general increase of mean algal cell size, appeared to affect the relative abundance of algae by the utilization of the small green algae as a food source. By the time the ice melted, the major component of the phytoplankton assemblage was Cryptomonas ovata and, to a lesser degree, small Chlorophytes.

Phytoplankton Standing Crop and Organic Carbon

The phytoplankton standing crop, expressed as cell volume per m^2 (Fig. 25) was generally greatest during July, August, and September of each year. Minimum values were generally observed under the ice. Anabaena flos-aquae reached the largest observed standing crop of 190,000 $mm^3 \cdot m^{-2}$ on 10 September 1973. The following year, the maximum crop of Anabaena was approximately 20 times less. Cryptophyceae standing crops were also observed to be greater during 1973-74, especially under the ice. Chrysophyta, principally Fragillaria crotonensis, had a slightly greater standing crop in the summer of 1974 as compared to 1973. However, both years exhibited an increase in standing crop shortly before the ice melted.

Chlorophyll concentrations, as mg Chl a $\cdot m^{-2}$ (Fig. 25), generally showed the same trends as the phytoplankton cell volume data. However, the magnitude of differences between chlorophyll values was much less than that observed for algal cell volume. This characteristic was especially apparent in April 1974, when chlorophyll values exceeded those measured in August 1974, but the total algal cell volume was twice as great in August. Also, the phytoplankton biomass was 20 times greater in August 1973 than in August 1974, but the chlorophyll values were only twice as great in August 1973. The relative amount of chlorophyll to phytoplankton carbon, calculated from cell volumes using the equations of Strathman (1967), generally were greater under the ice than during the ice-free months (Fig. 25). The lowest ratios, 5 to 10 µg Chl·mg

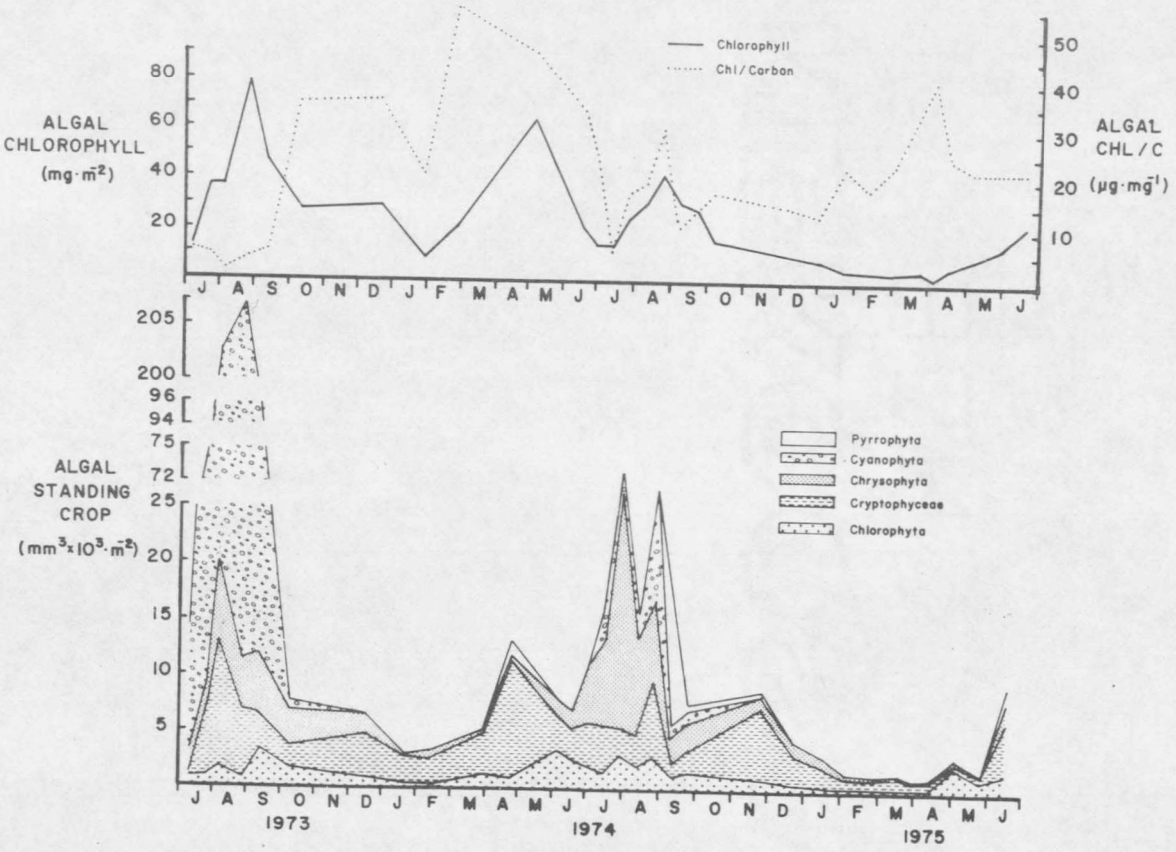


Figure 25. Seasonal Distribution of Algal Chlorophyll, Algal Chlorophyll to Carbon Ratio, and Standing Crop of the Major Phytoplankton Devisions from Georgetown Lake, Montana, 1973-75.

phytoplankton carbon^{-1}, were observed during the large Anabaena bloom in 1973. The 1974 summer ratios ranged between 10 and 30 µg Chl·mg C^{-1}. Winter ratios were typically between 15 and 55 µg Chl·mg C^{-1}. These chlorophyll to carbon quotients encompassed the entire ranges reported by Steele and Baird (1961, 1962) and Healey and Hendzel (1979) for algal cultures of variable ages. Changes in the chlorophyll to phytoplankton carbon ratios have been interpreted as either: a)a 'Chlorella type' light adaptation, which is characterized by an inverse relationship between light intensity and chlorophyll content (Soeder and Stengel 1974); b) a density dependent relationship (McQuate 1956; Wright 1960), which presumably results from decreased availability of nutrients, primarily nitrogen (Healey and Hendzel 1979); or c) to a lesser extent, a temperature dependent variation which results in a lower chlorophyll content per cell at lower temperatures (Harris 1978). The seasonal trend of chlorophyll per phytoplankton carbon in Georgetown Lake clearly rules out the reported temperature affect. However, light adaptation and/or density dependent nutrient responses probably account for the observed variation. These two phenomena probably were responsible for the overestimate of the mean chlorophyll concentration using total phosphorus as the independent variable (Table 8).

Based upon the results tabulated by Likens (1975), the mean summer chlorophyll and phytoplankton biomass concentrations indicate that Georgetown Lake may be classified as meso-eutrophic to eutrophic. However,

comparison of chlorophyll vertical distribution and total organic carbon variability in the water column (Fig. 26) indicates that organic carbon distribution was not well defined with respect to phytoplankton abundance. Furthermore, throughout most of the two-year period, phytoplankton carbon contributed less than 5% to the total organic carbon pool (Fig. 27). The only exception was during the 1973 Anabaena bloom when, at maximum, the phytoplankton contributed approximately 50% of the total carbon mass. Another, somewhat independent indicator of the minor contribution of phytoplankton to the total organic carbon mass was the correlation ($r=0.58$, $p<0.01$) of total organic carbon to the vertical extinction coefficient of light (Fig. 28). Phytoplankton concentration, as measured by chlorophyll, showed little relationship to light extinction. These comparisons indicate that, although Georgetown Lake was relatively rich with respect to phytoplankton, other sources of organic matter probably dominated the system.

As with nutrients, organic matter may be of allochthonous or autochthonous origin. Organic inputs to Georgetown Lake via surface waters were probably negligible, due to the low concentrations of organic carbon in the tributaries (Table 4) and a net loss of organic carbon from the system (Knight et al. 1976). Autochthonous sources reported by Wetzel and Rich (1973) from Lawrence Lake, Michigan, a small, temperate, hardwater lake, were 25.4% from the phytoplankton, 22.1% from the epiphytic algae, 1.2% from epipelic algae, and 51.3% from the macrophytes. Presumably,

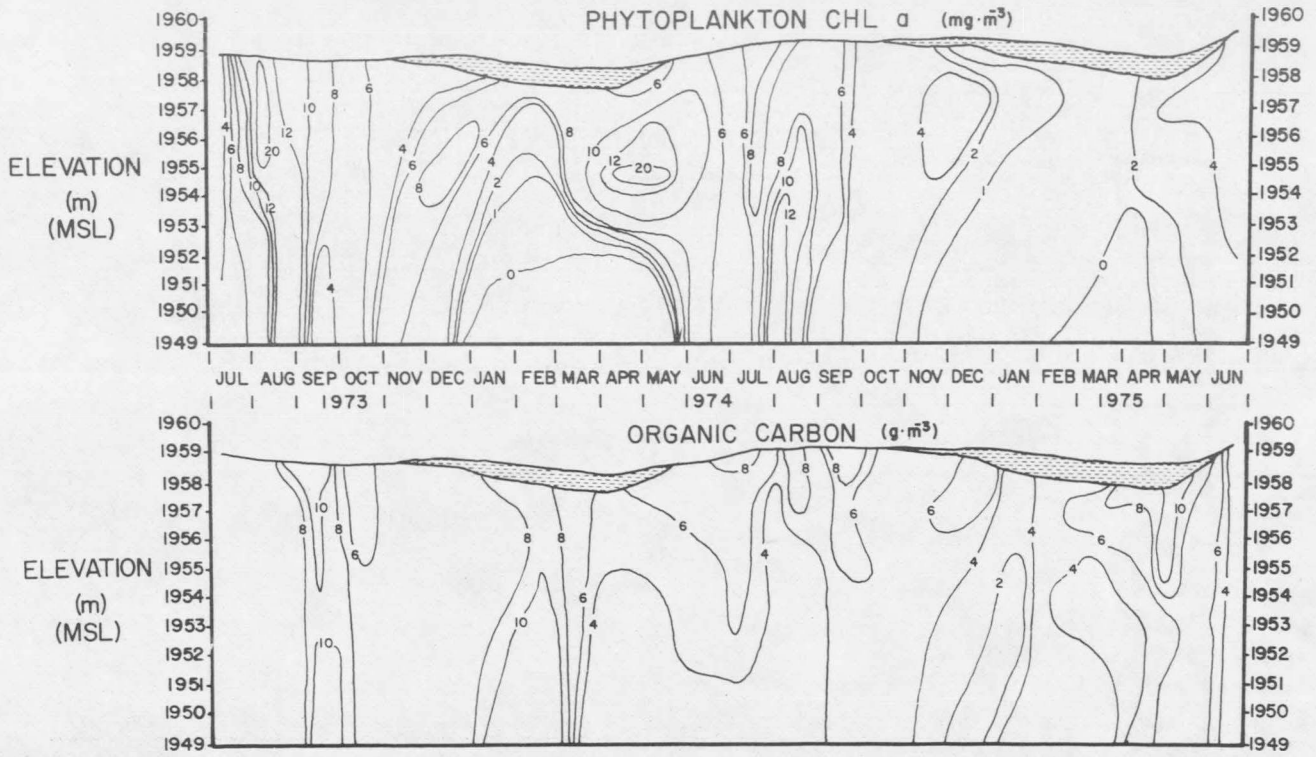


Figure 26. Seasonal and Vertical Distribution of Phytoplankton Chrlorophyll and Total Organic Carbon Concentrations in Georgetown Lake, Montana, 1973-75.

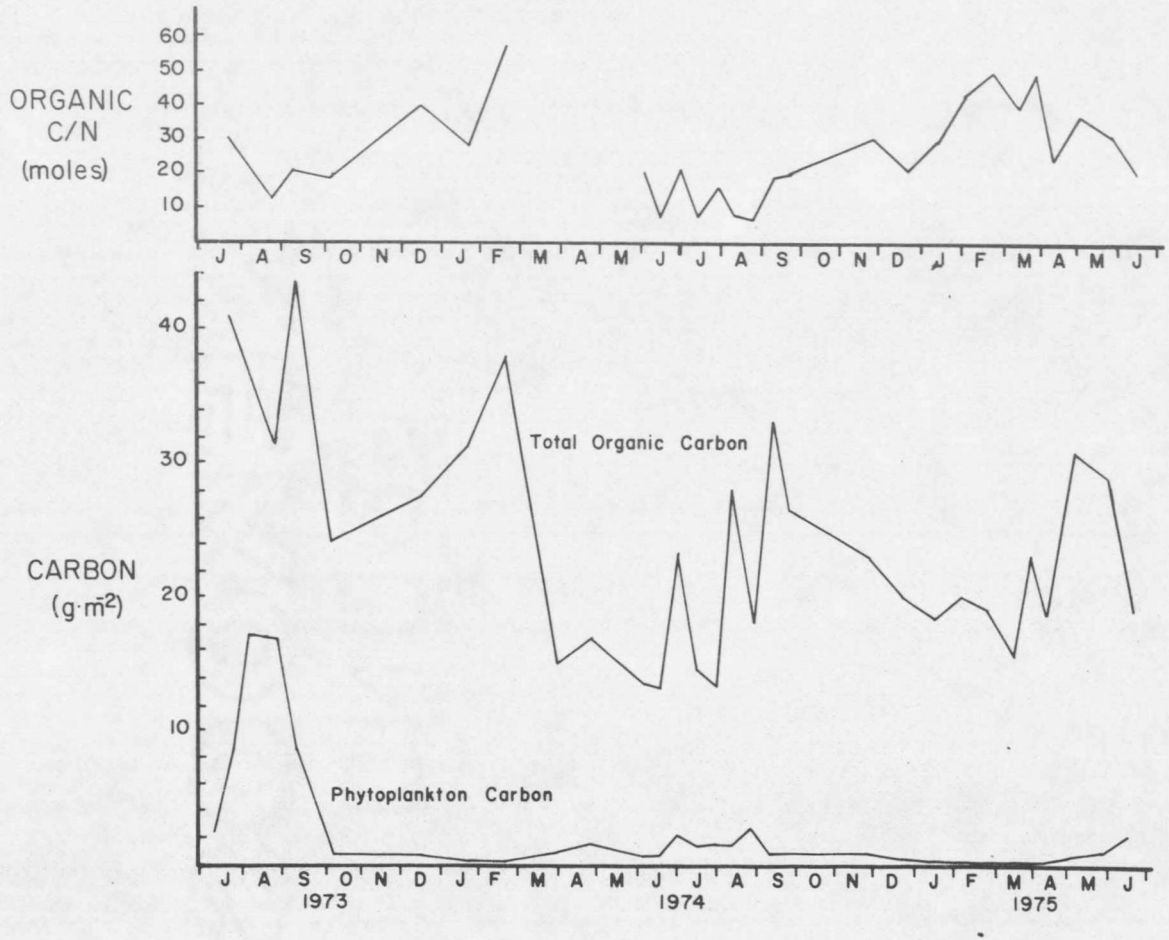


Figure 27. Seasonal Distribution of Organic Carbon to Organic Nitrogen Ratios, Total Organic Carbon, and Phytoplankton Carbon in Georgetown Lake, Montana, 1973-75.

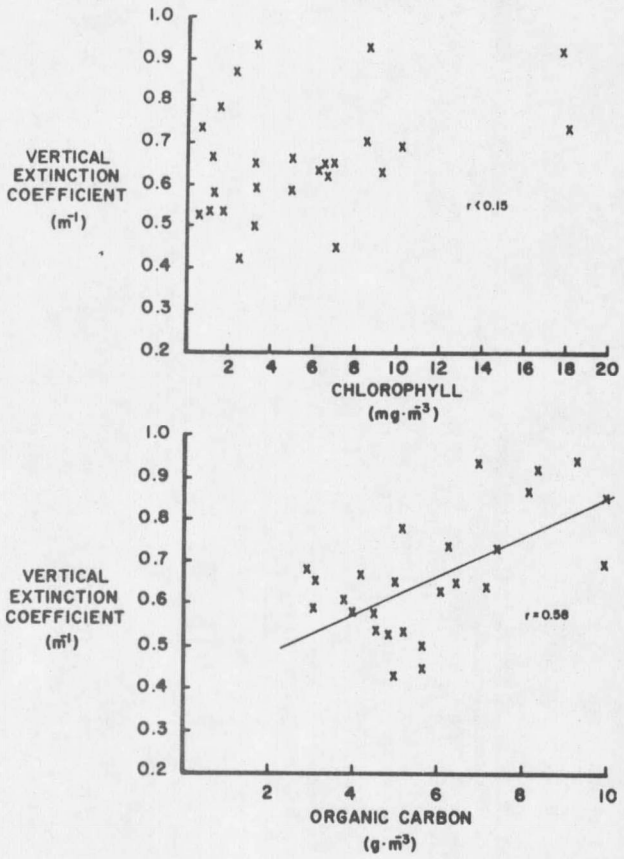


Figure 28. Vertical Extinction Coefficient of Light as a Function of Algal Chlorophyll and Organic Carbon Concentrations in Georgetown Lake, Montana, 1973-75.

because of the extensive macrophyte beds, autochthonous inputs to Georgetown Lake would be somewhat similar to those estimated for Lawrence Lake. The Georgetown summer carbon to nitrogen ratios, which ranged between 10:1 and 30:1 (Fig. 27), were generally indicative of the macrophyte C/N ratios of 20:1 (Wetzel 1975) and 26:1 (calculated from Hutchinson 1975) rather than phytoplankton ratios of 3:1 to 6:1 presented by Strickland (1960), Stumm and Morgan (1970), Banse (1974), and Healey and Hendzel (1979). However, as pointed out by Golterman (1975) and Rich and Wetzel (1978), the measured mass of detrital carbon is a function of turnover rate (i.e., input rates and bacterial decomposition). The organic carbon turnover rates during the ice-free season in Georgetown were probably substantial as evidenced by greater fluctuations of the organic carbon and the C/N ratios (Fig. 27). During the period of ice cover, organic carbon exhibited more gradual changes and the carbon to nitrogen ratio generally increased to a maximum value of 60:1. These data suggest that inputs and/or decomposition rates were reduced relative to summer turnover rates, and that nitrogen was used preferentially, leading to an accumulation of refractory organic compounds, (Stumm and Morgan 1970; Wetzel 1975).

Even though the phytoplankton were not considered the major source of organic carbon, the large Anabaena bloom observed in the summer of 1973 did contribute a substantial portion of the organic carbon pool (Fig. 27). The difference in the total phytoplankton standing crop

between the two summers is probably indicative of nutrient availability. Since the incident light and temperature were similar both years (Figs. 3 and 5), and the concentrations of nitrogen and phosphorus were not substantially different (Fig. 18), the hypothesis of nutrient availability is consistant with the concept of internal loading presented in the Nitrogen and Phosphorus section. Within the limits of the light, temperature, and mixing regimes, phosphorus is usually considered to set the maximum algal standing crop (Lean and Charlton 1977; Schindler 1977; Scavia 1979). As mentioned previously, major sources of phosphorus to the water column were probably sediment exchange and macrophytes. However, at lower water levels, the area available for phosphorus exchange (sediments and particularily macrophytes) would increase relative to the water volume. Such a morphometric change would have a net effect of increased phosphorus availability to the plankton. A comparison based on the relative differences between summer mean depths and total phosphorus, (Table 11) indicates that the percent difference of mean depth (6.85%) was large enough to increase the available phosphorus (18.5%). This comparison tends to support Rawson's (1939) hypothesis that the contribution of the littoral area (i.e., internal loading) geometrically increases as the mean depth decreases. However, the algal carbon to total phosphorus quotients (Table 11) substantially deviate from Stumm and Morgan's (1970) average algal ratio of 106 moles carbon to one mole of phosphorus. This deviation could possibly reflect phosphorus deficiency

Table 11. Comparison of Summer Maximum Phytoplankton Standing Crops and Maximum Total Phosphorus to the Mean Depths of Georgetown Lake, Montana, 1973 and 1974.

Algal Standing Crop ($gC \cdot m^{-2}$)		Total Phosphorus ($mgP \cdot m^{-2}$)	Algal Carbon ÷ Total Phosphorus (Molar)	Mean Depth (m)
1973 Summer Maximum	17.0	205	219	4.35
1974 Summer Maximum	2.7	173	43	4.67
Difference	14.3	32	-	-0.32
Percent Difference	517%	18.5%	-	6.9%

during the 1974 summer algal bloom, luxury uptake the second summer, or that all of the measured total phosphorus was not available to the algae.

Within the limits of phosphorus availability, nitrogen appeared to be the most deficient nutrient as evidenced by the presence of an algal species capable of nitrogen fixation, in this case Anabaena flos-aquae. This apparent nitrogen deficiency is again consistent with the concept of nutrient turnover, since, as originally suggested by Birge and Juday (1934), nitrogen liberation, hence turnover, was considered to be substantially less than for phosphorus. The use of isotopes (P^{32} and/or N^{15}) have provided estimates of phosphorus turnover as low as 1-3 minutes and of nitrogen turnover on the order of tens of minutes or longer (Rigler 1956, 1964; Peters and Lean 1973; Lean and Nalewajko 1976; Lean and Charlton 1977; DePinto and Verhoff 1977; Liao and Lean 1978). These short turnover times were generally reported where concentrations were low but nutrient demand was high, which appeared to be the case in Georgetown. One other interesting note contrasting the phytoplankton standing crop between the two summers is that the nitrogen content in the water column was essentially the same both summers (Fig. 18), even though the Anabaena crop was 20 times larger. This comparison, in addition to the low chlorophyll to carbon ratios observed during the summer of 1973 (Fig. 25), indicate that nitrogen fixation was substantially less on a per cell basis in 1973. Lean and Charlton (1977) attributed similar decreases of nitrogen fixation rates to iron deficiences at times of high production and biomass.

Phytoplankton Production and Community Respiration

Throughout previous sections of this report, the implication was made that phytoplankton were not the dominant primary producer in Georgetown Lake. However, since the understanding of biological productivity may be regarded as the central theme of limnology, the intent of this section is to evaluate the overall phytoplankton production with respect to lake metabolism. This discussion must be confined to the period from June 1974 to June 1975 since in situ rate measurements were not made the first year.

Daily rates of photosynthesis expressed on an areal basis were calculated from volume weighted rate measurements linearized with the total daily incident light intensity (Table 12). Utilizing a direct proportionality of photosynthesis to light intensity would tend to slightly overestimate the daily photosynthetic rate (Strickland 1960; Vollenweider 1974). Daily respiration rates were based upon measured hourly rates expanded to 24 hours (Table 12). Since all three techniques were subject to numerous errors (Harris 1978), the daily gross photosynthetic rates measured by the oxygen and pH (CO_2) methods were compared to the daily total ^{14}C (particulate and filtrate fractions) uptake rates. Relatively good agreement ($r = 0.95$, molar ratio=1.06 O_2:1 C) was found between total ^{14}C uptake and oxygen gross photosynthesis (Fig. 29). Gross photosynthesis, measured by the pH method, exhibited more variability than the oxygen method, but the relationship to total ^{14}C was statistically significant ($r=0.88$, $p < 0.01$).

Table 12. Daily Rates of Phytoplankton Production and Community Metabolism Measured by the Light and Dark Bottle Oxygen, pH, and ^{14}C Methods in Georgetown Lake, Montana, 1974-75.

	RESPIRATION			PHOTOSYNTHESIS				MASS	
DATE	O_2 dark bottle $gO_2 \cdot m^{-2} \cdot day$	pH dark bottle $gC \cdot m^{-2} \cdot day$	Estimated 10% P_{max} $gC \cdot m^{-2} \cdot day^{-1}$	Gross O_2 light & dark $gO_2 \cdot m^{-2} \cdot day^{-1}$	Gross C pH light & dark $gC \cdot m^{-2} \cdot day^{-1}$	C^{14} part + filtrate $gC \cdot m^{-2} \cdot day^{-1}$	C^{14} particulate $gC \cdot m^{-2} \cdot day$	phytoplankton $gC \cdot m^{-2}$	organic carbon $gC \cdot m^{-2}$
5 June 74	3.46	2.59	0.315	2.13	0.692	0.628	0.310	0.641	13.6
17 June 74	3.84	2.77	0.145	1.20	0.225	0.150	0.094	0.551	13.4
1 July 74	2.47	4.39	0.231	0.648	0.174	0.209	0.078	2.150	23.5
15 July 74	3.00	3.14	0.139	0.724	0.493	0.234	0.181	1.424	14.8
29 July 74	6.93	2.68	0.666	2.63	0.711	0.966	0.282	1.537	13.5
12 Aug 74	2.81	0.383	0.259	1.84	0.163	0.384	0.281	1.389	28.2
26 Aug 74	2.43	1.25	0.163	0.998	0.174	0.212	0.180	2.754	17.3
10 Sept 74	0.993	0.844	0.222	1.25	0.550	0.390	0.291	0.673	33.4
24 Sept 74	1.33	1.54	0.226	0.951	0.375	0.361	0.255	0.852	26.5
25 Nov. 74	1.80	0.540	0.052	0.401	0.169	0.044	0.028	0.927	23.3
21 Dec 74	1.51	0.105	0.062	0.137	0.072	0.019	0.012	0.554	20.7
13 Jan 75	0.799	1.69	0.023	0.079	0.031	0.010	0.007	0.342	18.7
2 Feb 75	0.910	0.403	0.006	0.066	0.020	0.003	0.002	0.214	20.8
23 Feb 75	1.21	1.29	0.007	0.050	0.036	0.003	0.003	0.184	19.3
17 Mar 75	0.361	0.954	0.018	0.012	0.006	0.007	0.004	0.185	16.0
29 Mar 75	1.36	0.891	0.002	0.042	0.057	0.001	0.001	0.130	23.3
12 Apr 75	1.37	0.686	0.004	0.217	0.077	0.005	0.001	0.135	18.9
3 May 75	1.45	1.75	0.018	0.427	0.265	0.046	0.033	0.360	30.7
26 May 75	3.90	1.33	0.050	0.110	0.079	0.056	0.033	0.582	29.1
16 June 75	1.87	4.20	0.148	1.45	0.452	0.500	0.320	1.041	19.0

RESPIRATION CALCULATIONS:

$$g \cdot m^{-2} \cdot day^{-1} = \frac{\Sigma R_i V_i}{A \cdot 1000} 24$$

where,

R_i = mean $mg \cdot m^{-3} \cdot hr^{-1}$ of the ith water strata (from dark bottle rates at two successive depths)

V_i = volume (m^3) of the ith water strata

A = lake area (m^2)

PHOTOSYNTHESIS CALCULATIONS:

$$g \cdot m^{-2} \cdot day^{-1} = \frac{\Sigma P_t V_i}{A \cdot 1000} \cdot \frac{I_d}{I_t}$$

where,

P_t = mean $mg \cdot m^{-3} \cdot t^{-1}$ of the ith water strata (from light and dark bottle rates)

t = time (hrs) of the in situ incubation period

V_i = volume (m^3) of the ith water strata

A = lake area (m^2)

I_d = incident light received per day ($Ly \cdot day^{-1}$)

I_t = incident light received per incubation period ($Ly \cdot t^{-1}$)

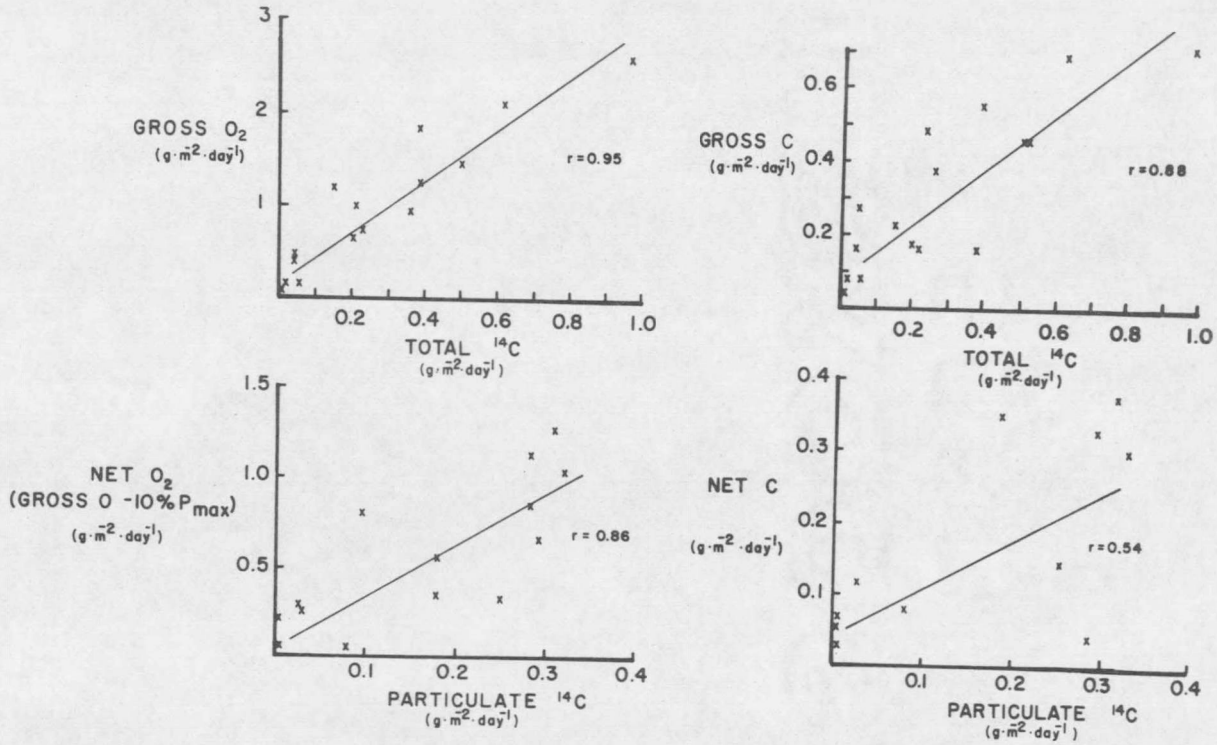


Figure 29. Comparison of the Daily Algal Photosynthetic Rates Measured by the Oxygen and pH Methods to the ^{14}C Uptake Method, Georgetown Lake, Montana, 1974-75.

Net phytoplankton production could not be calculated directly from the light and dark bottle measurements since community respiration was consistently greater than gross photosynthesis (Table 12). However, phytoplankton respiration typically ranges between 5 and 20% of the maximum photosynthetic rate (Harris 1978). Therefore, a mean daily value of 10% of P_{max}, reported by McAllister et al. (1964), was subtracted from the gross photosynthetic rates and regressed against the rates calculated from the particulate ^{14}C fraction (Fig. 29). Even though both the oxygen and pH (CO_2) 'net production' rates were statistically significant ($r=0.86$, $p<0.01$ and $r=0.54$, $p<0.025$, respectively) with respect to the ^{14}C particulate method, variability was much greater than observed for gross photosynthesis relationships. This variability was probably the result of assuming a constant 10% P_{max} value for algal respiration, and the assumption that the particulate fraction retaining ^{14}C measured net photosynthesis. Many authors, as reported by Strickland (1960), Vollenweider (1974), and Harris (1978), seem to agree that ^{14}C retained on filters is a measurement somewhere between net and gross photosynthesis, depending upon the rate of reassimilation of expired CO_2. In addition, under conditions of high pH, Schindler and Fee (1973) reported CO_2 depletion in the incubation bottles, which would tend to reduce the measured uptake of ^{14}C as compared to photosynthetic rates, which, in their case, was proportional to the rate of CO_2 invasion from the atmosphere. Conversely, if bicarbonate was used as a carbon source, calcium carbonate

precipitation (which would not be measured as ^{14}C on the filter due to the acid wash) would tend to reduce the expected pH change. In view of all the possible errors and assumptions, gross photosynthetic rates as measured by all three techniques were reasonably close. However, net production rates, which for this discussion will be assumed equal to the particulate ^{14}C fraction, cannot be calculated since actual algal respiration appeared to be a minor component of the community respiration (Table 12).

The seasonal trend of gross phytoplankton production (Fig. 30) indicated that approximately 90% of the yearly plankton photosynthesis occurred during the ice-free period (Table 13). The initial increase of gross production immediately after the ice melted was probably associated with favorable nutrient conditions and rapidly increasing light intensities. As was evidenced by increased nitrogen to phosphorus ratios (Fig. 24), phosphorus was probably depleted, which resulted in a decreased photosynthetic capability and a substantially reduced phytoplankton turnover rate (Fig. 31) in late June and early July. Gross production and phytoplankton turnover rate (based on net production per unit biomass) increased throughout July, suggesting greater nutrient availability. Zooplankton, which reached maximum population values at that time (Fig. 24), could have influenced nutrient recycling as reported by Liao and Lean (1978) and Scavia (1979). Phytoplankton gross photosynthesis and turnover rates decreased throughout August. This decrease

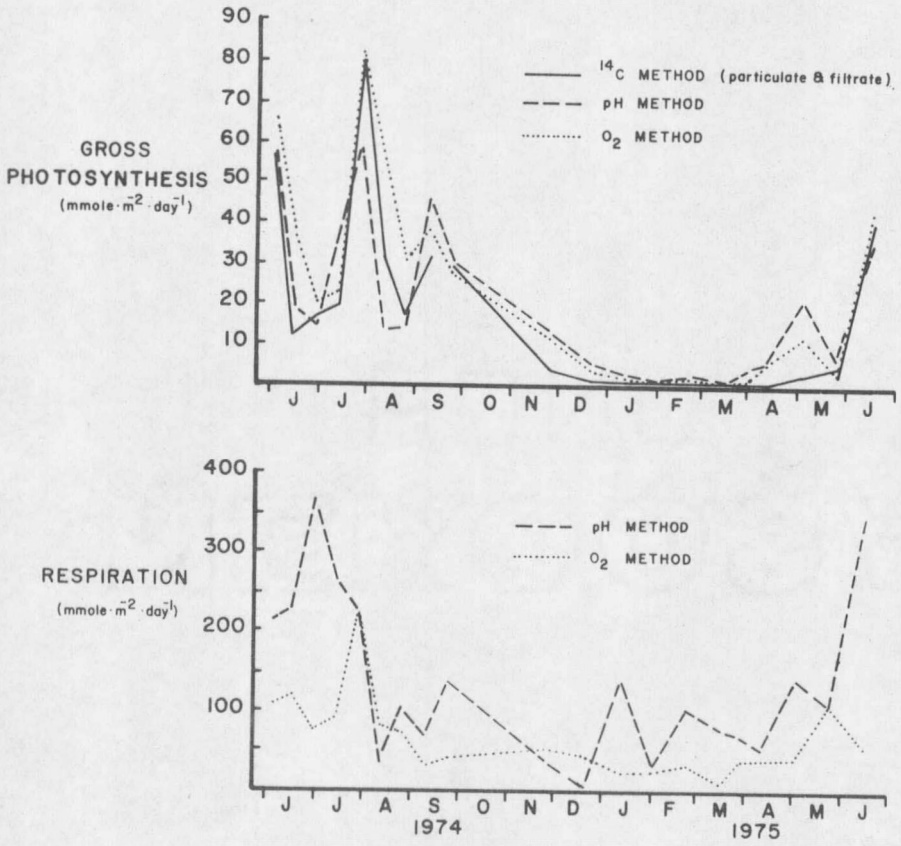


Figure 30. Seasonal Distribution of Daily Phytoplankton Gross Photosynthesis and Planktonic Respiration in Georgetown Lake, Montana, 1974-75.

Table 13. Mean Seasonal Photosynthetic and Respiratory Rates of the Plankton in Georgetown Lake, Montana, 1974-75.

	Mean Daily Rates ($g \cdot m^{-2} \cdot day^{-1}$)		Season Total ($g \cdot m^{-2}$)		Annual ($g \cdot m^{-2} \cdot yr^{-1}$)
	Ice-Free	Ice-Covered	Ice-Free	Ice-Covered	
Photosynthesis					
Gross O_2	1.38	0.15	211	32	243
Gross Carbon	0.40	0.08	61	17	78
Net Carbon (^{14}C)	0.25	0.01	38	2	40
Respiration					
O_2	2.91	1.47	445	312	757
Carbon	2.68	0.96	364	204	568

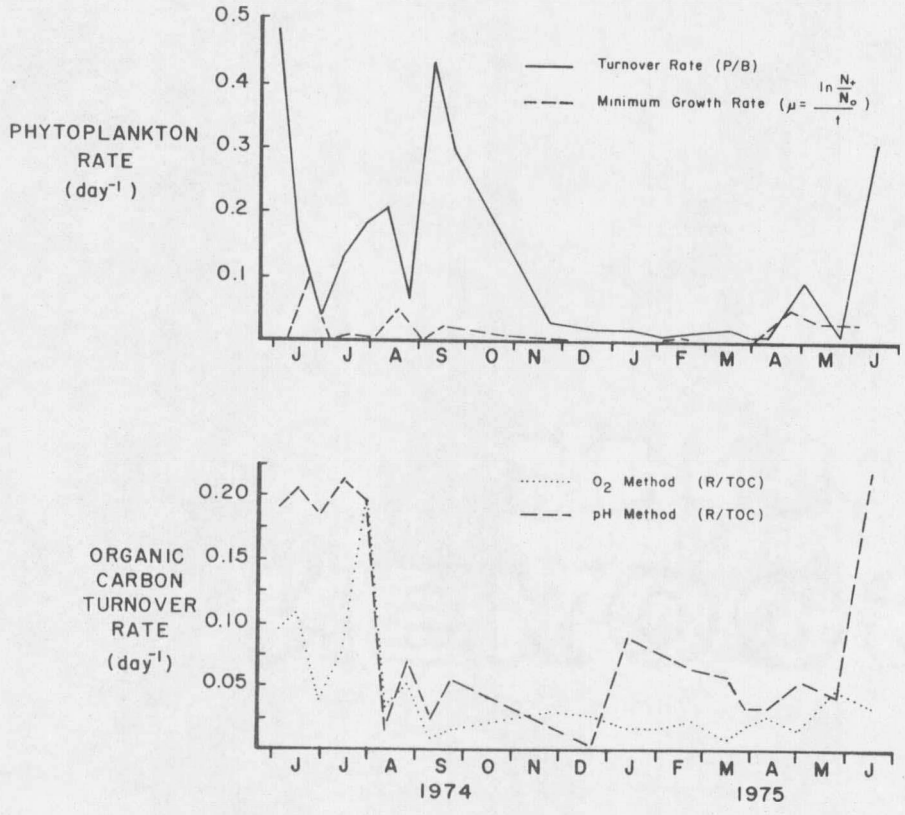


Figure 31. Seasonal Distribution of Phytoplankton Turnover Rates (P/B), Minimum Growth Rates, and, Organic Carbon Turnover Rates Calculated from Georgetown Lake, Montana, 1974-75.

was associated with the Anabaena pulse, which according to Paerl and Kellar (1979), compensated lower carbon fixation rates to fix molecular nitrogen. In September, algal production and turnover rates again increased in coincidence with the pulse of Cyclotella bodanica and small chlorophytes. Throughout most of the period of ice cover, gross production and turnover rates of the algae were greatly reduced, probably as a result of low temperatures and very low light levels. However, in May, when light intensities increased under the ice and inorganic nutrient concentrations were highest, the gross photosynthesis and turnover rates of the green algae (Fig. 24) increased. Previously, heterotropic growth was postulated for cells found under the ice. However, the turnover rate, which was based upon net autotrophic production, was consistently greater than the minimum calculated growth rate (Fig. 31). These data support the findings of Morgan and Kalft (1975), who attributed the dark survival of Cryptomonas erosa under the ice to reduced respiration rates utilizing stored carbodydrates. However, as they point out, heterotrophic growth cannot be ruled out, especially with the inaccuracies of the production and respiration measurements at such low metabolic rates.

The most striking aspect of the observed in situ light and dark bottle measurements was the consistently greater community respiration rates as compared to plankton gross photosynthetic rates (Table 12). Since the dark bottle oxygen and pH (CO_2) changes were entered into the calculations for gross photosynthesis, with which good agreement was

found with respect to the ^{14}C technique, the respiration rates would appear to be valid. However, the measured respiratory quotients (R.Q.) averaged 2 moles CO_2/mole O_2 throughout the ice-free season, and 1.75 mCO_2/mO_2 under the ice (Fig. 30). These quotients suggest that anaerobic respiration dominates the entire year. During the winter, when oxygen concentrations decreased to undetectable limits, anaerobic decomposition would be expected. However, summer oxygen concentrations were generally at saturation levels (Fig. 10), suggesting aerobic metabolism. A similar discrepancy in the interpretation of R.Q. values was addressed by Rich (1979), who maintained that the degree to which the community R.Q. was greater than 0.85 reflected the amount of metabolism for which oxygen was not the terminal electron acceptor and that the R.Q. of communities with mixed aerobes and anerobes depend more on the nature of the oxidizing agent. This analogy implies that the summer plankton community, of which bacteria appeared to be a substantial portion, was possibly utilizing other terminal electron acceptors or substrates which were decarboxylated and not completely oxidized.

Since daily respiraton rates (R_s) were observed to be consistently greater than daily phytoplankton gross production, organic sources other than phytoplankton, dominate in Georgetown Lake. The respiration rates were generally greater during the summer (Fig. 30), reflecting either substrate availability and/or warmer temperatures. The organic turnover rates, calculated as R_s/TOC, which represent the minimum turnover, were

generally greatest for two months after the ice melted (Fig. 31). These rates were similar to the turnover rates reported by Seepers (1977), Wetzel and Manny (1972), and Hall et al. (1972) for dissolved organic carbon. White and Wetzel (1975) found that organic material resuspended during the spring circulation period in Lawrence Lake, Michigan, presumably adsorbed and/or coprecipitated with $CaCO_3$ the previous summer. Reddy (1975) also observed that organics coprecipitated with calcium carbonate, although the organics reduced the growth rate of $CaCO_3$ aggregates. Hough and Wetzel (1975) reported varying dissolved organic carbon excretion rates from macrophytes (4 to 40% of gross photosynthesis) at various times throughout the growing season, which appeared to be dependent upon specific taxa and the degree of scenescence. Since portions of macrophytes of varying ages were decaying throughout the entire growing season (Lehman and Sangren 1978), continual input of particulate and dissolved organics probably contributed to the total organic pool. The measured respiration (decay) rates within the water column could account for all of the decrease of the total organic mass (Fig. 27), but the continual input rate of organics to the water column was probably at or near the respiration rate to account for the maintenance of the observed organic carbon concentrations. Although macrophyte production, decay, and release of organics were not measured in Georgetown, the continual decrease of $CaCO_3$ from the water column throughout the ice-free period (Fig. 13) indicates a positive net production for the entire

lake, presumably by macrophytes and epiphytic algae. Additional evidence for the dominance of autochthonous production and subsequent detrital (with associated bacteria) formation, independent of the phytoplankton, is that the seasonal production (gross or net) of phytoplankton (expressed as a dry weight (d.w.) $\cdot m^{-2} \cdot day^{-1}$) could not account for the large zooplankton production rates measured by Geer (1977) (Fig. 32). As suggested previously, the zooplankton had a pronounced effect on the phytoplankton populations, but at the time of maximum zooplankton production (5.5 g (d.w.)$\cdot m^{-2} \cdot day^{-1}$) (Fig. 32) neither the phytoplankton net production (0.45 g(d.w.)$\cdot m^{-2} \cdot day^{-1}$, nor the algal gross production (0.8 g(d.w.)$\cdot m^{-2} \cdot day^{-1}$) was great enough to sustain the zooplankton increase. Throughout the remainder of the ice-free period, the zooplankton production averaged approximately 50% of the phytoplankton production. Such efficiences are highly doubtful (Slobodkin 1961). This comparison also suggests the minor contribution of phytoplankton to the overall autochthonous production within Georgetown Lake.

TROPHIC RELATIONSHIPS

A summary of the available yearly production, respiration, fish yield, and allochthonous inputs (Table 14) indicates that Georgetown Lake was very productive. The three methods used to estimate sport fish yield in Georgetown resulted in very similar values. These estimates of fish yield were very high compared to those presented by Ryder et al. (1974) and Oglesby (1977), being exceeded by some tropical lakes, carp ponds,

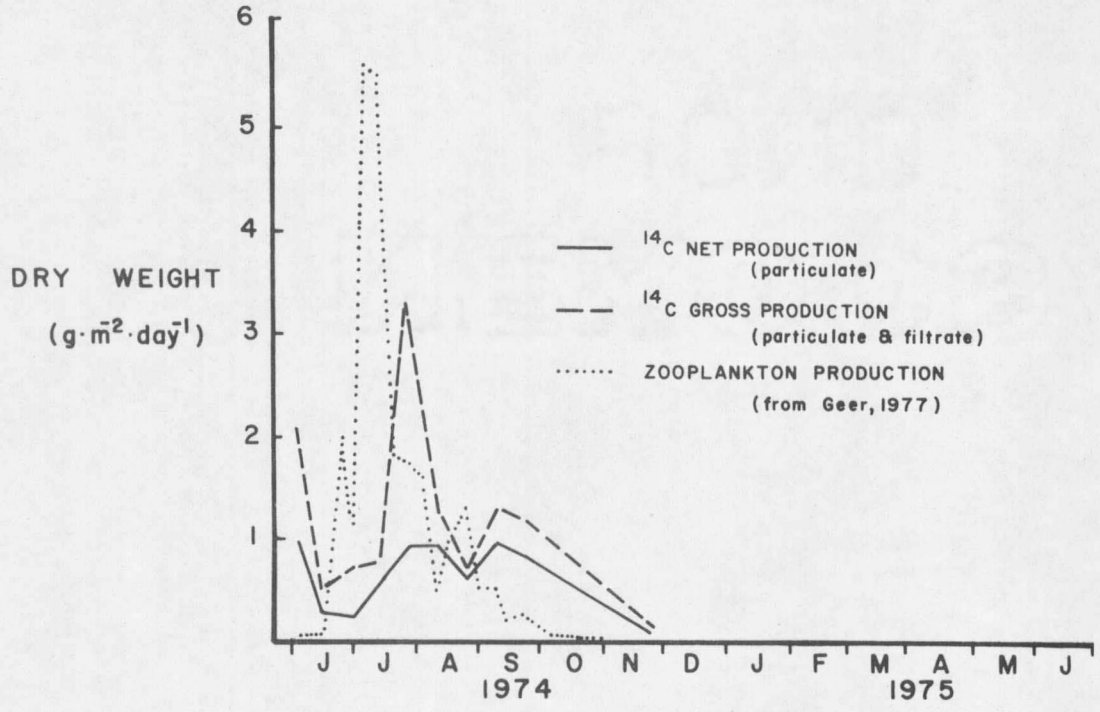


Figure 32. Seasonal Distribution and Comparison of Zooplankton Production (from Geer 1977) to Phytoplankton Gross and Net Production in Georgetown Lake, Montana, 1974-75.

Table 14. Comparison of the 1974 Annual Phytoplankton and Zooplankton Production, Estimated Fish Yield, Respiration, and Allochthonous Carbon for Georgetown Lake, Montana.

	MEASURED UNITS	CONVERSION TO ENERGY UNITS	ESTIMATED YEARLY PRODUCTION AND/OR YIELD
PHYTOPLANKTON:			
(THIS STUDY)			
GROSS PRODUCTION O_2 METHOD	243 $gO_2 \cdot m^{-2} \cdot yr^{-1}$	1 gO_2=14.7 kJ	3572 $kJ \cdot m^{-2} \cdot yr^{-1}$
C^{14} METHOD	78 $gC \cdot m^{-2} \cdot yr^{-1}$	1 gC=41.8 kJ	3260 $kJ \cdot m^{-2} \cdot yr^{-1}$
NET PRODUCTION		(Burgis and Dunn, 1978)	
C^{14}	40 $gC \cdot m^{-2} \cdot yr^{-1}$		1672 $kJ \cdot m^{-2} \cdot yr^{-1}$
ZOOPLANKTON: (GEER, 1977)			
NET PRODUCTION	161 $g(d.w.) \cdot m^{-2} \cdot yr^{-1}$	1 g(d.w.) = 21 kJ (Burgis and Dunn, 1978)	3381 $kJ \cdot m^{-2} \cdot yr^{-1}$
FISH YIELD			
MONTANA FISH & GAME DEPT. CREEL SURVEY, 1970-72	32 $lbs\ (f.w.) \cdot acre^{-1} \cdot yr^{-1}$		
(in, GEORGETOWN LAKE PRESTUDY, 1973)	3.59 $g(f.w.) \cdot m^{-2} \cdot yr^{-1}$		15 $kJ \cdot m^{-2} \cdot yr^{-1}$
CALCULATED FROM MORPHO-EDAPHIC	23 $lbs.(f.w.) \cdot acre^{-1} \cdot yr^{-1}$	1 g(f.w.)=4.18 kJ	
EQUATIONS OF RYDER (1964)	2.58 $g(f.w.) \cdot m^{-2} \cdot yr^{-1}$	(Burgis and Dunn, 1978)	11 $kJ \cdot m^{-2} \cdot yr^{-1}$
CALCULATED FROM MORPHO-EDAPHIC	33.8 $lbs\ (f.w.) \cdot acre^{-1} \cdot yr^{-1}$		
EQUATIONS OF HAYES & ANTHONY (1965)	3.79 $g\ (f.w.) \cdot m^{-2} \cdot yr^{-1}$		16 $kJ \cdot m^{-2} \cdot yr^{-1}$
RESPIRATION (THIS STUDY)			
O_2 METHOD	757 $gO_2 \cdot m^{-2} \cdot yr^{-1}$	1 gO_2=14.7 kJ	11,128 $kJ \cdot m^{-2} \cdot yr^{-1}$
pH METHOD	568 $gC \cdot m^{-2} \cdot yr^{-1}$	1 gC=41.8 kJ	23,742 $kJ \cdot m^{-2} \cdot yr^{-1}$
SURFACE WATERS (Knight et al., 1976)			
INFLOW ORGANIC CARBON	31 $gC \cdot m^{-2} \cdot yr^{-1}$		1333 $kJ \cdot m^{-2} \cdot yr^{-1}$
OUTFLOW ORGANIC CARBON	49 $gC \cdot m^{-2} \cdot yr^{-1}$		2048 $kJ \cdot m^{-2} \cdot yr^{-1}$

culture ponds, or some lakes which were fished commercially. Based upon the classical 'energy pyramids' first outlined by Lindeman (1942), the yearly fish yield of salmonids in Georgetown theoretically could have been sustained by the zooplankton, phytoplankton, or allochthonous inputs with direct conversion efficiences of 0.4, 0.8, and 1%, respectively. However, direct salmonid utilization of phytoplankton or detrital carbon as a primary food source seems unlikely. Furthermore, as pointed out earlier, the phytoplankton production was probably unable to sustain the high zooplankton production rates. Consequently, planktonic algae was probably not the primary 'food base' for the fish. Although the fish yield estimates provide a base for comparison, these values undoubtedly underestimate the actual fish production in the lake. Calculation of fish production from fish yield in Georgetown Lake is complicated by the stocking program (e.g., approximately 60% return of the total number of 4 to 6 inch rainbow trout stocked per year (Georgetown Pre-Study 1973)), and the natural reproductive, survival, and growth rates of game and non-game species. Furthermore, the ecological efficiences necessary to support the Georgetown fishery would also be dependent upon the knowledge of the 'food web' in the lake. But the yearly planktonic respiration rates, decrease of calcium carbonate during the ice-free period, net loss of organic carbon from the reservoir, and net accumulation of organic carbon to the sediments (Garrison 1976), all suggest very high production rates of the macrophytes and associated epiphytic algae. These sources of organic

carbon probably provide both a direct source for herbivorous grazers and an indirect source for the detrital consumers, as suggested by Rich and Wetzel (1978). Both modes of energy transfer to salmonids probably involve non-game species, which would provide the actual forage base for the game fish. An approximation of the minimum net production rates of the macrophytes and associated epiphytic algae during the ice-free season may be estimated by the following equation:

$$\delta C_i = \delta R_p + \delta R_{sed} + \delta C_a - \delta P_{m+e} - \delta P_p - \delta C_{ca}$$

where,

δC_i = average daily change of the total inorganic carbon (=-29 mmole $C \cdot m^{-2} \cdot day^{-1}$, from Fig. 13)

δR_p = average daily planktonic respiration rates (=198 mmole $C \cdot m^{-2} \cdot day^{-1}$, from Table 13)

δR_{sed} = average daily sediment respiration rates and associated diffusion rates to the free water (unknown)

δC_a = average daily CO_2 invasion rates from the atmosphere (unknown)

δP_{m+e} = average daily net production rates of the macrophytes and epiphytic algae

δP_p = average daily gross production rates of the phytoplankton (33 mmole $C \cdot m^{-2} \cdot day^{-1}$, from Table 13)

δC_{ca} = average daily change of inorganic carbon due to solubility product with calcium (=-12 mmole $C \cdot m^{-2} \cdot day^{-1}$, from Fig. 13)

Solution of the equation yields:

$$\delta P_{m+e} = 2.18 gC \cdot m^{-2} \cdot day^{-1} + \delta R_{sed} + \delta C_a$$

However, the implicit assumption of the equation is that all rates are instantaneous. But, as Garrison (1977) indicated, the sediments exhibited a net yearly gain of organic matter and, since respiration rates were greater than photosynthesis under the ice, the contribution of carbon dioxide from the sediments and/or atmosphere during the summer months must have been substantial to enable such accumulation and subsequent delayed decomposition.

SUMMARY

Georgetown Lake, a 1479 ha reservoir formed by an impoundment on Flint Creek at an elevation of 1960 m (msl), is located in the Clark Fork drainage 17 miles west of Anaconda, Montana. Rights to the water in Georgetown Lake are shared by the Montana Power Company, the Anaconda Mining Company, and irrigation concerns in the Phillipsburg Valley. In addition to supplying water, the Georgetown Lake watershed provides permanent residence for approximately 300 people. However, the substantial year long recreational demands were estimated to increase at a rate of 18% per year (Georgetown Pre-Study 1973). Area use analysis indicated that the principal recreational demands are fishing (slightly less than 4% of the total fishing in Montana), camping, picnicing, boating, and snowmobiling. Residents have become increasingly concerned about the eutrophication of Georgetown Lake but little information was available to assess its trophic status. Therefore, this investigation was conducted to provide baseline data to assess the principal limnological factors in Georgetown Lake.

At full pond elevation, Georgetown Lake has a maximum depth of ten meters, and a mean depth of 4.89 meters. Throughout the sampling period, July 1973 through June 1975, the lake level fluctuated one meter. Typically, the maximum lake levels were reached following the snowmelt period in May. The level gradually decreased throughout the summer due to evaporation and power and irrigation demands. The water pumped to Silver Lake by Anaconda

Mining Company from December through March reduced lake levels to the minimum yearly values. Direct precipitation inputs were minimal during the ice-free period, but snow accumulation on the ice contributed to increased water levels at the time of ice melt. Yearly surface run-off and groundwater contributions were estimated to be 22% and 68%, respectively, of the total annual water contribution to the lake.

The yearly heating cycle in Georgetown Lake was typical of a temperate, dimictic lake. However, due to the shallow depth and relatively deep light penetration (1% light depth averaged 7.2 meters during the ice-free season), the lake did not thermally stratify during the ice-free period. Typical winter stratification patterns were developed since ice cover prevented wind induced mixing and substantially reduced light penetration (55-82% reduction). As was evidenced by a lag in the water temperature relative to the equilibrium temperature, the heating and cooling rates of the water column during the ice-free season were a function of meteorological conditions (e.g., solar radiation, cloud cover, air temperature, humidity, and wind). The formation, thickness, and duration of ice cover (average of seven months per year) was also a function of meteorological conditions, but the gradual increase of water temperature under the ice was principally due to heat input from the sediments. The large sediment heat budget (16.4% of the annual budget) reflected the large seasonal amplitude in temperature of the water which, in the absence of a stratified water column, came in contact with the

entire lake substrate. The annual heat budget of 20,000 $g \cdot cal \cdot cm^{-2} \cdot yr^{-1}$ was similar to other temperate, dimictic lakes, but 30.4% of the annual heat budget was required for the latent heat of fusion to covert ice and snow to liquid water. In addition, the reservoir was considered a heat trap since 10% of the annual heat income was required to heat the inflowing, advected water to ambient reservoir conditions. Overall, in addition to enabling an estimate of the groundwater contribution (critical for nutrient loading estimates), the annual heating and cooling regime of the lake had pronounced effects on the atmospheric exchange of gases, principally O_2 and CO_2, the light penetration, and the development of density currents. These factors greatly influenced the chemical and biological properties of the lake.

Georgetown Lake was characterized by relatively high dissolved solids, e.g., yearly mean conductivity of 212 $\mu mhos \cdot cm^{-2}$, principally as calcium-magnesium carbonates. This general composition was indicative of the limestone-clay-gravel characteristic of the watershed. Sodium and chloride concentrations were very low, indicating negligible contributions from human activities.

Chemical stratification was not observed during the ice-free season. During this time, dissolved oxygen was at or above saturating concentrations while carbon dioxide was typically below saturation. In addition, calcium carbonate was precipitated from the water column throughout the

summer months. These data suggest high biological production rates throughout the ice-free period. However, the measured planktonic respiration rates were greater than the phytoplankton gross production rates, suggesting very high primary production rates of the macrophytes and associated epiphytic algae. Substantial exchange of CO_2 and O_2 between the water column and the atmosphere and sediments during the summer months was suggested by the average daily loss of inorganic carbon, calcium carbonate precipitation, and planktonic photosynthetic and respiratory rates.

In contrast, the ice cover prevented atmospheric exchange of carbon dioxide and oxygen during the winter. Since decomposition rates exceeded photosynthetic rates under the ice, oxygen concentrations were gradually depleted at a rate of 7 mmole $O_2 \cdot m^{-2} \cdot day^{-1}$, while inorganic carbon initially increased at a rate of 6.5 mmole $C \cdot m^{-2} \cdot day^{-1}$. The rate of inorganic carbon accumulation increased to 15.7 mmole $C \cdot m^{-2} \cdot day^{-1}$ at the time when anoxic conditions reached the 1954 m lake contour. This elevation coincided with the depth of maximum sediment area exposed to the corresponding water strata volume. This data indicates, in addition to anaerobic metabolism, that density currents flowed along the lake bottom and accumulated dissolved material in the deeper portions of the lake. Even though the use of this water by Montana Power Company tended to remove the anoxic water, the rate of accumulation was greater than the flow rates of the Montana Power hydroelectric plant. As anoxic

conditions persisted, the oxidation-reduction potential was decreased at least to a point which enabled the reduction of sulfate. As a consequence of anaerobic metabolism and subsequent equilibrium changes, carbon dioxide, iron, phosphate, nitrite, ammonia, bicarbonate, and calcium concentrations increased in the water column. These increases reflected the loss of adsorptive properties of the sediment as well as the chemical reduction of oxidized compounds to more soluble reduced forms. The decrease in pH, which resulted from increased carbon dioxide concentrations, solubilized calcium carbonate.

With the melting of the ice cover, reaeration of the water column and associated loss of CO_2 from the system resulted in the rapid precipitation of insoluble, oxidized compounds, and the reformation of an oxidized microzone on the sediment-water interface. At this time, orthophosphate decreased, but the total phosphate in the water column remained constant suggesting rapid uptake of phosphorus by algae rather than a substantial loss of phosphate as a chemical complex (e.g., $FePO_4$).

Total phosphate averaged 26 $\mu g \cdot \ell^{-1}$ throughout the year while the yearly total nitrogen mean concentration was 370 $\mu g \cdot \ell^{-1}$. Except for an increase of inorganic nutrient concentrations (e.g., orthophosphate, nitrate, nitrite, and ammonia) during the anoxic period, inorganic levels were at or below the detection limits. Organic phosphorus and nitrogen, expressed as $mmole \cdot m^{-2}$, exhibited wider fluctuations during the ice-free

period than under the ice. Such fluxes in the organic forms could not be attributable to the corresponding changes in the inorganic species. In addition, the calculated nutrient loading, including groundwater, could not account for the observed fluxes. Furthermore, utilization of the Georgetown nutrient inputs in nine loading models typically predicted Georgetown Lake to be oligotrophic, whereas the measured algal standing crop values were in the meso-eutrophic classification. Together with a net annual loss of phosphorus and nitrogen from the reservoir, these data all suggest that internal nutrient availability and recycling were the dominant mechanisms controlling the measured nutrient levels.

The relationships of Georgetown annual mean total phosphorus to the annual means of carbon, nitrogen, and chlorophyll are well within the ranges presented by Schindler (1977). This comparison indicates that, on a yearly average, the nutrient ratios were a function of primary production and subsequent decomposition (i.e., biological activity). The specific mechanisms and associated rates of nutrient availability to the plankton were not measured, but direct nutrient release rates from the sediment or via the macrophytes and subsequent sedimentation rates, either as organic or inorganic chemical complexes, probably controlled the measured levels of total nutrients in the water column.

The typically higher inorganic nitrogen to phosphorus ratios during the first summer compared to the ice-free period in 1974, and the higher

organic nitrogen to phosphorus ratios observed the second summer, indicate that phosphorus availability was greater the first summer despite high demand by algae. These ratios, in conjunction with the much higher standing crop of Anabaena flos-aquae the first summer, suggest that phosphorus availability and subsequent turnover rates determine the maximum standing crop of algae, while the availability of nitrogen influences the taxonomic composition. In Georgetown Lake, nitrogen deficiences with respect to phosphorus enabled Anabaena flos-aquae to achieve much higher standing crops the first summer when phosphorus was more available and it could fix atmospheric nitrogen. The second summer, however, was characterized by a much lower standing crop of Anabaena. This probably reflected less phosphorus availability, especially relative to nitrogen. The difference in phosphorus availability between the two summers was attributed to lower lake levels the first summer. The lower water level would tend to increase the exposed surface area of the sediment and macrophytes relative to the water volume, again suggesting internal nutrient cycling as the dominant nutrient source.

The yearly phytoplankton assemblage was composed of at least 110 algal taxa. While the seasonal succession throughout both sampling years was similar, the standing crops of the dominant forms were typically greater during the period from July 1973 through May 1974. After the ice melted, small chlorophytes and Cryptomonas ovata dominated the phytoplankton biomass. Coincidental with a decline of those forms and a sub-

stantial increase of the inorganic nitrogen to phosphorus ratio, Dinobryon sertularia reached maximum abundance. In mid-July, when zooplankton were at peak population levels, substantial zooplankton grazing was evident from a shift to a larger mean phytoplankton cell size. Following the zooplankton maximum and coinciding with the increase of Fragillaria crotonensis, the average phytoplankton surface to volume ratios reached maximum values. This shift suggests high nutrient demand and possible nutrient deficiencies. The decrease of the algal surface to volume ratio, a lower inorganic nitrogen to phosphorus ratio, and the dominance of Anabaena flos-aquae probably reflected higher phosphate availability but increased nitrogen deficiencies which occurred as F. crotonensis settled out of the water column. The late summer-early fall phytoplankton populations were dominated by Cyclotella bodanica and Cryptomonas ovata. Under the ice, Cryptomonas was the primary taxon observed, with a small pulse of Stephanodiscus astrea. Cryptomonas survival under low light and temperature conditions has been reported to be a function of low respiration rates and the utilization of stored products accumulated when conditions were favorable. The rapid increase of small chlorophytes in April and May probably resulted from the high availability of nutrients and increased light intensity prior to the ice melting. The difference in phytoplankton standing crop the first sampling year was probably a function of the lower lake levels.

The phytoplankton standing crops, expressed as cell volume$\cdot m^{-2}$ or

cell carbon$\cdot m^{-2}$, were greatest during the ice-free period. Even though chlorophyll concentrations were also generally higher during the summer, chlorophyll content per cell carbon appeared to be a function of '*Chlorella* type' light adaption and/or density dependent nutrient deficiencies. This trend was most apparent during the summer months when chlorophyll to algal carbon ratios were typically lower than the corresponding ratios under the ice. Similarily, chlorophyll to algal carbon ratios were lower the first summer as compared to the second summer, indicating nutrient deficiencies with high algal biomass. These lower ratios and similar total nitrogen values during both summers indicate a greater nitrogen deficiency the first summer which could have resulted from a decreased per cell nitrogen fixation rate by *Anabaena*. Lean and Charlton (1977) reported reduced nitrogen fixation rates per algal standing crop to be a function of a deficiency of a co-factor required for nitrogen fixation, e.g., iron.

On the basis of average summer phytoplankton standing crop (i.e., 17.0 $gC\cdot m^{-2}$ and 2.7 $gC\cdot m^{-2}$ for 1973 and 1974 respectively), Georgetown Lake may be classified as a eutrophic or mesotrophic lake. However, the total organic carbon content in the water column did not appear to be a function of the phytoplankton biomass. The algal biomass averaged less than 5% of the total organic carbon. In addition, the summer organic carbon to nitrogen ratios ranged between 10:1 and 30:1, which were indicative of macrophyte C/N ratios, not the C/N ratios of 6:1 reported

for phytoplankton. Organic carbon to nitrogen ratios increased to a maximum value of 60:1 under the ice, indicating that nitrogen was used preferentially, leading to an accumulation of refractory compounds. The measured mass of organic carbon is a function of the input rates and the decomposition rates of carbon compounds. Since the planktonic respiration was consistently greater than phytoplankton gross photosynthetic rates, the primary input of organic material to the water column was not a function of the phytoplankton. In addition, allochthonous inputs were minor. These results lead to the conclusion that organic loading to the water column was a function of macrophytic and associated epiphytic autochthonous inputs, either directly or indirectly from the sediment as detritus.

Planktonic respiration (i.e., decomposition) rates averaged 2 to 2.4 times greater during the ice-free period than under the ice. The mean respiration quotient (CO_2/O_2) of 2.0 throughout the year indicated substantial anaerobic metabolism, even in an aerobic water column. However, comparison of the rate of total inorganic carbon gain to the water column under the ice (6.48 to 15.7 mmole$\cdot m^{-2}\cdot day^{-1}$) and oxygen loss (6.96 mmole$\cdot m^{-2}\cdot day^{-1}$) to mean planktonic respiratory rates (0.080 mmole C$\cdot m^{-2}\cdot day^{-1}$ and 0.046 mmole $O_2\cdot m^{-2}\cdot day^{-1}$) suggest that the sediment was the major site of decomposition.

The three methods used to measure phytoplankton photosynthetic rates

(i.e., pH change, oxygen change, and ^{14}C uptake) yielded similar values for the daily gross production rates. Net phytoplankton production, however, could not be measured directly due to the dominance of plankton respiration. Estimates of net production, assuming phytoplankton respiration was 10% of the maximum photosynthetic rates, yielded statistically significant correlations with particulate ^{14}C uptake, but were much more variable than the gross photosynthetic comparisons. The calculated mean net production during the ice-free period of 0.25 $gC \cdot m^{-2} \cdot day^{-1}$ or total summer phytoplankton production of 38 $gC \cdot m^{-2}$ were, according to the classification of Likens (1975), indicative of oligotrophic conditions. However, the calculated summer phytoplankton turnover rates (production per unit biomass) were far greater than the minimum growth rates required for the observed standing crop changes. Thus, the relatively high standing crops imply that most of the phytoplankton production was required for maintenance of the populations, possibly related to the rate of nutrient availability and subsequent turnover. Under the ice, daily autotrophic production rates were at subsistence levels due to the very low light intensities, although heterotrophic growth could not be ruled out completely.

Comparison of the measured organic fluxes in Georgetown Lake, expressed as energy equivalents, illustrate that the yearly phytoplankton net production was approximately 50% of the total zooplankton production. At the time of peak zooplankton production (5.5 g (d.w.) $\cdot m^{-2} \cdot day^{-1}$),

phytoplankton production was less than one-fifth the zooplankton production. Allochthonous input, although less than the organic carbon discharge from the reservoir, was slightly less than the yearly phytoplankton net production. These data, in conjunction with the very high respiration rates, suggest that the major organic carbon sources in the reservoir were the macrophytes and/or associated epiphytes. However, whether these organic carbon sources were utilized directly or indirectly via the detrital pathway is not known. Fish yields in Georgetown Lake were very high compared to other cold water sport fisheries, however, the fish production in Georgetown Lake could not have been supported by a system based on the phytoplankton alone. Zooplankton production, which was primarily based upon detrital utilization, could theoretically account for the high fish yields. Macrophytes and epiphytes undoubtedly contribute substantially to the fishery.

In conclusion, Georgetown Lake was a very dynamic system. Meteorological events provided the boundary conditions by regulating the formation and duration of ice cover which, in turn, reduced the light availability and prevented gaseous exchange with the atmosphere. In addition, the amount of precipitation, principally as accumulated snow pack in the watershed, influenced the lake water level. The morphometry of the basin and subsequent lack of summer stratification provided continual contact of the entire water column with the sediment. These factors, in addition to the limestone geology of the watershed, influenced the biological

activities and, subsequently, the chemical characteristics within the reservoir. The key to the understanding of the phytoplankton responses within the reservoir appear to be a function of the rate at which nutrients, particularily phosphorus and nitrogen, become available, and a distinction between macrophyte and/or sediment contributions of those nutrients. Since the internal 'recycling' rates were the dominant factors contributing to the phytoplankton species succession and standing crop values, water level throughout the summer period had a pronounced effect on the phytoplankton populations. The degree of oxygen depletion under the ice was primarily a function of the water level prior to ice formation and the amount of accumulated autochthonous organic material produced the previous summer.

Fisheries management practices should attempt to maintain the macrophyte populations, since, the high sport fish yields were supported by the macrophyte community. However, to reduce blue-green algal blooms during the summer, and, to minimize a potential fish kill under the ice, water levels should be maintained at the highest, practical level.

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