# Field and Experimental Winter Limnology of Three Colorado Mountain Lakes

Robert W. Pennak

**Vaartaja, Olli.** 1962. Ecotypic variation in photoperiod of trees with special reference to *Pinus resinosa* and *Thuja occidentalis*. Can. J. Bot. **40**: 849–856.

**Van Huystee, Robert.** 1964. Cold acclimation and accompanying metabolic changes in red-osier dogwood with emphasis on proteins. Ph.D. Thesis. University of Minnesota, St. Paul, Minn. 106 p.

**Wareing, P. J.** 1963. Growth studies on woody species. V. Photoperiod in dormant buds of *Fagus sylvatica* L. Physiol. Plant. **6**: 592–706.

# FIELD AND EXPERIMENTAL WINTER LIMNOLOGY OF THREE COLORADO MOUNTAIN LAKES[1]

ROBERT W. PENNAK

*Department of Biology, University of Colorado, Boulder, Colorado*

*Abstract.* Physical, chemical, and plankton conditions were studied during two winters in three Colorado mountain lakes. Black Lake is mesotrophic, Pass Lake is highly oligotrophic, and Tea Lake is shallow, eutrophic, and pondlike.

The lower waters of Black and Pass lakes absorb heat from the basin so that their winter temperatures are above 4.0°C and as high as 5.4°C. The substrate and bottom waters reach equilibrium in late February or March. Thereafter the lower waters cool toward 4.0°C.

Black and Pass lakes had thick snow covers and no photosynthesis for 5–7 months, but Tea Lake had little snow and intermittent photosynthesis during all winter months. Black and Pass lakes are summer-oligotrophic and winter-eutrophic. They became so highly anaerobic by March and April that trout populations died. Such winter kills are thought to occur frequently in many small mountain lakes.

All three lakes had negligible winter populations of diatoms and green and blue-green algae, but the populations of μ-algae attained winter maxima of 1–14.5 million cells per liter. Such maxima had no consistent seasonal pattern. The importance of winter algal heterotrophy is discussed.

Winter copepod and cladoceran populations were negligible; densities seldom exceeded one adult per liter. Rotifer populations were usually dense, commonly exceeding 500 per liter, especially during December and January before the onset of severe anaerobiosis in Black and Pass lakes, and during all months in Tea Lake.

Seston varied much more widely than during the months of open water. The seston of large lake-water samples stored in the dark at 3°C for 30 days ranged from a 20% decrease to a 350% increase over the original seston content.

Winter plankton had an average respiratory rate *in situ* of about twice that of the plankton in corresponding water samples kept in a dark refrigerator at 3°C.

Water samples treated with antibiotics had a lower plankton respiratory rate during 30 days in a dark refrigerator at 3°C than did refrigerated control samples. After an interval of 60 days, however, comparable samples treated with antibiotics had a respiratory rate higher than that of controls. It is postulated that the inhibition of bacteria by antibiotics makes nutrients available to yeasts, molds, mutant antibiotic-resistant bacteria, and μ-algae(?), which, after a lag phase, grow and collectively attain a high respiratory rate after the longer experimental interval.

These results on seston and plankton show that the metabolism of small, enclosed experimental water samples is highly variable and poorly understood, especially in the dark at low temperatures.

## INTRODUCTION

Because of the difficulties involved in taking water samples through ice during the cold months, comparatively little is known about winter limnology in temperate and high latitudes. The situation is even more discouraging in high mountainous areas where winter field work is often plagued by unpredictably high winds, snow, and severe cold. Furthermore, because most secondary access roads are not plowed, field trips to mountain lakes usually involve wearing skis or snow-

[1] Contribution No. 45, Limnology Laboratory, University of Colorado.

shoes and hauling equipment on sledges. Most of our knowledge of midwinter limnological conditions in mountainous areas is therefore restricted to small amounts of data collected during one or two trips to only a few bodies of water. Examples of such studies are Leutelt-Kipke (1934), Olszewski (1948, 1951), Morandini (1949), Rodhe (1962), and Suchlandt and Schmassmann (1935).

The results reported here derive from a midwinter investigation of three Colorado mountain lakes. They are especially an attempt to trace the development of limnological conditions under thick ice and snow. Each of these three lakes was

liters taken with the Kemmerer sampler at each of

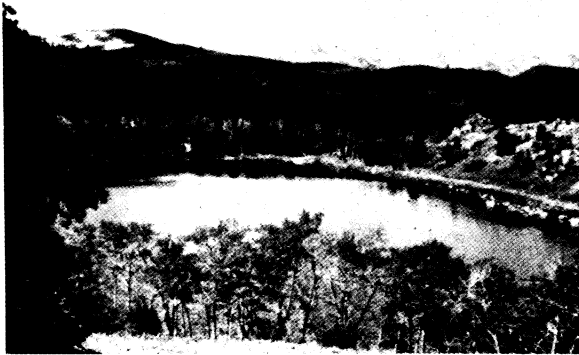water is presumably released through contraction

FIG. 1.  Tea Lake, Colorado, looking southwest; June.

visited about every 3 weeks during the winters of 1962–3 and 1963–4.

## DESCRIPTION OF LAKES

Tea Lake (Fig. 1) is 21 km (13 miles) northwest of the University of Colorado at Boulder, in the montane zone at an altitude of 2,686 m.  In the strict sense it is a pond, since it has an area of only 0.7 ha and a maximum depth of 1.3 m. The south and part of the east margins are sedgy and mucky, but the rest of the periphery is composed of gravel, sand, and boulders with little organic material.  During the summer months aquatic vegetation grows over about 60% of the bottom.  There is no inlet stream, and only a small outlet during a few weeks in the spring.  The shape is elongate with length about three times maximum width, and the bottom is flat but slopes gently upward near the periphery.  The water has a color of 200–280 on the platinum-cobalt scale. Total residue averages 32 mg per liter, about 60% of this being organic matter.  By these characters it is obviously in Pennak's (1945) category of semidrainage lakes.

Black Lake (Fig. 2) is on the west side of the Continental Divide at an altitude of 3,195 m at the juncture of the montane and alpine zones and
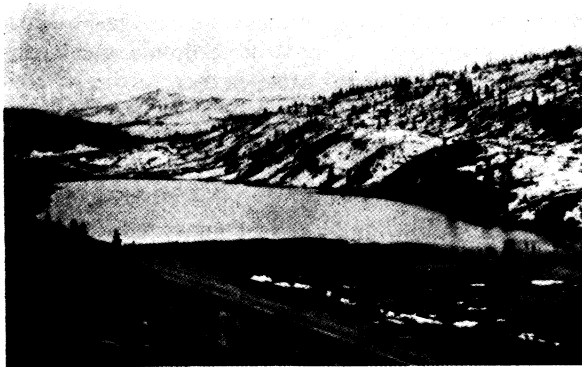


FIG. 2.    Black Lake, Colorado, looking southwest; October,
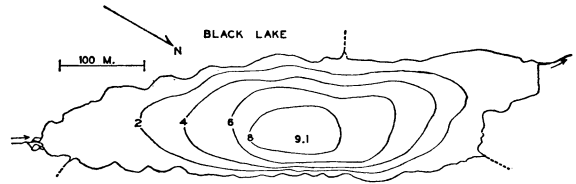


FIG. 3.   Depth contours of Black Lake, Colorado.

about 100 km (60 miles) west-southwest of Boulder.  It is adjacent to a main highway and is accessible during all months of the year.  The basin is long and narrow, and the deepest part of the lake (9.1 m) is greatly limited (Fig. 3).  Total area is 6.33 ha.  During summer the inlet and outlet are small brooks about 1.2 m wide and about 6 cm deep, but during midwinter the inflow and outflow are reduced by more than 90%. About 95% of the shoreline is rocky, and there is only a small amount of rooted aquatic vegetation near the south end.  Total residue averages 59 mg per liter.  Black Lake is probably best classified as mesotrophic.

Pass Lake lies near Loveland Pass on U. S. Highway 6 about 66 km (41 miles) from Boulder in a direct line.  Although it is easily accessible



FIG. 4.  Pass Lake, Colorado, looking southeast; October.
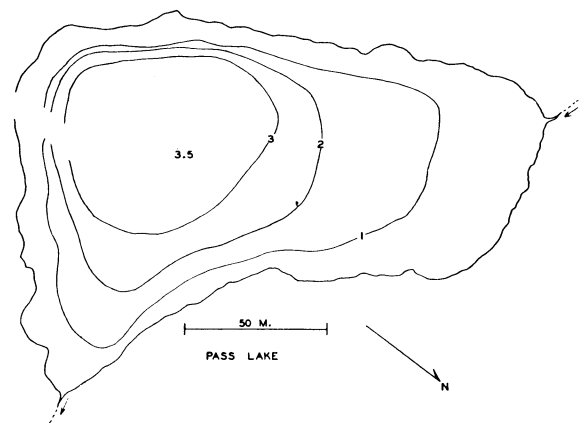


FIG. 5.   Depth contours of Pass Lake, Colorado.

by vehicle during the warm months, one must snowshoe about 500 m during the winter. The altitude is 3,608 m, and Pass Lake is a typical barren oligotrophic alpine lake with rock and gravel shores (Fig. 4), no aquatic vegetation, and a negligible summer plankton population. The area is 1.56 ha, maximum depth is only 3.5 m, and the basin is quite flat (Fig. 5). Total residue averages about 19 mg per liter. There is no regular inlet stream, all inflow being derived from local melting snow and rain. Inflow and outflow are negligible during the winter.

### FIELD AND LABORATORY METHODS

Field equipment was hauled to the deepest water area with a toboggan-like "snowboat" for all sampling. In fine weather when the air temperature was above freezing and when there was little wind, samples could be conveniently taken in the open merely by shoveling a space clear and drilling through the ice. During colder, snowy, and windy weather, however, all operations were done in a 9- by 9-ft heated tent. Although the tent had an outside supporting aluminum frame, accessory stakes were driven into the ice and apparatus was strategically arranged to hold the tent in place in windy weather. A square hole was cut in the floor cloth, and during each field trip a circular hole 14 cm in diameter was cut through the exposed ice with a fisherman's broad-blade Swedish auger. This hole was large enough for water samplers, thermometers, and long plankton sampling tubes. All samples were brought back to the laboratory in Boulder in refrigerator chests for immediate analysis.

Temperatures were taken with custom-made thermistor thermometers standardized in the laboratory before each use and checked against an accurate mercury thermometer in the field. Carbon dioxide determinations were made with the usual phenolphthalein and methyl orange methods. Dissolved oxygen was determined by the unmodified Winkler method, with proper corrections for altitude. Chemical analyses were made at the surface, mid-depth, and 10 cm above the bottom at Pass and Black lakes, but only at mid-depth at the shallow Tea Lake. All samples for chemical analyses were taken with a 2-liter Kemmerer sampler.

Other aspects of this study are the qualitative and quantitative estimates of zooplankton populations, especially since so little is known about under-ice conditions. At Black Lake a composite 10-liter zooplankton sample was derived from 2.5 liters taken with the Kemmerer sampler at each of four evenly spaced depths from top to bottom. At the shallower Pass and Tea lakes two or three top-to-bottom replicates were taken with the plankton tube sampler (Pennak 1962) at each visit. Concentrated samples were counted in Sedgwick-Rafter chambers. Usually the populations were so sparse that all of the organisms in each sample were enumerated.

Phytoplankton populations were determined from centrifuged composite top-to-bottom samples from each lake. Either 1 or 2 liters were run through the Foerst centrifuge for each visit. Centrifugates were counted in Sedgwick-Rafter chambers.

Seston determinations were also obtained from 2-liter composite samples run through the Foerst centrifuge.

Samples for experimental laboratory studies on plankton respiration were taken in the field with the Kemmerer sampler. Such water was run into ground-glass stoppered bottles with an average capacity of 128 ml and with stoppers coated with vaseline to prevent water and air leakage. Methods of treating these samples are discussed in the section *Plankton respiration under laboratory conditions.*

### RESULTS AND DISCUSSION

#### *Ice and snow cover*

Little is known about the variations in snow and ice thickness in mountain lakes from one month to another, despite the dependence of plankton respiration and photosynthetic efficiency on these factors. Table 1 summarizes snow and ice measurements during two winters at each of the three lakes. The snow data in this table are misleading. Actually the total snowfall for the three lakes is heavy, but winds blow much of the snow off the ice, and many days of bright sunshine and low humidities sublimate snows rapidly. These factors, plus the generally low precipitation in the lower montane zone, explain the small amounts of snow recorded for Tea Lake. Protected 1-m drifts in the forest around Tea Lake persist for months. Only about 11 km southwest at an altitude of 2,700 m, the University of Colorado Institute of Arctic and Alpine Research recorded total precipitation of 22.6 and 18.7 cm between December 1 and March 15 in 1962–3 and 1963–4, respectively. Data kindly supplied by John Marr, Director of the Institute. These figures are roughly equivalent to 226 and 187 cm of snow.

As pointed out by Olszewski (1951) and other European investigators, the late winter and spring ice cover of high mountain lakes commonly has alternate layers of ice, snow, and water. The water is presumably released through contraction cracks in ice weighted by heavy snow. This condition developed during January or February at

TABLE 1. Snow and ice thickness

| | 1962–3 | | | 1963–4 | | |
| | | Thickness (cm) | | | Thickness (cm) | |
| Lake | Date | Snow | Ice | Date | Snow | Ice |
|------|------|------|-----|------|------|-----|
| Tea | Dec. 8, '62 | 0 | 14 | Dec. 14, '63 | 0 | 17 |
| | Jan. 5, '63 | 6 | 24 | Jan. 10, '64 | 0 | 24 |
| | Jan. 28, '63 | 0 | 27 | Jan. 30, '64 | 1 | 30 |
| | Mar. 16, '63 | 0 | 24 | Mar. 14, '64 | tr | 31 |
| Pass | Nov. 17, '62 | tr | 18 | Nov. 16, '63 | tr | 16 |
| | Nov. 23, '62 | tr | 30 | Dec. 7, '63 | 10 | 34 |
| | Dec. 14, '62 | tr | 40 | Jan. 6, '64 | 27 | 53 |
| | Jan. 21, '63 | 20 | 54 | Jan. 23, '64 | 8 | 56 |
| | Feb. 9, '63 | 15 | 82 | Feb. 15, '64 | 23 | 60 |
| | Mar. 2, '63 | 45 | 90 | Mar. 7, '64 | 40 | 80 |
| | Mar. 23, '63 | 25 | 90 | Mar. 28, '64 | 33 | 111 |
| | Apr. 13, '63 | 20 | 99 | Apr. 19, '64 | 27 | 130 |
| | May 4, '63 | 10 | 97 | May 9, '64 | 23 | 124 |
| | May 25, '63 | 0 | 79 | | | |
| Black | Dec. 1, '62 | 3 | 25 | Nov. 30, '63 | 5 | 12 |
| | Dec. 22, '62 | 45 | 20 | Dec. 18, '63 | 12 | 29 |
| | Jan. 24, '63 | 45 | 41 | Jan. 16, '64 | 13 | 31 |
| | Feb. 16, '63 | 35 | 76 | Feb. 9, '64 | 28 | 56 |
| | Mar. 9, '63 | 55 | 97 | Feb. 29, '64 | 17 | 81 |
| | Mar. 30, '63 | 21 | 112 | Mar. 19, '64 | 22 | 116 |
| | Apr. 20, '63 | 9 | 103 | Apr. 11, '64 | 20 | 120 |



FIG. 6. Winter temperatures of Pass Lake, Colorado, 1963–4. Scale arranged so that 1°C (horizontally) is equivalent to 1 meter (vertically).
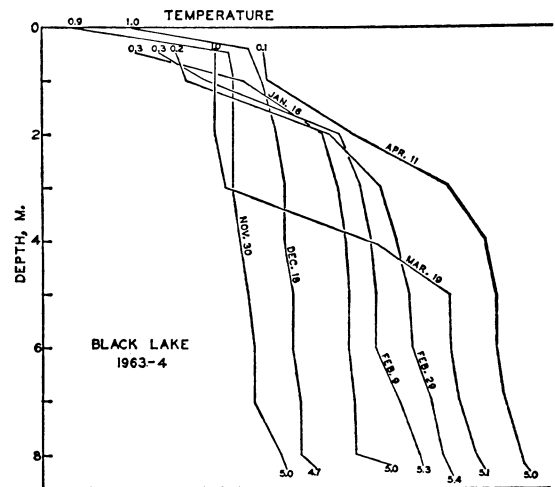


FIG. 7. Winter temperatures of Black Lake, Colorado, 1963–64. Same scale as Figure 6.

Black and Pass lakes and persisted until the spring melt. An opaque layer of slush, 5–25 cm thick, occurred between the ice and the dry snow cover. In Table 1, the layer of slush is included in the thickness of the ice. Rodhe (1955) also reported intermediate layers of slush in Swedish Lapland lakes.

From the data given by Neess and Bunge (1957), and by interpolating the extensive data summarized by Greenbank (1945), it can be assumed that the light transmission through ice and snow cover of Tea Lake averaged 10 or 20%. Thus, photosynthesis could presumably occur from top to bottom in this shallow lake during most winter days. Albrecht (1964), however, claims that sufficient light for photosynthesis can penetrate no more than 2 cm of snow. Wright (1964) found that only 0.19% of the incident radiation penetrated 29 cm of snow and 41 cm of ice in Beaver Pond in Massachusetts.

The combination of thick ice and snow in Pass and Black lakes from December through April or May undoubtedly inhibited all photosynthesis. For practical purposes, therefore, there is no algal primary (photosynthetic) production in the winter, and the oxygen present in the water in November or December is slowly exhausted until the disappearance of snow and ice in May or June returns the lakes to photosynthetic conditions. The zooplankton that survives in Pass and Black lakes depends for nutrition on the residual autumn phytoplankton and on heterotrophic algae, bacteria, and tripton.

## Water temperatures

The most noteworthy feature of temperature conditions in Pass and Black lakes is the marked warming above 4°C in the lower half of these lakes (Figs. 6 and 7). Accounts of such warming during periods of ice cover are widely scattered and not common in the literature, and are usually based on single vertical temperature series. Buchanan (1879) may have been the first to record this phenomenon in a (nowadays) naive fashion: "In Linlithgow Loch which was entirely frozen over, the very great rise in temperature near the bottom was caused by the immense quantity of filth contained in its water and in the mud on the bottom." Buchanan's temperatures were as follows: 3 ft—2.2°C, 36 ft—3.8°C, 42 ft—4.8°C, and 45 ft—5.6°C.

More recent reports of midwinter warming of lower waters (excluding meromictic conditions) are given by Brönsted and Wesenberg-Lund (1911) for Furesö, Birge and Juday (1911) for Lake Mendota (one record), Rossolimo (1932) for Lake Beloje, Hutchinson (1941) for Linsley Pond, Morandini (1949) for several Italian alpine lakes, and Leutelt-Kipke (1934) for several Tyrol lakes. The most extensive records published to

date are contained in Yoshimura (1936) where one vertical midwinter series for each of 15 lakes shows near-bottom temperatures ranging from 4.19° to 6.70°C.

Aside from meromictic and spring-fed lakes, there are two chief means by which bottom waters are heated during periods of ice cover: (1) There may be heating of shallow water under the ice, especially near the periphery of a lake. Such water, when warmed to 4.0°C, "slides downhill" away from shore and along the bottom as a density current to the nearest deep point in the lake basin. In Pass and Black lakes, however, it is extremely doubtful that this mechanism is operative after December 1, by which time the thick ice and snow prevent all light penetration, even near shore. (2) As shown by the pioneer work of Birge, Juday, and March (1928) and other more recent investigators, heat absorbed by the bottom mud during the warm months is transmitted back into the lowermost cold stratum of water during winter stagnation. As this water warms above 4.0°C, it rises and produces minor vertical turbulence so that the stratum of water above 4.0°C may be surprisingly thick. In Pass Lake, for example, up to 1.5 m of bottom water was above 4.0°C (Fig. 6), and in Black Lake this layer attained a maximum thickness of about 6.0 m on December 18 (Fig. 7). As explained by Hutchinson (1941), there is no midwinter "overturn" of the water mass because the lowermost warm water shows a slight chemical stratification which increases the density sufficiently to keep the warmer water in place at the bottom of the lake basin.

In Pass Lake the warming progressed upward until the 4.0°C isotherm reached a depth of 1.9 m below the surface on January 6, and in Black Lake 2.3 m below the surface on December 18. By these dates most of the sedimentary heat had been transferred to the water, and the 4.0°C isotherms thereafter progressed slowly downward in both lakes as the continued cooling below the ice became evident (Figs. 6 and 7). Likens and Ragotzkie (1965) demonstrate these phenomena clearly.

There remains the possibility of warming of bottom waters by inlet streams, but for Black and Pass lakes this mechanism cannot operate because the midwinter temperatures of the negligible inlets ranged from 0.0° to 2.0°C.

Undoubtedly winter heating from the lake basin is common in small lakes of cold latitudes and altitudes. Presumably such records are not abundant in the literature because cold weather discourages midwinter limnology and because critical temperature series are seldom taken.

Temperature conditions in the very shallow Tea Lake require little comment. Since the maximum depth was only 0.9–1.3 m, the influence of the ice cover was manifest from top to bottom. Temperatures at mid-depth ranged from 1.0° to 3.0°C, and the temperature 5 or 10 cm above the bottom ranged from 3.3° to 3.9°C, except in one series on March 14, 1964, when the bottom water reached 4.5°C. Possibly such warming at this late date was due to solar radiation, because there was only a skiff of snow in small scattered areas on the ice.

### Carbon dioxide

During both winters the waters of Black Lake showed progressive stagnation brought on by lack of photosynthesis and continuing respiratory activities of the plankton (Table 2). Free carbon dioxide in the surface waters increased from 1.5 to 4.7 ppm between December 1, 1962 and April 20, 1963, and from 2.6 to 5.5 ppm between November 30, 1963 and April 11, 1964. Carbon dioxide in the bottom waters during the same two periods increased from 4.7 to 16.5 and from 4.1 to 14.9 ppm, respectively. Mid-depth values were roughly intermediate. The half-bound (methyl

TABLE 2. Midwinter carbon dioxide conditions in Black Lake, ppm

| Date | Free carbon dioxide | | | Half-bound carbon dioxide | | |
| --- | --- | --- | --- | --- | --- | --- |
| | Surface | Mid-depth | Bottom | Surface | Mid-depth | Bottom |
| Dec. 1, '62............ | 1.5 | 2.7 | 4.7 | 13.8 | 12.8 | 14.0 |
| Dec. 22, '62........... | 1.7 | 3.0 | 6.2 | 14.0 | 13.3 | 19.2 |
| Jan. 24, '63........... | 3.6 | 5.2 | 7.5 | 12.5 | 14.8 | 20.0 |
| Feb. 16, '63........... | 3.1 | 5.8 | 13.5 | 11.6 | 14.6 | 25.1 |
| Mar. 9, '63........... | 3.0 | 7.9 | 16.7 | 10.5 | 16.9 | 30.0 |
| Mar. 30, '63........... | 3.0 | 8.0 | 13.3 | 11.0 | 14.6 | 24.6 |
| Apr. 20, '63........... | 4.7 | 7.6 | 16.5 | 12.0 | 17.5 | 28.7 |
| Nov. 30, '63........... | 2.6 | 2.6 | 4.1 | 14.7 | 13.5 | 15.1 |
| Dec. 18, '63........... | 2.0 | 4.3 | 6.0 | 13.9 | 14.8 | 18.0 |
| Jan. 16, '64........... | 3.2 | 6.0 | 9.0 | 13.4 | 15.1 | 21.5 |
| Feb. 9, '64........... | 4.1 | 6.0 | 14.3 | 13.4 | 15.5 | 27.1 |
| Feb. 29, '64........... | 5.1 | 6.9 | 13.5 | 14.3 | 16.6 | 30.5 |
| Mar. 19, '64........... | 5.0 | 7.5 | 20.0 | 14.7 | 16.7 | 31.5 |
| Apr. 11, '64........... | 5.5 | 7.5 | 14.9 | 14.2 | 16.5 | 31.4 |

orange) carbon dioxide varied only slightly in the surface waters, but it increased in the bottom waters from 14.0 to 28.7 ppm in 1962–3 and from 15.1 to 31.4 ppm in 1963–4. Mid-depth values were intermediate.

Comparable conditions were found in Pass Lake (Table 3) even though it is much shallower than Black Lake. Perhaps the most striking difference is the fact that the bottom waters reached only 11.0 and 11.1 ppm of free carbon dioxide during the latter parts of the two winters. In comparison with other "typical" alpine lakes of Colorado, the half-bound carbon dioxide deter-

TABLE 3. Midwinter carbon dioxide conditions in Pass Lake, ppm

| Date | Free carbon dioxide | | | Half-bound carbon dioxide | | |
|---|---|---|---|---|---|---|
| | Surface | Mid-depth | Bottom | Surface | Mid-depth | Bottom |
| Nov. 23, '62 | -1.0 | -0.5 | 1.0 | 18.2 | 17.5 | 17.5 |
| Dec. 14, '62 | 1.0 | 0.8 | 0.7 | 20.3 | 20.0 | 19.5 |
| Jan. 21, '63 | 1.8 | 2.0 | 3.8 | 22.0 | 22.0 | 21.8 |
| Feb. 9, '63 | 3.8 | 3.8 | 4.9 | 21.2 | 22.1 | 23.5 |
| Mar. 2, '63 | 4.3 | 4.3 | 6.2 | 22.5 | 22.4 | 23.9 |
| Mar. 23, '63 | 4.5 | 5.0 | 7.3 | 22.0 | 22.6 | 24.5 |
| Apr. 13, '63 | 5.9 | 7.0 | 9.5 | 23.9 | 22.4 | 26.1 |
| May 4, '63 | 6.6 | 7.3 | 9.0 | 25.5 | 24.0 | 27.0 |
| May 25, '63 | 3.7 | 4.5 | 11.0 | 16.0 | 22.3 | 26.2 |
| Nov. 16, '63 | -1.9 | -1.5 | -1.1 | 18.7 | 19.2 | 18.0 |
| Dec. 7, '63 | 1.1 | 1.2 | 1.3 | 20.7 | 19.2 | 19.3 |
| Jan. 6, '64 | 1.3 | 1.7 | 2.4 | 20.7 | 19.7 | 21.5 |
| Jan. 23, '64 | 2.0 | 2.4 | 4.1 | 22.5 | 21.7 | 21.7 |
| Feb. 15, '64 | 2.8 | 2.5 | 5.5 | 23.9 | 22.5 | 23.9 |
| Mar. 7, '64 | 3.3 | 3.5 | 6.8 | 22.0 | 23.4 | 25.0 |
| Mar. 28, '64 | 4.3 | 5.1 | 6.1 | 23.0 | 23.5 | 26.0 |
| Apr. 19, '64 | 8.9 | 8.1 | 9.7 | 24.6 | 24.6 | 28.3 |
| May 9, '64 | 8.3 | 10.5 | 11.1 | 26.0 | 26.8 | 29.0 |

TABLE 4. Dissolved oxygen in Black Lake, ppm

| Date | Depth | | |
|---|---|---|---|
| | Surface | Mid-depth | Bottom |
| Dec. 1, '62 | 8.95 | 8.06 | 5.32 |
| Dec. 22, '62 | 8.38 | 3.53 | 1.71 |
| Jan. 24, '63 | 6.57 | 3.56 | 0.20 |
| Feb. 16, '63 | 5.79 | 2.50 | 0.00 |
| Mar. 9, '63 | 4.85 | 0.10 | 0.00 |
| Mar. 30, '63 | 4.36 | 0.58 | 0.00 |
| Apr. 20, '63 | | 0.10 | 0.00 |
| Nov. 30, '63 | 7.64 | 7.04 | 5.48 |
| Dec. 18, '63 | 7.44 | 5.37 | 2.12 |
| Jan. 16, '63 | 5.23 | 3.37 | 0.03 |
| Feb. 9, '63 | 4.37 | 2.25 | 0.00 |
| Feb. 29, '63 | 5.60 | 1.59 | 0.00 |
| Mar. 19, '63 | 2.62 | 0.00 | 0.00 |
| Apr. 11, '64 | 1.95 | 0.23 | 0.00 |

TABLE 5. Dissolved oxygen in Pass Lake, ppm

| Date | Depth | | |
|---|---|---|---|
| | Surface | Mid-depth | Bottom |
| Nov. 23, '62 | 10.30 | 10.71 | 8.04 |
| Dec. 14, '62 | 9.50 | 9.42 | 9.27 |
| Jan. 21, '63 | 9.67 | 9.29 | 6.98 |
| Feb. 9, '63 | 7.70 | 6.61 | 4.32 |
| Mar. 2, '63 | 5.97 | 6.07 | 2.73 |
| Mar. 23, '63 | 4.94 | 4.80 | 1.09 |
| Apr. 13, '63 | 3.78 | 3.48 | 0.51 |
| May 4, '63 | 2.68 | 2.47 | 0.38 |
| May 25, '63 | | 1.75 | 0.34 |
| Nov. 16, '63 | 9.32 | 9.30 | 9.19 |
| Dec. 7, '63 | 9.67 | 9.20 | 9.08 |
| Jan. 6, '64 | 8.33 | 7.26 | 6.85 |
| Jan. 23, '64 | 6.77 | 6.48 | 6.27 |
| Feb. 15, '64 | 6.07 | 5.19 | 2.46 |
| Mar. 7, '64 | 3.84 | 4.34 | 0.20 |
| Mar. 28, '64 | 2.32 | 1.56 | 0.07 |
| Apr. 19, '64 | 0.27 | 0.25 | 0.00 |
| May 9, '64 | 0.17 | 0.00 | 0.00 |

minations are relatively high. Usually they are less than 15 ppm.

In view of the very low zooplankton and phytoplankton counts, it is remarkable to find pronounced and progressive changes in the carbon dioxide conditions for both Pass and Black lakes. Undoubtedly the bacterial populations were more significant than usual.

Only mid-depth samples were taken at Tea Lake, and the carbon dioxide conditions can be summarized briefly. During 1962–3 the free carbon dioxide increased from 4.4 to 16.6 ppm, and in 1963–4 from 3.3 to 4.1. Half-bound carbon dioxide increased from 38.6 to 57.5 during 1962–3 and from 38.2 to 65.0 ppm in 1963–4. Carbon dioxide accumulations were therefore much more pronounced than in the two deeper lakes, in spite of intermittent periods of photosynthesis. Because several vertical series of temperatures showed sharp stratification in Tea Lake, it can be assumed that carbon dioxide also was sharply stratified, with unusually large quantities of free and half-bound carbon dioxide immediately above the mud-water interface. It should be revealing to conduct similar studies during midwinter ice cover in a wide variety of comparable ponds.

### Dissolved oxygen

Dissolved oxygen concentrations in Black Lake (Table 4) dropped markedly during ice cover. In December 1962 the surface water contained 8.95 ppm (101.0% saturation) of dissolved oxygen, and by March 30, 1963 it had dropped to 4.36 ppm. Mid-depth oxygen dropped rapidly and reached a minimum of 0.10 ppm on March 9 and April 20. The bottom water lost its oxygen

much more quickly than had been anticipated for a mountain lake of this kind and size. No oxygen was found in the bottom waters after January 24. Oxygen conditions for 1963–4 were similar to those of the previous winter except that the surface waters had lost a much greater fraction of dissolved oxygen by winter's end.

Despite pronounced summer oligotrophy, Pass Lake was also characterized by marked reduction of oxygen content (Table 5). In 1962–3, for example, the surface waters had only 2.68 ppm by May 4, and subsequent to March 23 there was less than 1.0 ppm in the bottom waters. In 1963–4 conditions were even more severe, with only 0.17 ppm in the surface water by May 9, 0.00 at mid-depth by May 9, and 0.00 ppm in the bottom water by April 19. The situation is all the more remarkable in view of the fact that Pass Lake

was supersaturated when the first samples were taken. Surface water on November 23, 1962 was 116.6% saturated, and on November 16, 1963 it was 115.0% saturated.

Although there was clear ice cover and little snow during both winters, Tea Lake did not have sufficient photosynthesis to maintain high concentrations of dissolved oxygen (Table 6). As will be shown in a subsequent section, limited winter primary production may be ascribed to low populations of algal cells. At any rate, the oxygen content of mid-depth water decreased from 8.30 ppm on December 8, 1962 to 0.39 ppm on March 16, 1963, and in the following winter from 5.27 ppm on December 14, 1963 to 3.60 ppm on March 14, 1964.

TABLE 6.  Dissolved oxygen in Tea Lake, ppm at mid-depth

| Date | Dissolved oxygen |
|---|---|
| Dec. 8, '62 | 8.30 |
| Jan. 5, '63 | 3.91 |
| Jan. 28, '63 | 5.58 |
| Feb. 23, '63 | 1.34 |
| Mar. 16, '63 | 0.39 |
| Dec. 14, '63 | 5.27 |
| Jan. 10, '64 | 1.21 |
| Jan. 30, '64 | 1.35 |
| Feb. 22, '64 | 1.06 |
| Mar. 14, '64 | 3.60 |

Midsummer (1962) profiles showed a range of 86–105% saturation from top to bottom for all three lakes. Thus the seasonal oxygen conditions are just the reverse of the situation in most stratified lakes, where the lower waters are anaerobic during late summer and more or less aerobic during winter. Indeed, if oxygen is used as the single criterion of lake typology, then Black and Pass lakes are oligotrophic during the summer and eutrophic during the long winter! To put it another way, the waters have a summer orthograde distribution and a winter clinograde distribution of oxygen. This situation does not yet appear to have been noted in the literature. As distinguished from an oligotrophic summer condition, Black and Pass lakes (and presumably many other small mountain lakes) may be classified as winter-anaerobic waters.

*Dissolved oxygen and fish populations*

Tea Lake is privately owned, and it is occasionally stocked with a few legal-sized rainbow trout (*Salmo gairdneri*). Most of these fish are quickly taken by angling, however, and the number of fish persisting from one season to the next is negligible.

Black and Pass lakes are open to public fishing and are heavily and frequently stocked with rainbow trout, usually of legal or near-legal size. Fishing pressure is heavy, but the "average" angler seldom gets more than four or five fish per day of fishing effort. Undoubtedly many trout are still in these lakes when the ice forms, although there are no means of making estimates.

A great deal of information is available in fisheries literature concerning winter-kills and minimum oxygen requirements, especially as related to numerous chemical, physical, and biological conditions associated with such kills (see Greenbank 1945 for a partial summary). Although various conclusions are reached (often depending on the species and size of the fish), the comments of Moore (1942) and Thompson (1925) are generally applicable. The former concluded that: "thresholds of many species of fresh-water fishes lie between 1.0 and 2.0 p.p.m. However, some of the less tolerant species may require up to 3.0 p.p.m. or possibly higher." The latter concluded that, at low temperatures, "dissolved oxygen concentrations between zero and two parts per million will kill all kinds of fishes." In view of the low oxygen or anaerobic conditions attained in Black and Pass lakes, a complete or nearly complete winter kill of trout is very probable.

In Pass Lake in 1962–3 the dissolved oxygen fell below 2 ppm toward the end of February at mid-depth and about the middle of December in bottom water. Such trout as persisted in this lake were therefore confined to the uppermost stratum of the lake for more than a month. Allowing about 90 cm for thickness of the ice, this stratum of water was only about 0.8 or 0.9 m thick. At the close of the winter of 1963–4, on the other hand, the entire water mass contained less than 2.0 ppm after about April 5, and during the subsequent 6 weeks it must be assumed that winter kill was essentially complete. Perhaps a few trout got through the winter near the small trickle forming the intermittent inlet.

Comparable conditions prevailed in Black Lake. By about February 20, 1963 the lower half of the lake contained less than 2.0 ppm dissolved oxygen, and by mid-April a stratum of surface water only about 2 m thick contained sufficient oxygen for trout. In 1963–4 conditions were even more critical, and by about April 5, 1964 none of the water mass contained as much as 2.0 ppm. Except for those trout that congregated at the small inlet, it can be assumed here also that there was a complete winter kill.

In the Colorado mountains Pass and Black lakes are typical of hundreds of small lakes having thick covers of snow and ice for 5–7 months every

winter plus sufficient dissolved and particulate organic matter to reduce, by bacterial action, the dissolved oxygen below a critical threshold for trout. It is my conviction, therefore, that the generally poor fishing in such lakes is a consequence of partial or complete winter kills every year. Unfortunately no good estimates of late autumn and early spring trout populations are available for any such lakes. The disaster of winter kills is often masked by the frequency with which many lakes are artificially stocked with hatchery-reared trout during the open-water months.

### Phytoplankton populations

Reports on frequent time series of reliable, quantitative, top-to-bottom plankton samples from mountain lakes in midwinter do not appear in limnological literature. In a sense, therefore, the data in this section are unique.

The "usual" population cycle for phytoplankton involves a pronounced decrease in numbers of cells once the ice begins to form in the autumn. Populations remain sparse under ice cover until the ice melts in spring, when the water usually undergoes a circulatory period during which nutrients are redistributed. Diatom and blue-green algal populations increase sharply thereafter. Such a sequence, however, did not occur in Black, Pass, and Tea lakes.

*Black Lake.*—Diatoms, green algae, flagellates, and ciliates formed only negligible elements of the phytoplankton populations. There were highly variable and sometimes extremely dense populations of cells (Fig. 8), however, that I have had to resort to calling *"Chroococcus,"* "spores," "very small green algae," "very small blue-greens," and "Chlorobacteriaceae." For the most part, these
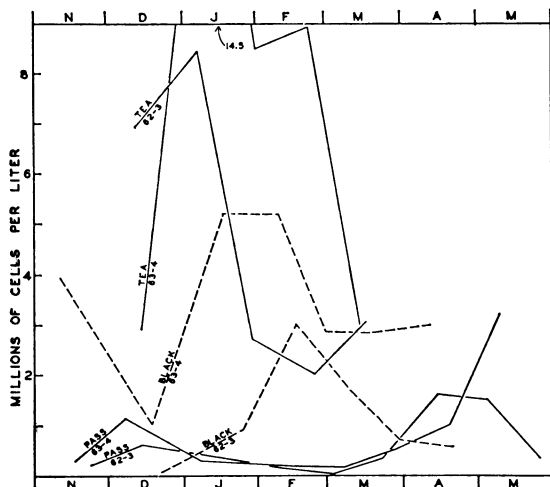


FIG. 8. Winter μ-algae populations of Tea, Black, and Pass lakes, Colorado.

cells defy identification. G. W. Prescott of Michigan State University examined a few samples and states: "As I feared, the organisms are some of the Chlorobacteriaceae—that demimond lying between blue-green algae and the bacteria—about which so little is known in this country . . . along with a scattering of *Chroococcus* sp. . . . many minute spores . . . and possibly *Thiophysa*." The separation of these minute cells into questionable taxonomic categories would be misleading, so they are simply lumped together into what Europeans are conveniently calling "μ-algae." It was assumed that 90% of the cells in the samples were metabolically active, the remainder being inactive spores or cysts, judging from the thickness of the cell walls.

Although phytoplankton samples were taken and treated as large quantitative top-to-bottom samples, the many single Kemmerer samples taken at various depths in Black and Pass lakes showed that the μ-algae were markedly concentrated in the lower anaerobic or near-anaerobic layers. Colleagues have reported to me orally that winter populations of μ-algae are found in railroad ice ponds in Wyoming mountains, and I have no reason to doubt their general occurrence in small bodies of water in the mountains where winter anaerobic conditions persist for several months in bottom waters. I did not find μ-algae in my earlier study of eight mountain lakes (Pennak 1955), but none of these has anaerobic waters during the winter. Nor did I find such algae in a year-round study of plains lakes where ice cover lasts less than 3 months and where the snow cover is negligible (Pennak 1949).

The diatoms in Black Lake were chiefly *Fragilaria, Tabellaria,* and *Synedra.* Green algae were mostly *Scenedesmus* and *Cosmarium.* Flagellates were usually *Mallomonas.*

*Pass Lake.*—In this lake diatoms and small flagellates were more abundant than in Black Lake. Diatoms were most common during the first half of the winter with only an occasional cell being found in samples taken during the latter half. Flagellates occurred sporadically with no seasonal pattern. The μ-algae were much less abundant than in Black Lake (Fig. 8). The same major morphological types were found, but *Clathrochloris sulphurica* (Szafer) Geitler (or a related undescribed species) was much more abundant than in Black Lake.

Diatoms in Pass Lake were mostly *Synedra;* flagellates were chiefly *Dinobryon* and *Mallomonas; Ankistrodesmus* was the only green alga found.

*Tea Lake.*—The μ-algae attained extreme densities in this lake (Fig. 8), and several other taxa

were much more common than in Black and Pass lakes. Flagellates, for example, were abundantly represented by *Euglena, Dinobryon, Ceratium, Peridinium, Trachelomonas, Glenodinium, Mallomonas,* and some colorless species. Large flagellate cysts, in contrast to the small μ-algae spores and cysts, were easily recognized. Green algae were mostly *Ankistrodesmus, Characium,* and *Scenedesmus.* Diatoms were scarce, being limited to a few *Synedra* cells. Ciliates were generally unidentifiable because of improper fixation. The phytoplankton picture for Tea Lake is thus decidedly pondlike and not limnetic.

Figure 8 shows the seasonal abundance for the μ-algae for both winters in the three lakes. Tea Lake had a single population maximum in both years, up to 14.5 million cells per liter on January 10, 1964 and 8.4 million cells per liter on January 5, 1963.

Black Lake had a clearly defined peak of 3 million on February 16, 1963, but in the following year the maximum of 5 million extended from mid-January to mid-February. An early winter maximum of 3.9 million cells per liter was also found in Black Lake on November 30, 1963. It is possible that this population developed very promptly after ice formation but before the ice was strong enough to hold our field party.

Pass Lake had by far the smallest population of μ-algae, and in both years there were two poorly defined maxima. In December of 1962 and 1963 densities reached 539,000 and 1.1 million cells per liter, respectively. In April and May maxima reached 1.5 million (in 1963) and 3 million (in 1964).

Judging from Figure 8, it can be concluded that, regardless of the specific makeup of the "μ-algae" category, maxima may be found 1) early in the winter when anaerobiosis is poorly developed, 2) in midwinter when anaerobiosis is rapidly developing, and 3) in late winter and spring when anaerobiosis and stagnation are completely established.

Rodhe (1955) was presumably the first to use the expression "μ-algae" in the broad sense; i.e., to include a variety of very small forms such as *Chlorella, Cryptomonas, Stichococcus,* and *Coccomyxa.* The scope of the term has been broadened by Drews, Prauser, and Uhlmann (1961) to include *Synechococcus,* and still further in the present paper, even to including unknown genera and species. In general, it would seem advisable to include under "μ-algae" only species of flagellates, greens, blue-greens, Chlorobacteriaceae, and unknown taxa that have maximum dimensions not exceeding 6 μ; in other words, the smallest nannoplankton cells. It should be pointed out that the

centrifugates of lake water in the present study containing large numbers of μ-algae were distinctly dark brownish, and definitely not green.

Lund (1961) never found μ-algae maxima during the winter, but his "μ-algae" includes chiefly *Chlorella, Coccomyxa, Kirchneriella, Ankistrodesmus,* and *Cyclotella.* None of these genera is included in μ-algae as I use the term.

Rodhe (1955, 1962) suggested a dual autotrophy-heterotrophy for a means of heterotrophic proliferation of μ-algae in darkness in Lapland and the Alps. In other words, these forms assimilate dissolved organic matter resulting from photosynthesis during light conditions in previous months. In the 1962 paper he demonstrates glucose acetate assimilation in the dark by a plankton cryptomonad, but no glucose assimilation.

Aside from μ-algae, the ability of certain algae to grow heterotrophically in the dark has been known for many years, the first report probably being that of Beijerinck (1890). Seilheimer and Jackson (1963) list numerous more recent reports. Provasoli's (1958) review emphasizes the ability of many facultative heterotrophic phototrophs to live in the dark indefinitely, including many Volvocales and Chlorococcales. Lund (1965) has much the same conclusion: "There are, then, considerable indications that heterotrophic growth may be more important in the ecology of predominantly photosynthetic algae than has been suggested."

One of the few reported unsuccessful attempts to grow an alga in the dark is that of Fogg and Belcher (1961). Such results, however, may be a reflection of the particular metabolism of their experimental species, *Chlorella pyrenoidosa.*

Rodhe, Hobbie, and Wright (1966) did winter limnological work on several lakes in Lapland, but their results are much different from our Colorado observations, especially their large winter populations of green algae and chrysomonads. They conclude from the combined thickness of snow and ice that midwinter photosynthesis may accompany some heterotrophy but, "Whether or not there are any true heterotrophic algae is extremely difficult to say." Unfortunately, no data are given for snow thickness (as distinct from ice thickness), which is by far the more critical limiting factor for photosynthesis. Presumably it must have been thin enough to transmit some light. They also state that ". . . some of the algae are living by phagotrophy, and this is probably the energy source for the large populations of *Peridinium aciculiferum* . . . but that it is probably not operating in the nannoplankton . . ."

The midwinter metabolism of μ-algae in Black and Pass lakes is probably chiefly a combination

of algal heterotrophy and secondary anaerobic heterotrophy of the sulfur Chlorobacteriaceae such as *Clathrochloris* and *Thiophysa*. In Tea Lake phototrophy is probably the dominant situation, although heterotrophy may have been operative within a few cm of the mud-water interface. Hobbie and Wright (1965) and Wright and Hobbie (1966) contend that bacteria are so effective in utilizing such substrates as glucose and acetate that heterotrophy by algae (*Chlamydomonas* and *Gymnodinium*) is drastically limited. In view of the large μ-algal populations in the three Colorado lakes, however, it appears doubtful that this generalization applies to the Colorado species of μ-algae.

Table 7 shows "average" standing crops of phytoplankton. These data should be used only for judging the general magnitude of such populations

TABLE 7. Average standing crops of major phytoplankton taxa in three Colorado mountain lakes, expressed as cells per liter. A dash signifies no data available; tr signifies less than 100 cells per liter

| Category | Period | Black Lake | Pass Lake | Tea Lake |
|---|---|---|---|---|
| μ-algae | winter 1962-3 | 1,008,900 | 529,400 | 4,650,000 |
| | winter 1963-4 | 3,376,000 | 793,800 | 7,576,000 |
| | open season,1962 | 431,000 | 168,100 | — |
| Diatoms | winter 1962-3 | 370 | 2,050 | 1,270 |
| | winter 1963-4 | 8,040 | 37,300 | 3,250 |
| | open season 1962 | 17,370 | 15,650 | — |
| Green algae | winter 1962-3 | 1,060 | tr | 50,000 |
| | winter 1963-4 | tr | 220 | 12,860 |
| | open season 1962 | tr | tr | — |
| Flagellates | winter 1962-3 | tr | 2,530 | 269,100 |
| | winter 1963-4 | tr | 13,200 | 318,400 |
| | open season 1962 | 960 | 11,150 | — |
| Ciliates | winter 1962-3 | tr | 0 | 23,800 |
| | winter 1963-4 | 1,150 | 0 | 27,300 |
| | open season 1962 | 0 | 0 | — |
| Filamentous blue-greens | winter 1962-3 | 0 | 0 | tr |
| | winter 1963-4 | 0 | 0 | 617,500 |
| | open season 1962 | 0 | 0 | — |

and for gross differences between the three lakes. Omitting the μ-algae from consideration, it is obvious that Tea Lake has a phytoplankton population quite different from those of Black and Pass lakes. The abundance of ciliates, green flagellates, and green algae, combined with sparse populations of diatoms, characterize Tea Lake's phytoplankton as pondlike.

Diatoms and green algal populations in Black and Pass lakes were extremely sparse, especially when compared with populations in other Colorado mountain lakes (Pennak 1955). Although the μ-algae populations appear dense, it should be borne in mind that the cells are minute, and consequently the total biomass is not large.

## Zooplankton populations

In spite of an abundance of seston and μ-algae, only negligible limnetic populations of copepods were present during both winters in all three lakes, and no copepods were found in about half of the samples. No definite seasonal population trends could be defined. On two occasions maximum densities of 1.5 adult *Diaptomus coloradensis* per liter were found in Black Lake. (Because of the accurate quantitative field methods and laboratory counting techniques, results are expressed to the nearest 0.1 of an entomostracan per liter.) Unidentifiable cyclopoid copepodids ranged up to 9.3 per liter, and there were usually less than 3.0 nauplii per liter except for 23.5 per liter on April 20, 1963. In Pass and Tea lakes no adult copepods were ever taken in the samples, but copepodids ranged up to 2.5 per liter and nauplii up to 1.6 per liter in the former, and up to 5.0 and 7.4, respectively, in the latter. The preponderance of immature stages presumably reflects hatching of eggs left over from the autumn reproductive period. Summer population densities of copepods were about 10 times the winter densities.

Cladoceran populations were similarly negligible. *Daphnia rosea* was found in all Black Lake samples, but densities ranged from only 0.1 to 5.0 individuals per liter. January and February samples had the densest populations. *Chydorus sphaericus* were found just once, in January, in Black Lake. The dominant summer cladoceran in Black Lake is *Daphnia pulex*. Except for an occasional *Chydorus sphaericus* (up to 1.1 per liter) and one *Alona quadrangularis*, no cladocerans were taken in Pass Lake. The chief summer cladocerans are *Bosmina*, *Ceriodaphnia*, and *Daphnia*. No cladocerans were found in the winter samples from Tea Lake. Small summer populations of *Chydorus*, *Bosmina*, and *Daphnia* are typical.

Winter rotifer populations were remarkable for their high densities (Tables 8–10). Indeed, the two or three numerically dominant species were more abundant than those in Colorado plains lakes (Pennak 1949) and more abundant than those in typical mountain lakes during the summer months (Pennak 1955). In Black Lake, for example, *Keratella quadrata* reached densities of 395 and 160 per liter, respectively, in January of 1963 and 1964. *Filinia longiseta* reached a sharp peak of 148 per liter in December of 1962 but only 50 in February of 1964. *Asplanchna priodonta* was abundant in the early winter of 1963–4 but present in only small numbers in 1962–3. *Synchaeta* sp. and *Polyarthra* sp., on the other hand, were found in 1962–3 but were absent in 1963–4. Maximum populations were always attained in early or mid-

winter, before severe anaerobic conditions developed.

Pass Lake contained small to dense populations of *Keratella quadrata, Filinia longiseta,* and *Poly-*

TABLE 8.　Seasonal winter populations of dominant rotifers in Black Lake expressed as numbers of rotifers per liter.　Dash signifies less than 1 rotifer per liter

| Date | Keratella quadrata | Filinia longiseta | Asplanchna priodonta | Synchaeta sp. | Polyarthra sp. |
|---|---|---|---|---|---|
| Dec. 1, '62 | 65 | 92 | 1 | 85 | |
| Dec. 22, '62 | 242 | 148 | 5 | | |
| Jan. 24, '63 | 395 | 2 | 4 | 1 | |
| Feb. 16, '63 | 65 | 4 | | — | 3 |
| Mar. 9, '63 | 28 | 2 | | 7 | 3 |
| Mar. 30, '63 | 24 | 4 | — | — | 1 |
| Apr. 20, '63 | 28 | 5 | 1 | 10 | 2 |
| Nov. 30, '63 | 4 | 5 | 6 | | |
| Dec. 18, '63 | 150 | 24 | 132 | | |
| Jan. 16, '64 | 160 | 40 | 12 | | |
| Feb. 9, '64 | 102 | 50 | 7 | | |
| Feb. 29, '64 | 16 | 26 | | | |
| Mar. 19, '64 | 12 | 7 | | | |
| Apr. 11, '64 | 3 | 3 | | | |

TABLE 9.　Seasonal winter populations of dominant rotifers in Pass Lake expressed as numbers of rotifers per liter.　Dash signifies less than 1 rotifer per liter.

| Date | Keratella quadrata | Filinia longiseta | Asplanchna brightwelli | Synchaeta sp. | Polyarthra sp. |
|---|---|---|---|---|---|
| Nov. 23, '62 | 1 | | | 2 | 5 |
| Dec. 14, '62 | 165 | 2 | | 3 | 104 |
| Jan. 21, '63 | 805 | 23 | | | 138 |
| Feb. 9, '63 | 111 | 7 | | | 2 |
| Mar. 2, '63 | 67 | 2 | | | 2 |
| Mar. 23, '63 | 9 | | | | |
| Apr. 13, 63 | 12 | | | | |
| May 4, '63 | 80 | — | | | |
| Nov. 16, '63 | 6 | 9 | | | 26 |
| Dec. 7, '63 | 49 | 269 | 3 | | 569 |
| Jan. 6, '64 | 42 | 22 | 3 | | 57 |
| Jan. 23, '64 | 10 | 11 | | | 43 |
| Feb. 15, '64 | 6 | 10 | | | 18 |
| Mar. 7, '64 | — | 5 | | | 5 |
| Mar. 28, '64 | 6 | 6 | | | 52 |
| Apr. 19, '64 | — | — | | | 3 |
| May 9, '64 | — | — | | | 1 |

*arthra* sp. during both winters, and only a few specimens of *Asplanchna* and *Synchaeta. Keratella quadrata* was much more abundant in 1962–3 than in 1963–4, but *Filinia longiseta* and *Polyarthra* sp. were more abundant in the latter year. Here again, all populations dwindled with the onset of severe anaerobiosis.

Except for the addition of a large population of *Brachionus calyciflorus* in 1962–3 and *Keratella cochlearis* in 1963–4, the same dominant species were found in Tea Lake. *Keratella quadrata* was more abundant during the latter winter and *Filinia longiseta* during the former winter. *Asplanchna brightwelli* was present in 1962–3 but absent in 1963–4, whereas the opposite situation obtained for *Synchaeta. Polyarthra major* attained an extreme density of 1,820 per liter on January 5, 1963, and 1,117 per liter on March 14, 1964. As shown in Table 10, populations sometimes held up well during the late winter, and this may be a reflection of the fact that dissolved oxygen did not approach depletion.

In addition to the species listed in Tables 8–10, small numbers of the following were also taken in the winter samples: *Keratella cochlearis* and *Lepadella patella* in Black Lake; *Asplanchna priodonta* and *Diurella* sp. in Pass Lake; and *Notholca acuminata, Lecane* sp., and *Lepadella patella* in Tea Lake.

Midsummer sampling showed the same dominant species as those in Tables 8–10. Species mentioned in the previous paragraph plus such common forms as *Pompholyx sulcata, Monostyla lunaris, Lecane luna,* and *Conochilus* sp. were also usually found in small numbers.

The material contained in these three tables emphasizes a generalization expressed in earlier studies on Colorado lakes—that rotifer populations exhibit remarkable short-term fluctuations and differ greatly from year to year within the same lake, even to the point of being abundant in a

TABLE 10.　Seasonal winter populations of dominant rotifers in Tea Lake expressed as numbers of rotifers per liter.　Dash signifies less than 1 rotifer per liter

| Date | Keratella quadrata | Filinia longiseta | Asplanchna brightwelli | Synchaeta sp. | Polyarthra major | Keratella cochlearis | Brachionus calyciflorus |
|---|---|---|---|---|---|---|---|
| Dec. 8, '62 | 5 | 80 | 9 | | 1,410 | 14 | 343 |
| Jan. 5, '63 | 23 | 106 | 66 | | 1,820 | | 228 |
| Jan. 28, '63 | — | 3 | — | | 79 | | 37 |
| Feb. 23, '63 | 3 | 366 | | | 114 | | |
| Mar. 16, '63 | 7 | 271 | | | 20 | | |
| Dec. 14, '63 | 78 | 3 | | 41 | 30 | 11 | |
| Jan. 10, '64 | 138 | 76 | | 49 | 158 | 113 | |
| Jan. 30, '64 | 50 | 217 | | 33 | 585 | 183 | |
| Feb. 22, '64 | — | 33 | | 267 | 1,000 | 583 | |
| Mar. 14, '64 | | 17 | | 167 | 1,117 | 100 | |

particular month of one year and absent (by ordinary sampling methods) the following year.

### Seston

Seston determinations have long been used in my laboratory as a general and valid indicator of productivity, especially when seasonal series are available for a particular body of water. Such data for Black, Pass, and Tea lakes are shown in Table 11, where each figure is a composite top-to-bottom value for a particular date. These data have not been increased by the 25% increment suggested earlier (Pennak 1949). They have, however, been corrected for carbonate loss on ignition.

Except for the unusual situation in Tea Lake in the winter of 1962–3, the seston determinations are comparable with summer seston data given for eight mountain lakes (Pennak 1955) and well below those obtained for seven Colorado plains lakes (Pennak 1949). On the other hand, it is clear that there was much more month-to-month variation from the mean under the ice than has been reported for other mountain lakes during the ice-free months. In view of the relatively stagnant conditions and the paucity of entomostracan grazers, these variable winter results are unexpected. Presumably winter bacterial action and the metabolic activities of the μ-algae are vagaries which require careful assessment. In 1962–3 the seston of Black Lake varied from 0.56 to 0.97 mg per liter and in 1963–4 from 0.48 to 1.83 mg per liter. Corresponding means were 0.80 and 1.03 mg per liter. Comparable data for the more oligotrophic Pass Lake are 0.43–1.65 and 0.13–0.63 mg per liter, with means of 0.81 and 0.40 mg per liter. The eutrophic conditions in Tea Lake produced mean seston determinations of 9.95 mg per liter in 1962–3 and 4.86 mg per liter in 1963–4. The former figure is high because of the exceptionally high seston (26.69 mg per liter) on January 28, 1963. Month-to-month trends showed no definite patterns, all seston maxima being found between January 16 and May 9.

In an attempt to clarify some of the wide variations shown in Table 11, laboratory experiments were set up whereby large (2-liter) aliquots of the original water samples were refrigerated in the laboratory for 30 days at 3°C in the dark, followed by second seston determinations. The results, shown in Table 12, are inconclusive. In five of the seven samples there was a decrease in the seston, ranging from 20 to 60%. The other two samples increased in seston by 350 and 78%. Undoubtedly such variations must depend on the uncertainties of autotrophic and heterotrophic nutrition of unicellular forms (Sorokin 1964; Rodhe

TABLE 11. Seston conditions in three Colorado mountain lakes during two winters

| Black Lake | | Pass Lake | | Tea Lake | |
|---|---|---|---|---|---|
| Date | Seston (mg/ liter) | Date | Seston (mg/ liter) | Date | Seston (mg/ liter) |
| Dec. 1, '62 | 0.97 | Nov. 23, '62 | 0.53 | Dec. 8, '62 | 7.93 |
| Dec. 22, '62 | 0.75 | Dec. 14, '62 | 0.43 | Jan. 5, '63 | 6.56 |
| Jan. 24, '63 | 0.74 | Jan. 21, '63 | 0.67 | Jan. 28, '63 | 26.69 |
| Feb. 16, '63 | 0.96 | Feb. 9, '63 | 0.40 | Feb. 23, '63 | 1.08 |
| Mar. 9, '63 | 0.82 | Mar. 2, '63 | 1.65 | Mar. 16, '63 | 7.50 |
| Mar. 30, '63 | 0.56 | Mar. 23, '63 | 1.23 | | |
| Apr. 20, '63 | 0.79 | Apr. 13, '63 | 1.06 | | |
| | | May 4, '63 | 0.64 | | |
| | | May 25, '63 | 0.72 | | |
| Avg | (0.80) | Avg | (0.81) | Avg | (9.95) |
| Nov. 30, '63 | 1.83 | Nov. 16, '63 | 0.57 | Dec. 14, '63 | 4.80 |
| Dec. 18, '63 | 0.73 | Dec. 7, '63 | 0.13 | Jan. 1, '64 | 3.74 |
| Jan. 16, '64 | 1.69 | Jan. 6, '64 | 0.47 | Jan. 30, '64 | 3.24 |
| Feb. 9, '64 | 0.69 | Jan. 23, '64 | 0.37 | Feb. 22, '64 | 6.92 |
| Feb. 29, '64 | 0.29 | Feb. 15, '64 | 0.21 | Mar. 14, '64 | 5.61 |
| Mar. 19, '64 | 1.53 | Mar. 7, '64 | 0.32 | | |
| Apr. 11, '64 | 0.48 | Mar. 28, '64 | 0.36 | | |
| | | Apr. 19, 64 | 0.50 | | |
| | | May 9, '64 | 0.63 | | |
| Avg | (1.03) | Avg | (0.40) | Avg | (4.86) |

TABLE 12. Effect of refrigerated storage on seston content of lake waters

| Lake | Date of sample | Original seston (mg/liter) | Seston of aliquot after 30 days in dark at 3° C |
|---|---|---|---|
| Black | Jan. 16, '64 | 1.69 | 0.74 |
| | Feb. 29, '64 | 0.29 | 1.30 |
| | Mar. 19, '64 | 1.53 | 1.22 |
| Pass | Mar. 7, '64 | 0.32 | 0.24 |
| | Mar. 28, '64 | 0.36 | 0.64 |
| Tea | Feb. 22, '64 | 6.92 | 2.73 |
| | Mar. 14, '64 | 5.61 | 3.85 |

1962). Certainly the negligible populations of diatoms and green algae had no measurable roles.

### Plankton respiration under laboratory conditions

Respiration by unmodified plankton.—Each time a lake was visited, replicate water samples were placed in Pyrex (standard taper) glass-stoppered bottles having an average capacity of 128 ml. In order to eliminate air and water leakage, the stoppers were set tightly with vaseline. These samples were refrigerated at 3°C (± 0.5°) for 30 or 60 days in the dark. At the end of the experimental interval, dissolved oxygen analyses were made, and the results were compared with dissolved oxygen conditions in situ at appropriate depths in each of the three lakes. Because the lakes were visited at 21-day intervals, in situ data were interpolated so that they could be directly compared with the 30- and 60-day refrigerated samples.

These measurements are an attempt to correlate winter plankton respiration in situ and the respi-

ration of the same plankton kept under (comparable) controlled laboratory conditions. The metabolism of enclosed plankton samples has been studied by other investigators who have been chiefly concerned with BOD readings, (dense) summer plankton, primary productivity, and nitrogen and phosphorus cycling. My observations are unusual in that: 1) they are concerned with plankton respiration at an exceptionally low temperature; 2) the entomostracan populations were negligible; and 3) the phytoplankton consisted chiefly of μ-algae and bacteria, with only small numbers of cells of the "usual" phytoplankton genera of diatoms and blue-green and green algae.

TABLE 13. Winter utilization of oxygen by plankton *in situ* and under controlled laboratory conditions (dark, 3°C). Results expressed as net ppm of oxygen consumed

| Lake | Depth | Oxygen consumed in 60 days (1962-3) | | Oxygen consumed in 30 days (1963-4) | |
|------|-------|-------------|---------|-------------|---------|
| | | in laboratory | *in situ* | in laboratory | *in situ* |
| Black | Surface | 1.65 | 2.27 | 1.36 | 1.37 |
| | Mid-depth | 0.37 | 2.73 | 0.85 | 1.74 |
| | Bottom | 0.31 | 2.36 | 0.80 | 2.12 |
| | Avg | (0.78) | (2.45) | (1.00) | (1.74) |
| Pass | Surface | 1.26 | 2.78 | 1.17 | 1.67 |
| | Mid-depth | 1.67 | 3.08 | 1.19 | 1.79 |
| | Bottom | 1.38 | 3.14 | 0.94 | 1.79 |
| | Avg | (1.44) | (3.00) | (1.10) | (1.75) |
| Tea | Mid-depth | 3.90 | 3.29 | 2.10 | 1.06 |

Each value in Table 13 is an average of five to nine different determinations. The results for Black and Pass lakes are the opposite of what were anticipated, namely that respiration *in situ* at all depths was more rapid than respiration in the same water maintained at comparable controlled laboratory conditions. Ordinarily, raw plankton samples kept in bottles in the dark have a relatively high oxygen consumption. The reason usually given is the fact that the surface of the glass serves as a favorable attachment substrate for bacteria, which then become relatively abundant and consume larger quantities of oxygen. I have no logical explanation of the lower respiratory rate (by about 50%) of the plankton of Black and Pass lakes when samples are enclosed in air-tight bottles in a dark refrigerator. Undoubtedly, however, these conditions markedly inhibit or otherwise alter the normal course of bacterial and μ-algal populations, and the whole technique emphasizes the unreliability of experimental data on small enclosed parcels of water. According to John Hobbie, ". . . in our experiments with the bacteria of lakes beneath ice cover,

we found that even at 2°C there was a drastic change in the bacterial flora within bottles within 24 hr."

In Tea Lake, on the other hand, the laboratory samples showed higher oxygen consumptions than water *in situ* in the lake, but these results are a reflection of the fact that some photosynthesis occurred intermittently throughout the winter, thus contributing to the available oxygen in the water and resulting in lower apparent oxygen consumed values in the lake.

In these experiments and in those to be described below every precaution was taken to ensure tight seals with vaseline, but several colleagues have suggested that there is a possibility that over the relatively long periods (30 or 60 days) of refrigeration there may be some "pumping" action of atmospheric air through the seals in spite of temperature variations of only ± 0.5°C in the refrigerator. In order to check this possible error, 12 blank samples were prepared and treated as follows: Tap water was boiled (to reduce the dissolved oxygen), placed in a 4-liter plastic jug, and cooled to 3°C for 24 hr. This (nonsterile) water was used to fill 12 sample bottles having stoppers sealed with vaseline. Six of these samples were refrigerated for 30 days and six for 60 days at 3° (± 0.5°) C. The results follow:

average dissolved oxygen initially: 3.53 ppm;
average dissolved oxygen after 30 days refrigeration: 3.52 ppm;
average dissolved oxygen after 60 days refrigeration: 3.32 ppm.

Thus there was no significant leakage of air (or oxygen) into the bottles through the vaseline seal, even though the water was only about 33% saturated. The anomalous plankton respiration results reported in this section are not therefore the results of experimental error but must be ascribed to metabolic peculiarities of the bacteria, μ-algae, and other phytoplankton groups.

*Plankton respiration as affected by antibiotics.*—Originally I intended to determine bacterial respiration in refrigerated plankton samples by adding broad-spectrum antibiotics to one set of samples and comparing oxygen utilization in these bottles with oxygen utilization in untreated bottles of lake water. The results, however, were not at all in keeping with expectations, but were so unusual that they are reported here in the hope that they will be of value to other investigators working on plankton metabolism.

Each time a lake was visited, pairs of water samples were placed in 128-ml bottles similar to those mentioned in the foregoing section. One bottle of each pair contained *7.7* mg terramycin

TABLE 14. Percentage of available oxygen used in antibiotic-treated lake-water samples as compared with untreated samples. All samples kept in dark at 3°C

| Lake | Year | Days kept in dark | Depth | | | | | |
|------|------|------|------|------|------|------|------|------|
| | | | Surface | | Mid-depth | | Bottom | |
| | | | Antibiotic added | Blank | Antibiotic added | Blank | Antibiotic added | Blank |
| Pass | 1963–4 | 30 | 6.2 | 20.4 | 11.8 | 21.2 | 28.9 | 30.8 |
| | 1962–3 | 60 | 46.9 | 34.3 | 44.2 | 38.1 | 35.9 | 24.1 |
| Black | 1963–4 | 30 | 19.0 | 40.2 | 18.5 | 38.3 | 23.6 | 37.4 |
| | 1962–3 | 60 | 44.9 | 22.1 | 64.6 | 49.1 | 75.0 | 67.3 |
| Tea | 1963–4 | 30 | | | 87.1 | 98.9 | | |
| | 1962–3 | 60 | | | 88.2 | 100.0 | | |

hydrochloride, 2.6 mg tetracycline hydrochloride, and 6.4 mg streptomycin sulfate (an equivalent total of 130 mg of antibiotics per liter). The first two antibiotics are bacteriostatic; the last is bactericidal. These broad-spectrum antibiotics should normally inhibit bacterial metabolism and reproduction, but their effects on μ-algae are not known. All samples were refrigerated in the dark at 3°C for 30 or 60 days, and at the end of these intervals dissolved oxygen determinations were made.

Each value in Table 14 is an average of three to nine separate determinations. The 30-day data for Pass and Black lakes all showed what would be expected under such conditions, namely that the oxygen consumption in the antibiotic-treated water was lower than in the untreated blanks. Presumably the bacterial respiration accounted for roughly half of the oxygen loss in the blanks, the remaining oxygen being used for respiration by the phytoplankton (chiefly μ-algae) and the negligible zooplankton (and yeasts and molds?).

When samples were refrigerated for 60 days, however, the situation became reversed, and there was greater cumulative oxygen consumption in bottles containing antibiotics than in the controls. Such results emphasize our lack of knowledge of gross plankton metabolism and the uncertainty of keeping natural water refrigerated for long periods. Perhaps these data may be explained by assuming that the early suppression of bacterial growth allowed other organisms (μ-algae?) to compete for the common nutrient pool more effectively, and that while early proliferation was slow, the population density of nonbacterial phytoplankton organisms may have been increasing exponentially by the time 40 to 60 days had passed.

The results discussed thus far in this section refer only to Pass and Black lake waters. In Tea Lake there were no significant differences between the 30- and 60-day refrigerated samples. Antibiotics decreased oxygen respiration by about 10 or 12%, but apparently the Tea Lake samples did not contain the same organisms in proper relative densities to produce the conditions found in Black and Pass lake waters.

*Millipore filtration and antibiotic treatment.*— In order to obtain a more accurate assessment of the effects of antibiotics on plankton respiration and to rule out wide variations in initial oxygen concentrations, a third set of simple observations was made during both winters. Immediately upon our return to the laboratory, we ran a liter of water from each sampling depth through a 2 μ Millipore filter. No special sterile techniques were used, since my chief purpose was to remove from the water all zooplankton and all "ordinary" phytoplankton. A filter of this porosity allows a few μ-algae and many bacteria to pass. When lake water is passed through a Millipore, the agitation and suction change the dissolved oxygen concentrations so that high concentrations are lowered and low concentrations are increased. The great majority of water samples contained from 3 to 5 ppm dissolved oxygen after passing through the filter. Three aliquots were used from the 1-liter sample. One aliquot was for an immediate oxygen analysis. A second sample of 128 ml was placed in a bottle (same as foregoing) and kept at 3°C in the dark for 30 or 60 days. The third aliquot was similar to the second except that antibiotics (as above) were added to it. Results, involving 290 samples, are summarized in Table 15.

In those samples refrigerated for 30 days at 3°C the results were approximately as expected. That is, there was greater oxygen consumption in samples not containing antibiotics, roughly 200 to 300% in Black and Pass lake waters. This difference indicates that the "residual" bacteria in the filtered water used two or three times as much oxygen as the very few "residual" μ-algae (and yeasts and molds?).

Although all samples were run through the filter in the same manner, it is notable that filter-passing cells in Tea Lake waters were sufficiently

TABLE 15. Oxygen utilization by Millipore-filtered water samples kept in the dark at 3°C expressed as ppm

| Lake | Initial dissolved oxygen | Dissolved oxygen in untreated samples after | | Dissolved oxygen in antibiotic-treated samples after | |
|---|---|---|---|---|---|
| | | 30 days | 60 days | 30 days | 60 days |
| Black | 4.21 | | 3.77 | | 2.77 |
| | 3.59 | 3.09 | | 3.40 | |
| Pass | 4.90 | | 4.30 | | 3.47 |
| | 4.39 | 3.74 | | 4.20 | |
| Tea | 4.28 | | 0.01 | | 0.47 |
| | 3.58 | 0.12 | | 1.88 | |

abundant to produce a much higher subsequent respiratory rate than in Black and Pass lake waters.

In the 60-day samples of Black and Pass lake waters the results are anomalous and comparable to those in the preceding section, with greater oxygen consumption in the antibiotic-treated water. Of the several possible reasons for this anomaly, the increased respiration by yeasts and molds (and μ-algae?) may be the most logical. In eliminating the competitive role of bacteria, antibiotics are known to enhance the growth of yeasts and molds (a phenomenon often referred to by microbiologists as "superinfection"). In the antibiotic-treated samples kept for 60 days at 3°C, therefore, it may be postulated that aquatic yeasts and molds, normally inhibited by bacterial competition for nutrients, can grow and become abnormally abundant, thus accounting for the greater oxygen consumption as compared with controls containing no antibiotics. Another (partial) explanation may be a familiar bacterial mechanism whereby the antibiotics eliminated all bacteria except a very few mutant cells that were antibiotic-resistant and were able, after a lag phase, to grow rapidly and use the available nutrients.

The anomalies in these last three sections are reported in order to call attention to the fact that enclosed experimental phytoplankton populations may produce a wide and unexpected range of ecological and competitive conditions, especially in the dark at low temperatures.

## ACKNOWLEDGMENTS

## LITERATURE CITED

Albrecht, M.-L. 1964. Der Einfluss von Licht und Temperatur auf die Sauerstoffproduktion im Wasser unter Eis und Schnee. Z. Fischerei 12: 167–182.

Beijerinck, M. W. 1890. Culturversuche mit Zoochlorellen, Lichengonidien und anderen niederen Algen. Bot. Z. 48: 725.

Birge, E. A., and C. Juday. 1911. The inland lakes of Wisconsin. The dissolved gases of the water and their biological significance. Bull. Wis. Geol. Natur. Hist. Surv. 22: 1–259.

Birge, E. A., C. Juday, and H. W. March. 1928. The temperature of the bottom deposits of Lake Mendota. Trans. Wis. Acad. Sci. Arts, and Lett. 23: 187–231.

Brönsted, J. N., and C. Wesenberg-Lund. 1911. Chemische-physikalische Untersuchungen der dänischen Gewässer. Int. Rev. ges. Hydrobiol. 4: 251–290.

Buchanan, J. Y. 1879. On the freezing of lakes. Nature 19: 412–414.

Drews, G., H. Prauser, and D. Uhlmann. 1961. Massenvorkommen von Synechococcus plancticus nov. spec., einer solitären planktischen Cyanophycee, in einem Abwasserteich. Beitrag zur Kenntnis der sogennanten "μ-Algen." Arch. Mikrobiol. 39: 101–115.

Fogg, G. E., and J. H. Belcher. 1961. Physiological studies on a planktonic μ-alga. Proc. Int. Assoc. Theor. Appl. Limnol. 14: 893–896.

Greenbank, J. 1945. Limnological conditions in ice-covered lakes, especially as related to winter-kill of fish. Ecol. Monogr. 15: 343–392.

Hobbie, J. E., and R. T. Wright. 1965. Competition between planktonic bacteria and algae for organic solutes. Mem. Ist. Ital. Idrobiol. 18: (Suppl.): 175–185.

Hutchinson, G. E. 1941. Limnological studies in Connecticut. IV. The mechanism of intermediary metabolism in stratified lakes. Ecol. Monogr. 11: 21–60.

Leutelt-Kipke, S. 1934. Ein Beitrag zur Kenntnis der hydrographischen und hydrochemischen Verhältnisse einiger Tiroler Hoch- und Mittelgebirgsseen. Arch. Hydrobiol. 27: 286–352.

Likens, G. E., and R. A. Ragotzkie. 1965. Vertical water motions in a small ice-covered lake. J. Geophysical Res. 70: 2333–2344.

Lund, J. W. G. 1961. The periodicity of μ-algae in three English lakes. Proc. Int. Assoc. Theor. Appl. Limnol. 14: 147–154.

———. 1965. The ecology of the freshwater phytoplankton. Biol. Rev. 40: 231–293.

Moore, W. G. 1942. Field studies on the oxygen requirements of certain fresh-water fishes. Ecology 23: 319–329.

Morandini, G. 1949. Richerche limnologiche sugli alti laghi alpini della Venezia tridentina (secondo contributo), Sella, Lagorai, Val delle Pozze. Boll. Pesca, Piscic. Idrobiol. 4: 75–115.

Neess, J. C., and W. W. Bunge, Jr. 1957. An unpublished manuscript of E. A. Birge on the temperature of Lake Mendota; Part II. Trans. Wis. Acad. Sci. Arts and Lett. 46: 31–89.

Olszewski, P. 1948. Winter stratification of oxygen in the larger Tatra lakes. Bull. Acad. Pol. Sci. Lett., Cl. Sci. Math. Nat., Ser. A, No. Somm. (1940–1946): 65–111.

———. 1951. The thermal conditions of mountain lakes. Bull. Acad. Pol. Sci. Lett., Cl. Sci. Math. Nat., Ser. A, Sci. Math. (1953): 239–290.

Pennak, R. W. 1945. Some aspects of the regional

limnology of northern Colorado. Univ. Colo. Studies, Ser. D, 2: 263–293.

———. 1949. Annual limnological cycles in some Colorado reservoir lakes. Ecol. Monogr. 19: 233–267.

———. 1955. Comparative limnology of eight Colorado mountain lakes. Univ. Colo. Studies, Ser. Biol. 2: 1–75.

———. 1962. Quantitative zooplankton sampling in littoral vegetation areas. Limnol. Oceanogr. 7: 487–489.

Provasoli, L. 1958. Nutrition and ecology of Protozoa and algae. Ann. Rev. Microbiol. 12: 279–308.

Rodhe, W. 1955. Can plankton production proceed during winter darkness in subarctic lakes? Proc. Int. Assoc. Theor. Appl. Limnol. 12: 117–122.

———. 1962. Sulla produzione di fitoplancton in laghi trasparenti di alta montagna. Mem. Ist. Ital. Idrobiol. Dott Marco de Marchi 15: 21–28.

Rodhe, W., J. E. Hobbie, and R. T. Wright. 1966. Phototrophy and heterotrophy in high mountain lakes. Proc. Int. Assoc. Theor. Appl. Limnol. 16: 302–313.

Rossolimo, L. 1932. Der Thermik der Bodenablagerungen des Beloje-Sees zu Kossino. Arb. Limnol. Sta. Kossino 15: 44–66.

Seilheimer, J. R., and D. F. Jackson. 1963. A comparison of algal growth in cultures exposed and unexposed to solar radiation. Trans. Amer. Micros. Soc. 82: 78–82.

Sorokin, J. I. 1964. On the trophic role of chemosynthesis in water bodies. Int. Rev. ges. Hydrobiol. 49: 307–324.

Suchlandt, O., and W. Schmassmann. 1935. Limnologische Beobachtungen an acht Hochgebirgsseen der Landschaft Davos. Z. Hydrol. (Hydrog. Hydrobiol. Fischereiwiss.) 7: 1–201.

Thompson, D. H. 1925. Some observations on the oxygen requirements of fishes in the Illinois River. Bull. Ill. Natur. Hist. Surv. 15: 423–437.

Wright, R. T. 1954. Dynamics of a phytoplankton community in an ice-covered lake. Limnol. Oceanogr. 9: 163–178.

Wright, R. T., and J. E. Hobbie. 1966. Use of glucose and acetate by bacteria and algae in aquatic ecosystems. Ecology 47: 447–464.

Yoshimura, S. 1936. A contribution to the knowledge of deep water temperatures of Japanese lakes. Part II. Winter temperatures. Jap. J. Astr. Geophys. 14: 57–83.

# STRUCTURAL CHARACTERISTICS OF BENTHIC ALGAL COMMUNITIES IN LABORATORY STREAMS

C. David McIntire

*Department of Botany, Oregon State University, Corvallis, Oregon 97331*

*Abstract.* Effects of light intensity and current velocity on the species composition and ecological properties of communities of benthic algae were investigated in laboratory streams. Of the 15 diatom taxa studied, only *Melosira varians, Meridion circulare,* and *Navicula radiosa* were more abundant in streams receiving 700 ft-c of illumination than in those receiving 150 ft-c. *Achnanthes exigua, A. minutissima, Meridion circulare, Rhoicosphenia curvata,* and *Navicula radiosa* were indifferent to current velocity, while current velocity had a positive effect on the abundance of *Nitzschia linearis, Achnanthes lanceolata, Navicula cryptocephala, N. minima, N. seminulum, Synedra ulna, Gomphonema parvulum, G. angustatum, Cocconeis placentula,* and the lanceolate *Nitzschia. Melosira varians* exhibited a negative response to current and was more abundant in standing water. Of the six taxa other than diatoms, *Anabaena variabilis* and *Tribonema minor* were more abundant in streams at the higher light intensity, but only one species, *Phormidium retzii,* was more abundant in streams with a current than in standing water.

At a particular season, light intensity, and current velocity, conditions in a laboratory stream allow the establishment of an algal community with a more or less unique species composition and a characteristic biomass, pigment concentration, and increment of export. In order to understand the factors which influence productivity in these communities, it is necessary to have some knowledge of the autecologies of the community constituents and the mechanisms which regulate species composition and diversity of the flora.

## INTRODUCTION

Studies of benthic algae and associated heterotrophic micro-organisms (i.e., periphyton) in flowing water environments have become more numerous within the last 10 yr, possibly as an indirect result of an increased demand for water pollution abatement in various streams and river systems and the concurrent development of new field and laboratory methods. In most of these studies, investigators have been concerned either with estimation of primary production and respiratory losses in the community unit (e.g., Cushing 1967; Duffer and Dorris 1966; Edwards and Owens 1962; McConnell and Sigler 1959) or with a descriptive analysis of species composition and the relationship between numbers of species and numbers of individuals (Patrick, Hohn, and Wallace 1954; Patrick 1961). Unfortunately, it is extremely difficult in field investigations to determine the factors and mechanisms that account