UNIVERSITY OF COLORADO STUDIES

Series in Biology
No. 2

COMPARATIVE LIMNOLOGY OF EIGHT COLORADO MOUNTAIN LAKES

BY
ROBERT W. PENNAK

University of Colorado Press
Boulder, Colorado, July, 1955

UNIVERSITY OF COLORADO STUDIES

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ROBERT W. PENNAK
PROFESSOR OF BIOLOGY
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UNIVERSITY OF COLORADO PRESS
BOULDER, COLORADO, JULY, 1955
Price $1.50

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COMPARATIVE LIMNOLOGY OF EIGHT COLORADO MOUNTAIN LAKES[1]

INTRODUCTION

Limnological literature contains many papers dealing with various phases of the limnology of mountain lakes and ponds, the past 20 years having demonstrated a greatly increased interest in such bodies of water, both in Europe and North America. Unfortunately, however, the great majority of such papers are brief and often superficial. Many are based on but single or sporadic visits to a lake and include only a few chemical and physical observations and notations on the plankton and bottom fauna. Our conception of the entire open season and of year-round chemical, physical, and biological conditions is therefore much more sketchy than is the case for lakes at lower elevations.

In North America, published investigations covering the limnology of mountain lakes over the entire open season are almost non-existent. Most papers are of a "reconnaissance" or "survey" nature. Two papers of Rawson (1942, 1953a) are notable exceptions.

The reasons for this situation are obvious. High lakes are often difficult of access and cannot be studied at frequent intervals, even in the summer months. In addition, the open season is very short, and there may be an ice cover extending through as long as seven to nine months. Since access roads are usually snowed in through this long winter period, it is impossible to visit such mountain lakes without undertaking an arduous journey on skis or snowshoes; and at such times it is difficult to carry even basic sampling equipment over the rough terrain. Frequently, therefore, even the most carefully planned investigations on mountain lakes are restricted to four to six months of the year. Few high-altitude lakes are so situated that they can be reached with automobile and field equipment through 12 months of the year.

European limnologists have been much more thorough in their investigations of mountain lakes, and quantitative data over the entire open season for numerous lakes, chiefly in the Alps, are included in the following typical papers: Baldi, Tonolli, and Pirocchi (1953), Findenegg (1953), Haempel (1923, 1926, 1932), Leutelt-Kipke (1934, 1935, 1936), Lotz (1929), Ruttner (1929/1930, 1937), Stirnimann (1926), and Suchlandt and Schmassmann (1938).

The present report is a contribution to our knowledge of the comparative limnology of eight northern Colorado mountain lakes which are located within a 40-mile radius of the Limnology Laboratory at the University of Colorado. These

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[1] Contribution No. 25, Limnology Laboratory, University of Colorado.

eight particular bodies of water were selected for study because they are typical examples of some of the many different varieties of lakes occurring in this geographic area. Field work extended from July 19, 1950 to April 13, 1954. Each lake was studied over a one-year period and was visited every three to four weeks during as much of the year as road and weather conditions would permit. Special emphasis was placed on seasonal qualitative and quantitative phytoplankton and zooplankton cycles, Secchi disc readings, free and bound carbon dioxide, dissolved oxygen, pH, temperature, and seston. In its aims, this investigation parallels the plains reservoir study published several years ago by the present author (Pennak, 1949). The main topics discussed are chiefly of a descriptive and comparative nature. No attempt is made to elaborate any special hypotheses. No theories are expounded to explain the *causes* of plankton cycles and variations.

This study was made possible through grants-in-aid from the Penrose Fund of the American Philosophical Society and the University of Colorado Council on Research and Creative Work. The Superintendent and Chief Naturalist of Rocky Mountain National Park were kind enough to issue the necessary collecting permit for working on Bear Lake. Robert McCollum, of Denver, generously granted permission to work on Manchester Lake. The office of the U. S. Bureau of Reclamation at Estes Park kindly allowed the author to make a copy of their survey of the Lake Estes site, from which a hydrographic map was easily constructed. A. W. Stromberg and David Abbott of the office of Denver Mountain Parks granted permission to use a boat on Summit Lake. Several colleagues and graduate students were most helpful on many field trips, often during the discomforts of high winds, rain, sleet, and snow.

DESCRIPTION OF LAKES STUDIED

Table I includes some of the gross chemical and physical features, the latter calculated on the basis of the high-water marks. Lake Estes, at an elevation of 2277 meters (7469 feet) lies just within the upper limit of the foothills zone (Pennak, 1941). Summit Lake, at an altitude of 3884 meters (12,740 feet), lies well above the lower limit of the alpine zone, and is the highest lake of any size in Colorado. The other six lakes range in elevation from 2540 to 3140 meters (8331 to 10,299 feet) and are situated within the montane zone.

With the exception of Manchester Lake, all of these bodies of water have soft waters, low residues, loss on ignition, and ash which are characteristic of northern Colorado mountain lakes (Pennak, 1945b). These data are indicated in the last three columns of Table I, where each figure represents an average of two to four separate determinations.

The lake outlines shown for the six hydrographic maps in the following pages were reproduced accurately from enlargements of U. S. Forest Service aerial

Fig. 1. Hydrographic map of Lake Estes, Colorado. Depths are indicated in meters.

photographs, but the depth contours were derived from series of sounding transects made from a boat.

Lake Estes. This body of water (Figs. 1 and 7) is unique in its comparative youthfulness. It was constructed previous to 1948 as one of the units in the multiple-purpose Colorado-Big Thompson project and fills much of a valley formerly traversed by the Big Thompson River. The lake is long and narrow from west to east, but the only deep water (up to 13.7 meters) is located in the easternmost third, just above the dam. Water entering the western end of the lake has two origins. Some is from the Big Thompson River, which passes through Estes Park Village just above the lake, and another portion originates west of the Continental Divide and enters the lake via a long tunnel through the mountains. When filled, this lake has a volume of 3,104,000 cubic meters, which is exceeded only by Grand Lake. The annual water-level fluctuation is not excessive, seldom being more than one or two meters. A growth of rooted aquatics has not yet become established. The surrounding terrain is covered with a typical "mountain park" growth of sparse grasses and herbs, with a few scattered yellow pines. The waters of this lake are stocked with trout regularly, usually of legal size.

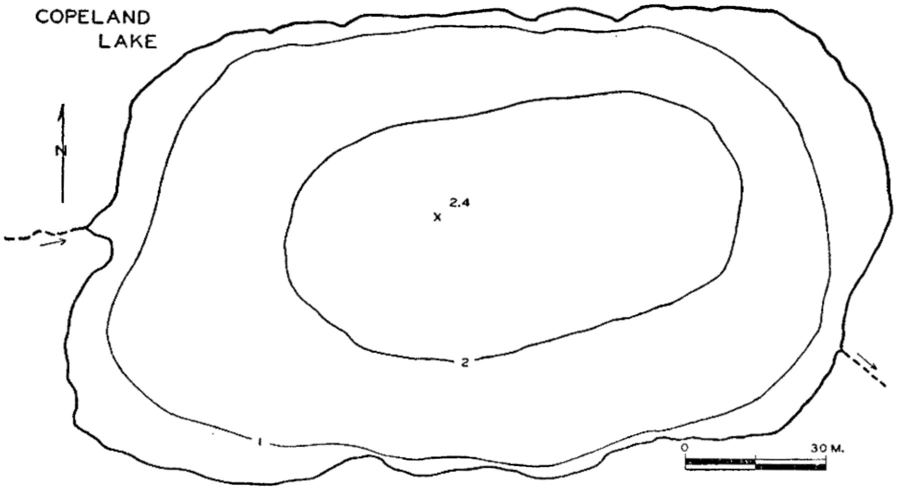

FIG. 2. Hydrographic map of Copeland Lake, Colorado. Depths are indicated in meters.

Copeland Lake. This is the smallest body of water in the group studied (Figs. 2 and 8), and actually it is nothing more than a shallow pond with a dense growth of *Chara* covering most of the bottom. The lake was formed in 1913 by the construction of a low dam at the eastern edge of a small depression. There is an intermittent inlet at the west end and a head-gate outlet at the east end. The level varies considerably. In years of unusually high run-off it may reach a maximum depth of 5 meters, but during the past several dry years the maximum depth has varied between 2.0 and 2.4 meters. The lake is surrounded by a forest of yellow pine and Douglas fir. Although Copeland Lake is occasionally stocked with trout, they do not maintain themselves, and there is only a small persistent population of suckers (*Catostomus*).

Grand Lake. This is the largest and deepest natural body of water in the state of Colorado (Fig. 9). It is situated in a steep-sided mountain valley on the west side of the Continental Divide at the head of the Colorado River drainage system. No hydrographic map is available, but numerous soundings show that the deep water covers a very large part of the lake, and the mean depth is unquestionably in excess of 50 meters. Grand Lake forms a part of the Colorado-Big Thompson project, and during much of the year water flows *into* the west end from Shadow Mountain Reservoir and *out* of the east end via the Adams tunnel, which carries water eastward through the mountains to Lake Estes on the Eastern Slope. In former times, of course, Grand Lake had a continuous outlet at the west end. The annual fluctuation in water level is less than 0.3 meter. A few small beds of potamogetons and *Chara* grow in the lake, which is regularly stocked with trout. Except for short sections of the north, west, and east shores, the lake is surrounded by typical montane forest.

Manchester Lake. This private lake (Figs. 3 and 10) was formed in 1900 by the construction of two earthen dikes at the east end of a double depression. Pre-

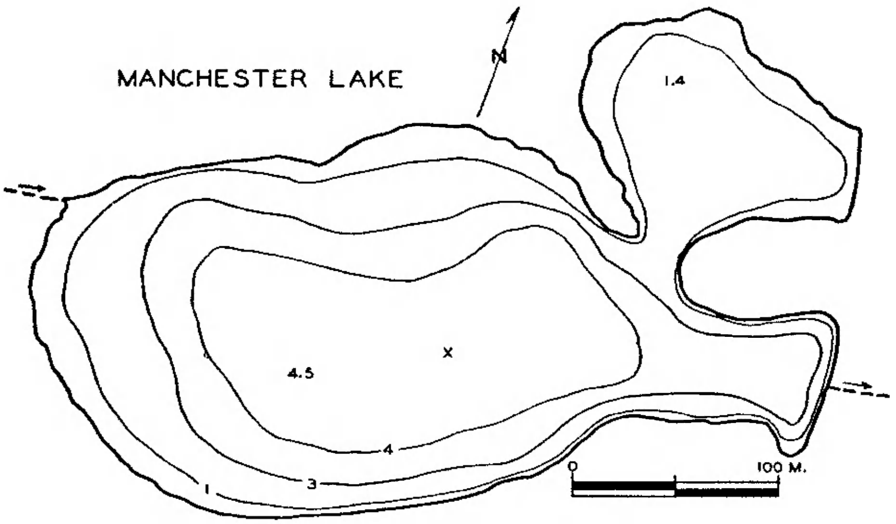

FIG. 3. Hydrographic map of Manchester Lake, Colorado. Depths are indicated in meters.

sumably it was originally intended chiefly for use as a fishing lake, since the outlet leads into a shallow, wet valley where irrigation water would be superfluous. Although there is an intermittent inlet at the west end, it seldom brings water into the lake. Nevertheless, the level remains remarkably constant, the annual variation in water level seldom exceeding 0.4 meter. It is possible that the lake contains some small springs. The main basin has a considerable growth of *Chara*, and the small northeast basin supports a dense growth of potamogetons. Manchester Lake is an unusual mountain lake in that it has a crayfish population, but the only fish seem to be stunted perch (*Perca flavescens*) and a few suckers. The lake is surrounded by an open yellow pine forest.

Beaver Reservoir. This reservoir lake (Figs. 4 and 11) was formed in 1892 by the construction of a high dike along the north edge of a large depression. In addition to local surface drainage, there is an intermittent inlet at the south end. A head gate is located at the east end of the dike, and a flow of water leaves the reservoir through this outlet during most of the year. Such water is carried by ditches to the plains zone 13 miles to the east, where it is used for irrigating fields. There is an overflow channel in the middle of the dike. This lake has a greater variation in water level than any of the other seven investigated, and during the period of study the maximum depth ranged from 2.8 to 10.1 meters. Much of the bottom is covered with fibrous peat which supports a poor benthic fauna. The fishing is disappointing. Although rainbow trout are planted frequently, they show poor growth and survival. Aside from the poor food supply, perhaps the few very large brown trout in the lake are responsible for keeping the rainbow population at a low level. There is also a dense population of suckers, most of which show a poor condition factor. Beaver Reservoir is surrounded by a montane forest.

Bear Lake (Fig. 12), like Grand Lake, is one of the best-known American mountain lakes from the standpoint of the general public. Photographs of it have appeared in many magazines and Sunday newspaper supplements. It also appears on calendars with surprising frequency. A hydrographic map of this body of water has already been published (Pennak, 1945a). The basin is a simple bowl-shaped depression with a shoreline development of only 1.12. There is an inlet at the west end and an outlet at the east end. The water level is constant and ordinarily does not vary more than 0.2 meter during the course of a year. The bottom near the east end consists of rubble and many large boulders, but much of the remainder of the substrate is organic. A few small scattered beds of potamogetons grow along the western shore. Bear Lake is heavily fished and frequently planted with rainbow trout, but the sucker population maintains complete numerical dominance, being three to ten times as abundant as the trout. A subalpine forest surrounds the lake.

Brainard Lake. To the average visitor, this body of water (Figs. 5 and 13) is deceptive in that it is much more shallow than one would guess. The deepest spot

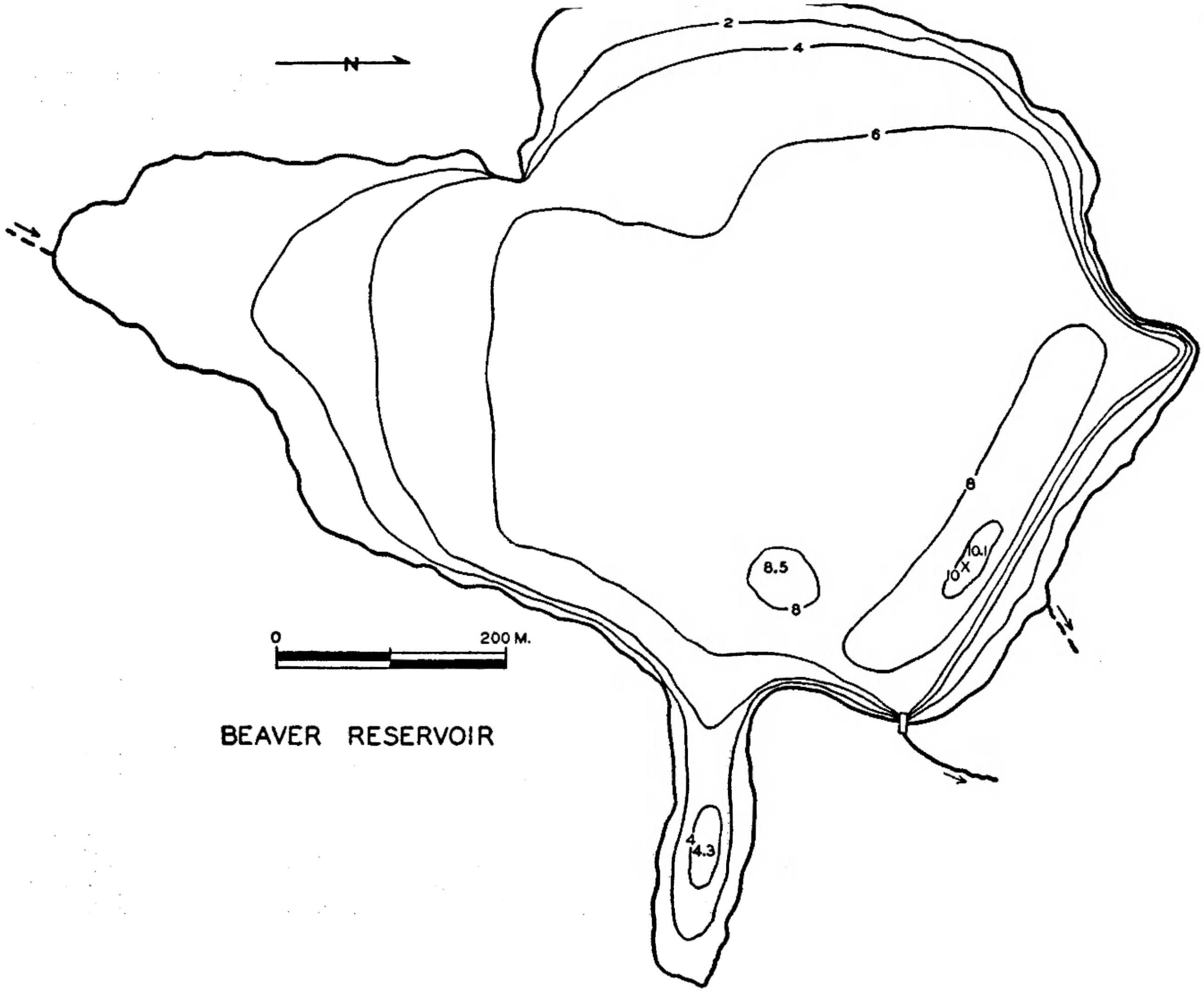

FIG. 4. Hydrographic map of Beaver Reservoir, Colorado. Depths are indicated in meters.

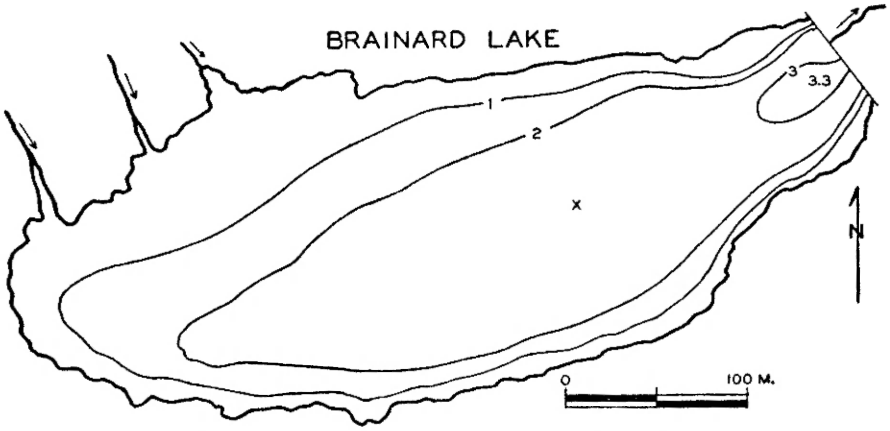

FIG. 5. Hydrographic map of Brainard Lake, Colorado. Depths are indicated in meters.

is 3.3 meters, and the mean depth only 1.6 meters, the lake having been made in 1892 by damming the South St. Vrain Creek at the east end of a gently sloping mountain meadow. This stream breaks up near the west end and enters Brainard Lake basin as three separate inlets. The water level shows an annual fluctuation of 0.2 meter or less. Much of the original gravel bottom now supports a continuous growth of *Chara*. A variable trout and sucker population is present, but there is a poor bottom fauna.

Summit Lake. This lake, near the top of Mount Evans, presented the greatest uncertainties for field work. It is 80 miles from the laboratory by mountain roads, and frequently upon our reaching the lake the wind would be blowing so violently that it was impossible to work from the sturdy aluminum rowboat; we could only turn around and make the return journey to the laboratory. The west end of Summit Lake (Figs. 6 and 14) lies at the foot of a rubble-strewn cirque, and the steep alpine terrain surrounding the basin consists mostly of exposed schists and gneisses. All of the water is derived from showers and melting snows in the immediate vicinity. The water level is stable, and there is a small stream carrying the outflow. Unlike the other seven lakes in this study, Summit Lake has two distinct depressions in its basin, one of 15.4 meters near the west end and another of 17.2 meters in the northeast arm. Except for Grand Lake, this body of water has the greatest mean depth (7.0 meters). Annual fluctuations in water level amount to only about 0.1 meter. The littoral areas are mostly gravel, rubble, and boulders. There are no rooted aquatics, and the bottom fauna is poor. Although the lake is stocked with trout, growth seems to be generally slow.

Estes and Bear lakes are located in Larimer County; Grand Lake is in Grand County; Summit Lake is in Clear Creek County; the other four lakes are all in Boulder County.

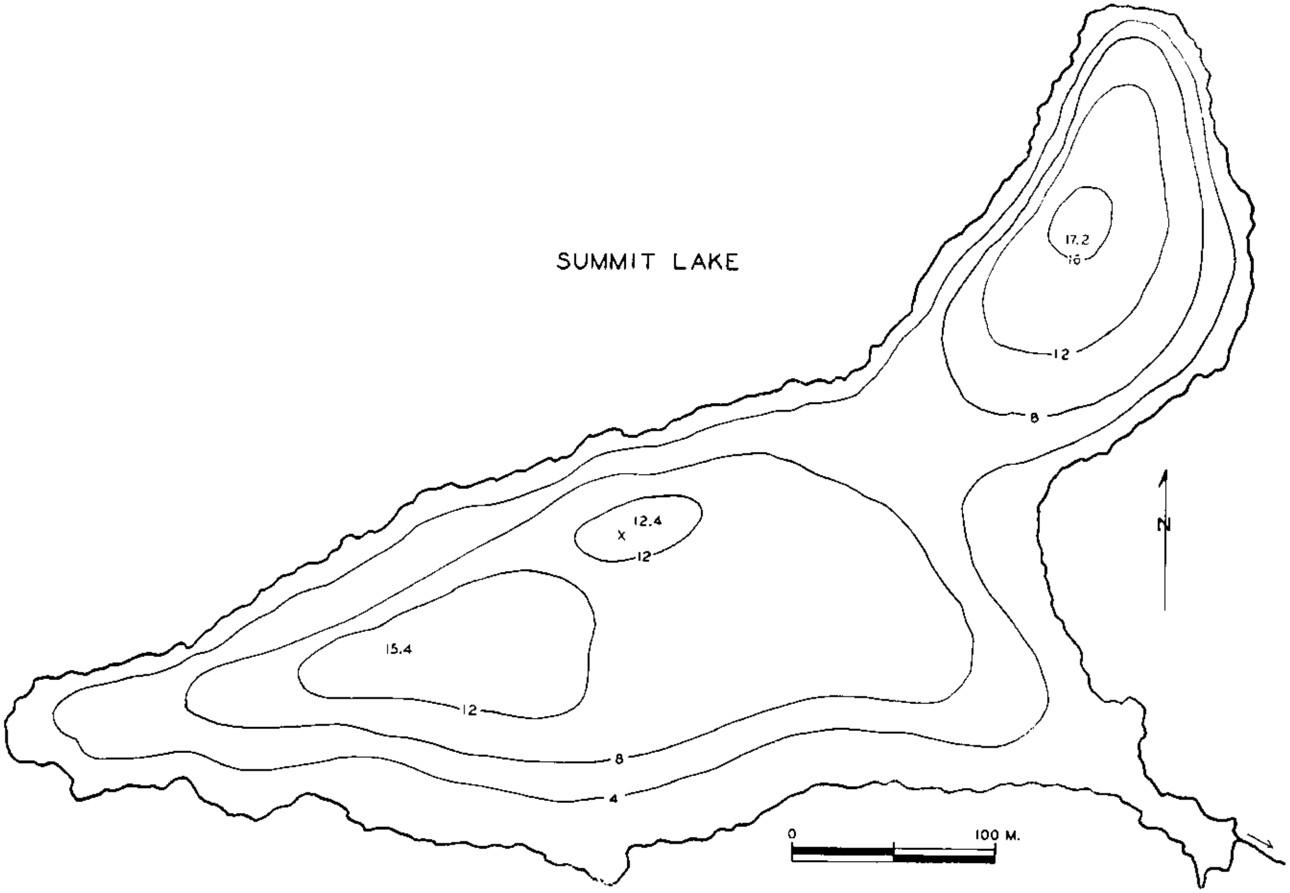

FIG. 6. Hydrographic map of Summit Lake, Colorado. Depths are indicated in meters.

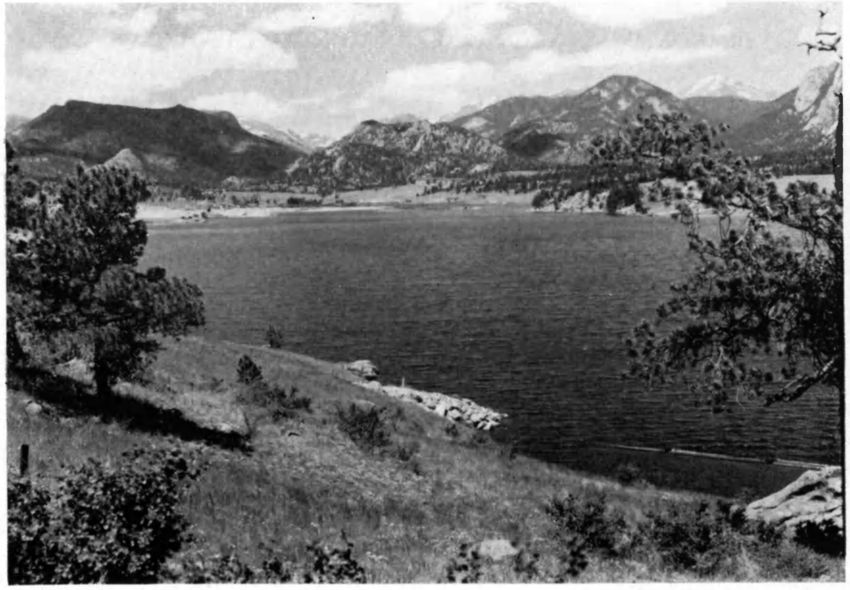

FIG. 7. Lake Estes, Colorado, looking west toward the village of Estes Park. Photograph taken on July 7.

FIG. 8. Copeland Lake, Colorado, looking west. Note inflated rubber boat at water's edge. Photograph taken on June 27.

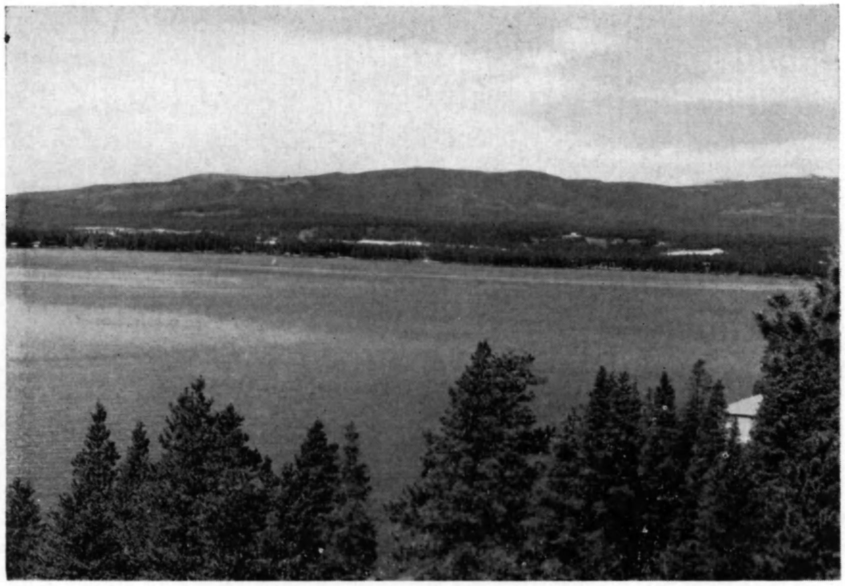

FIG. 9. Grand Lake, Colorado, looking west. The Continental Divide lies several miles directly behind the photographer. Photograph taken on August 21.

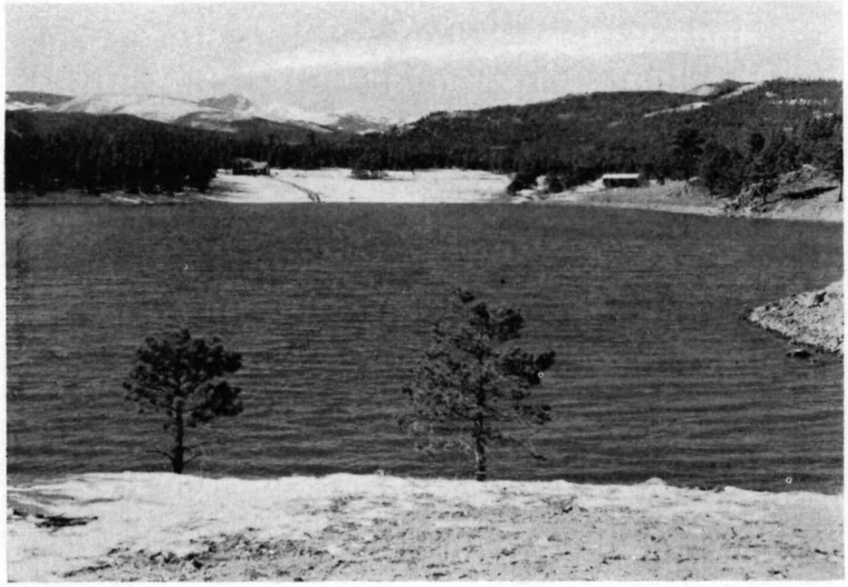

FIG. 10. Manchester Lake, Colorado, looking west toward the Continental Divide. Photograph taken on November 14.

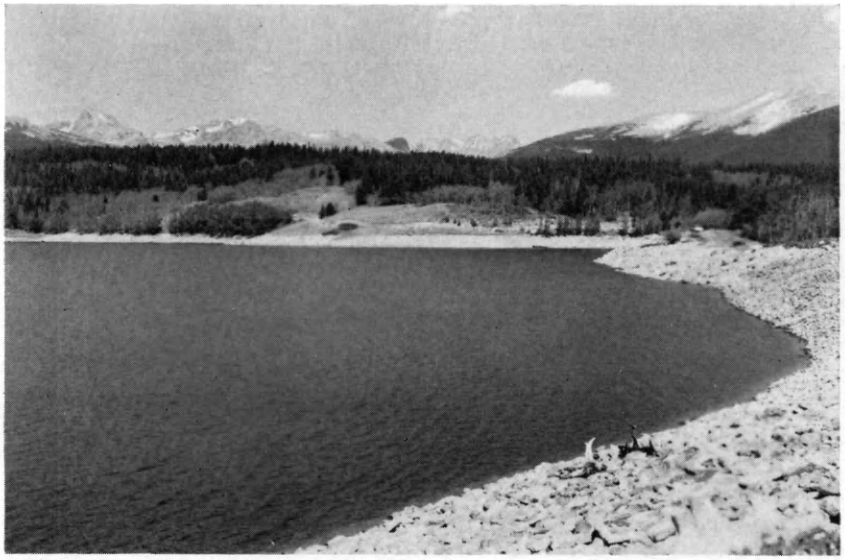

FIG. 11. Beaver Reservoir, Colorado, looking west toward the Continental Divide. Photograph taken from the east end of the dike which forms much of the northern margin of the lake.

FIG. 12. Bear Lake, Colorado, looking SSE toward Long's Peak. Photograph taken on November 30.

FIG. 13. Brainard Lake, Colorado, looking west toward the Continental Divide. Outlet dam shown at the extreme right. Photograph taken on June 23.

FIG. 14. Summit Lake, Colorado, looking west from the extreme northeast shore. Photograph taken on August 30 just after the last of the snowbanks had disappeared.

METHODS AND MATERIALS

A regular sampling station was established for each of the eight lakes, usually near the deepest spot. These points are marked with an "X" on each of the contour maps. Essentially all sampling was done from an anchored metal rowboat, but Manchester Lake was also visited during the period of ice cover, and samples were taken through a hole chopped in the ice at the appropriate depth. In order to avoid fouling, the lowermost sample was always taken in such a fashion that the center of the sampler was about 0.25 meter from the water-substrate interface.

Temperatures were taken with a reversing thermometer, and transparency readings with a standard Secchi disc. For chemical determinations water samples were taken at evenly spaced depth intervals between surface and bottom with a two-liter Kemmerer water bottle. Copeland Lake is so shallow, however, that usually only two samples were taken for each series (at the surface and 2.2 meters, for example). Three depths (top, mid-water, and bottom) sufficed regularly for Manchester and Brainard lakes. Samples at Grand Lake were widely spaced. A typical series included depths of 0, 19, 38, 57, and 76 meters. Bear Lake samples were usually taken at depths of 0, 3.2, 6.4, and 9.6 meters, while the Summit Lake depths were usually 0, 2.5, 5.0, 7.5, and 10.2 meters. Because of fluctuating water levels the number of samples and depths for Beaver Reservoir and Lake Estes varied, but ordinarily samples were taken at two- to three-meter intervals. Water for dissolved oxygen analysis was run from the sampler into glass-stoppered bottles, the customary precautions being used, but water for the other determinations was transported to the laboratory in gallon jugs.

In the laboratory hydrogen-ion determinations were made with permanent Hellige discs and appropriate indicator solutions. This method has a usual error of ±0.1 of a pH unit, but this is not serious for general limnological work.

The standard Winkler method was used for dissolved oxygen determinations, and results were calculated in terms of parts per million (ppm.) and per cent saturation, the latter always being corrected for altitude.

Free and bound carbon dioxide were determined with sodium hydroxide and hydrochloric acid titrations, by use of phenolphthalein and methyl orange indicators, respectively. Although these two titrations have inherent errors and limitations, they are usually considered sufficiently accurate for routine analyses. The terminology used in these determinations is explained by Pennak (1949).

Series of samples for zooplankton counts were taken at the same depths as other water samples with a ten-liter Juday plankton trap, rigged with number 25 bolting silk. Long usage, replicate sampling, and many types of checks with this sampler at the University of Colorado Limnology Laboratory have increased our confidence in it as a quantitative instrument, especially when zooplankton estimates are based

TABLE I. *Basic physical and chemical data for eight northern Colorado mountain lakes*

Name of lake	Approximate year of construction	Period of field work	Altitude, meters	Area, hectares	Area, acres	Maximum depth, meters	Mean depth, meters	Volume, cu. meters	Total residue, mg./l.	Loss on ignition, mg./l.	Ash, mg./l.
Lake Estes	1948	Aug. 2, 1950 July 28, 1951	2277	57.27	141.4	13.7	5.4	3,104,100	36.44	10.66	25.78
Copeland L.	1913	Apr. 27, 1952 Nov. 4, 1952	2540	1.52	3.8	2.4	1.4	21,900	23.80	12.07	11.73
Grand L.	—	May 28, 1953 Oct. 27, 1953	2550	205.18	507.0	80.8	>50.0		23.60	8.92	14.68
Manchester L.	1900	Apr. 28, 1953 Apr. 13, 1954	2610	24.89	61.5	4.5	2.6	163,800	102.74	22.78	79.96
Beaver Res.	1892	May 27, 1952 Oct. 31, 1952	2798	39.10	96.6	10.1	5.0	1,964,500	55.65	19.77	35.88
Bear L.	—	June 3, 1952 Oct. 28, 1952	2892	4.50	12.3	10.0	3.6	160,300	23.59	11.22	12.37
Brainard L.	1892	July 26, 1950 July 21, 1951	3140	6.85	16.9	3.3	1.6	110,200	23.77	7.35	16.42
Summit L.	—	July 19, 1950 July 14, 1951	3884	10.54	26.1	17.2	7.0	737,700	17.38	5.37	12.01

on an adequate vertical series of ten-liter samples in *small* lakes. In medium and large lakes trap samples taken at a single station are sometimes not representative because of differential horizontal concentrations of the plankton species. Incidentally, the work of Kurasawa, Kitazawa, and Shiraishi (1952) and of Kurasawa and Shiraishi (1954) shows a remarkable homogeneity in the horizontal distribution of both phytoplankton and zooplankton in Lake Suwa, a large body of water in Japan.

Zooplankters were identified to species and counted in a one-milliliter Sedgwick-Rafter counting chamber; for this purpose the 4 and 8 mm. objectives of a compound microscope equipped with a mechanical stage were used. Most ten-liter samples were counted in their entirety, even though the process of counting thereby became unusually tedious. In a few samples, however, the zooplankters were so very abundant that an aliquot was counted.

Phytoplankters were concentrated by running a 500-milliliter sample through a Foerst centrifuge. When properly used, and especially when the water is not run through too rapidly, this apparatus removes all but a negligible number of phytoplankton cells from the water. Concentrated samples were stored in four-dram vials of ten per cent formalin. Quantitative population estimates were derived by counting aliquots of these samples in a Sedgwick-Rafter cell; an 8 mm. microscope objective was used. Results were expressed in terms of "cells per liter", and justification of this method is discussed in an earlier paper (Pennak, 1949).

Seston determinations were also derived for the same depths at which phytoplankton, zooplankton, and chemical determinations were made for each field trip. A discussion of these methods is also contained in the 1949 plains reservoir paper.

The eight lakes investigated fall naturally into three groups with respect to depth, and much of the discussion which follows is organized from this standpoint. Copeland, Manchester, and Brainard, for example, are all very shallow. Estes, Beaver, Bear, and Summit are of medium depth. The great depth of Grand Lake puts it into a class by itself.

RESULTS AND DISCUSSION

Physical Conditions

TEMPERATURES

Temperature conditions in Copeland, Manchester, and Brainard lakes were roughly comparable (Fig. 15), chiefly owing to their shallowness. There was, however, a correlation between summer maximum temperatures and altitude which may be of some fundamental significance. The surface of Copeland Lake (altitude 2540 meters), for example, reached 21.5° on June 9, but comparable readings for Manchester Lake (2610 meters) and Brainard Lake (3140 meters) were only 17.8° on July 24 and 12.1° on September 6, respectively. This altitudinal difference is further borne out if mean temperatures for the June–September period are calculated. These corresponding figures were 17.6°, 15.4°, and 8.3°.

On successive sunny days during unusually calm weather the surface temperatures of these three lakes often became as much as two degrees warmer than the bottom temperatures, but with the onset of winds or in more normal weather the surface-bottom differences were seldom more than one-half degree.

On April 15 the temperature of Copeland Lake was homothermous at only 3.1°. On June 23, the surface and bottom of Brainard Lake were 2.7° and 2.5°, and on October 19 these corresponding temperatures were 3.0°. If these late autumn and early spring temperatures were any indication, both Copeland and Brainard lakes must have unusually low winter temperatures, perhaps averaging near 1.0°.

Manchester Lake, being deeper, probably had more typical winter temperatures. Readings taken in October and January showed temperatures of 2.0° to 4.0°.

Judging from the few records available, Copeland, Manchester, and Brainard lakes have a complete ice cover for about five, four and one-half, and seven and one-half months, respectively.

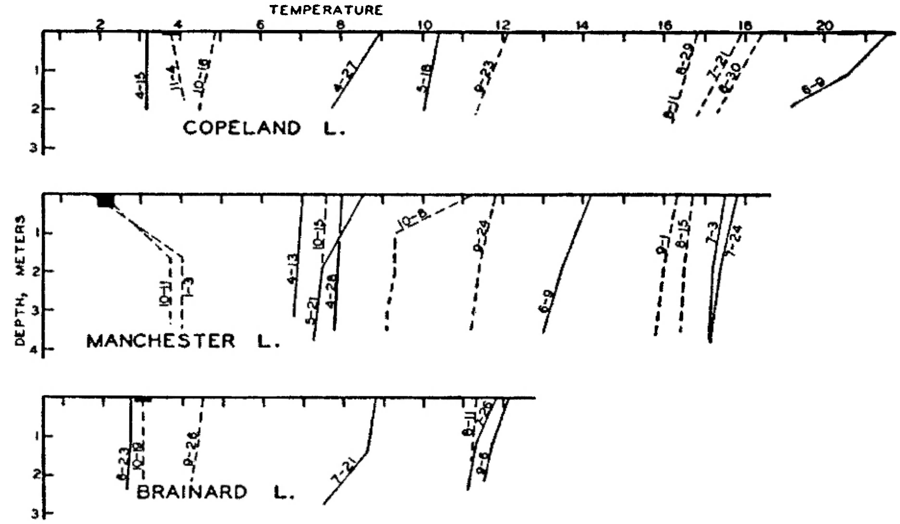

FIG. 15. Open-season temperature conditions in three shallow Colorado mountain lakes. Solid curves indicate periods of warming; broken curves indicate periods of cooling. Month and day of month indicated on each curve.

Temperature conditions in Estes, Beaver, Bear, and Summit lakes may be discussed together, since these four bodies of water are of similar depth. Lake Estes (Fig. 16) was the only one of the four that did not show a definite thermocline at any time, even though its general morphometry would indicate the likelihood of the formation of a thermocline. It is possible that this situation may in part be due to the fact that the winds, frequently strong, are chiefly from the west and sweep through the open valley and the long axis of the lake in such a violent fashion as to cause much more mixing than would usually be the case. In addition, Lake Estes has a large inflow and outflow, and these produce definite currents which may cause sufficient turbulence to inhibit thermocline formation. In fact, these currents were sufficiently well developed to inhibit ice formation along a narrow channel of much of the north shore of Lake Estes, even though the center of the lake had a thick layer of ice in midwinter. The highest reading attained for the bottom water of Lake Estes was 11.4° on August 23.

A well-defined thermocline appeared in Beaver Reservoir (Fig. 16) during July and August between depths of 3 and 6 meters. Following mid-August a great deal of water was drawn out of this lake through the head gate at the bottom of the

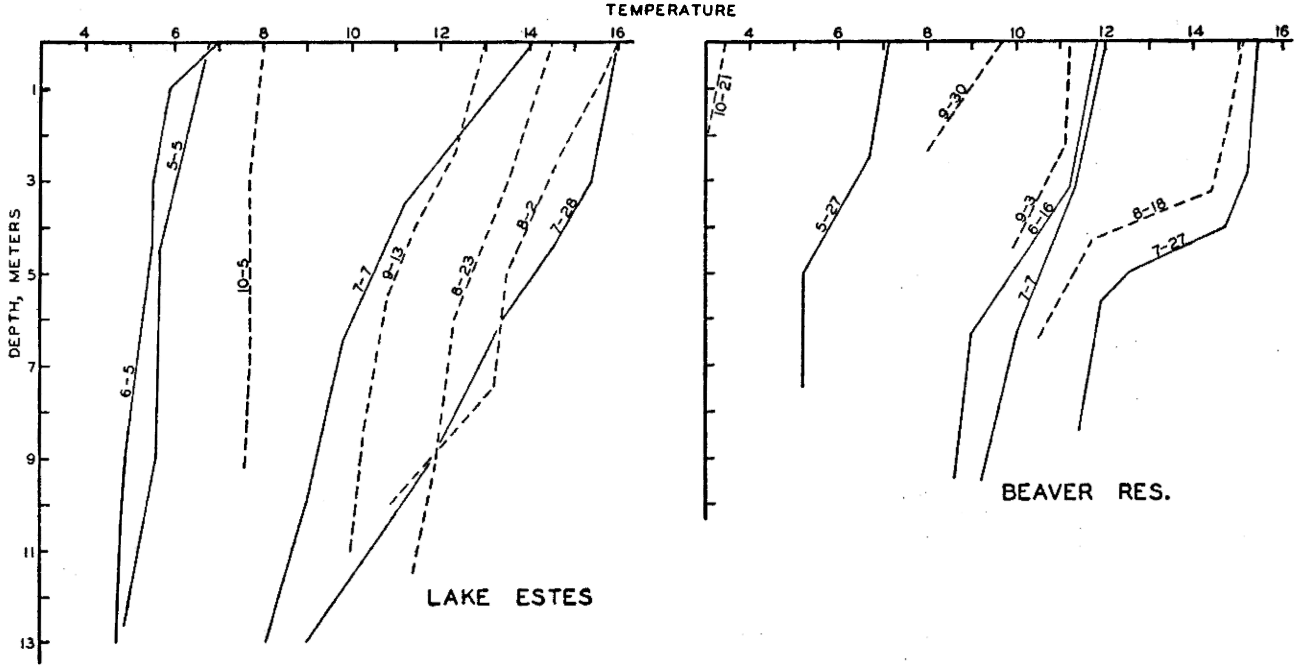

FIG. 16. Open-season temperature conditions in two Colorado mountain lakes. Solid curves indicate periods of warming; broken curves indicate periods of cooling. Month and day of month indicated on each curve.

dam, the net result being the progressive disappearance of hypolimnetic and thermocline water through September and October. Winter temperature conditions in Beaver Reservoir are unknown.

Temperature conditions in Bear Lake (Fig. 17) were more nearly typical than in any of the other three lakes of this depth group. There were a well-developed epilimnion, thermocline, and hypolimnion during late June, July, and August. During early June and October, however, near-homothermy obtained. On June 6 a temporary "epilimnetic thermocline" was found between the surface and 2 meters. This condition sometimes occurs in larger mountain lakes on sunny days when there is little wind and when the high insolation brings about a very rapid warming of the surface waters (see especially Trener *et al,* 1936). Such surface thermoclines quickly disappear when the wind comes up. The bottom water reached a maximum of 10.6° on July 14.

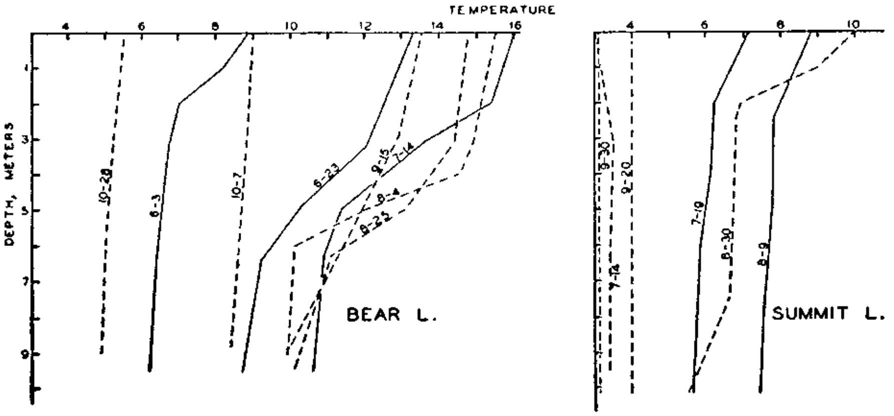

FIG. 17. Open-season temperature conditions in two Colorado mountain lakes. Solid curves indicate periods of warming; broken curves indicate periods of cooling. Month and day of month indicated on each curve.

Another epilimnetic thermocline is shown for Summit Lake on August 30 (Fig. 17). This situation was found after ten days of unusually sunny and calm weather, when the surface water reached a summer maximum of 10.0°. All of the other temperature curves for this body of water showed homothermy or near-homothermy, and this situation is in contrast to temperature conditions in similar lakes of the Alps where there is often a difference of three to five degrees or more between surface and bottom in midsummer. Between late September and the middle of July the mean temperature of Summit Lake is undoubtedly well below 4.0°. On September 30, for example, the surface and bottom temperatures were 3.1°, and

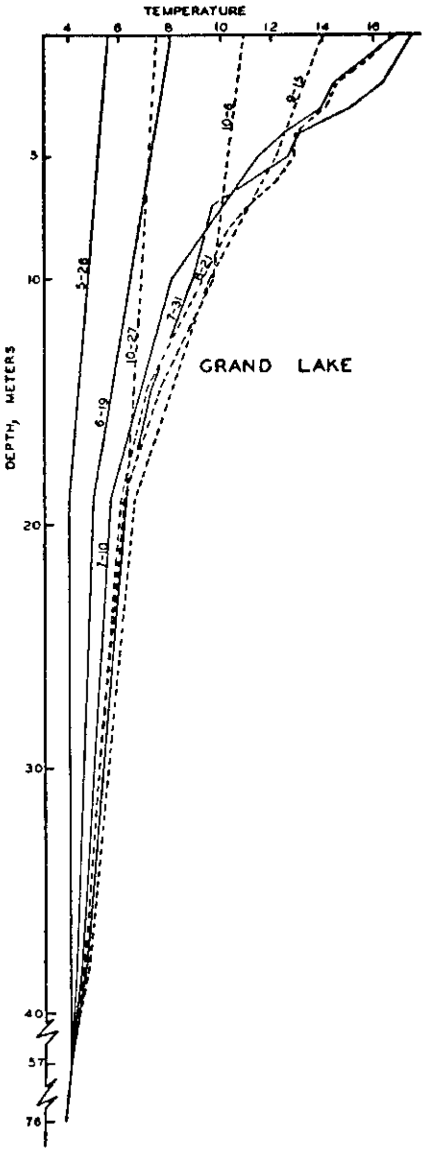

FIG. 18. Open-season temperature conditions in Grand Lake, Colorado. Solid curves indicate periods of warming; broken curves indicate periods of cooling. Month and day of month indicated on each curve.

on July 14 they were 3.0° and 3.4°, respectively. The period of open water on Summit Lake is remarkably short and probably averages only about two and one-half to three months. The ice cover is known to exceed 100 cm. in thickness.

Calculated mean June-September water temperatures for the four lakes indicated in Figures 16 and 17 are not well correlated with altitude. From lowest to highest altitude these data are as follows: Estes, 11.2°; Beaver Reservoir, 11.2°; Bear Lake, 11.5°; Summit Lake, 5.5°. There is, nevertheless, a partial explanation for this lack of correlation. The large volume of cold stream water coming into Lake Estes undoubtedly keeps the lake temperatures unusually low, and the loss of cold hypolimnetic water from Beaver Reservoir via the irrigation head gate results in a calculated mean which is undoubtedly a little high.

Because of its comparably large volume, Grand Lake has an unusually long open season. It freezes over in December and is open by May 1 or 15. Warm-season temperatures, however, are somewhat typical of those obtaining in very deep cold lakes. Although fresh water has its maximum density at 4.0°, it was interesting to find that owing to the "pressure effect", the temperature at 76 meters in Grand Lake remained at 3.8° throughout the sampling period. At 57 meters the temperature ranged from 3.9° to 4.4°, and at 38 meters from 4.0° to 4.7° (Fig. 18). The midsummer epilimnetic region had unusual temperature conditions as shown by three series of temperatures taken between July 10 and August 21. Instead of a near-homothermous condition in the epilimnion as would be expected, there was a regular drop in temperature between the surface and 5 meters, amounting to as much as four to five and one-half degrees. This situation is not comparable with the surface thermocline of only one or two meters' thickness found in smaller lakes. Instead, it is felt that, at least in part, the temperature curve for the top five meters is the result of partial mixing of warm water coming into Grand Lake through the large west inlet. This water is derived from a much larger, shallow (and warmer) body of water, Shadow Mountain Lake, immediately southwest of Grand Lake. On the other hand, the midsummer curves are remarkably similar to those shown for Maligne, Bow, and Waskesiu lakes in Canada (Rawson, 1936, 1942), and for certain Italian Alpine lakes (Trener *et al*, 1936).

By way of summary, these eight lakes, aside from the lower summer maximum temperatures as related to altitude, show few important temperature differences from those of lakes of similar depths at lower elevations.

COLOR

All eight lakes were relatively colorless, as determined with platinum-cobalt color standards. Brainard and Summit lakes never exhibited more than a trace of color. The color of Lake Estes and Grand Lake ranged from a trace to 10, Copeland from 8 to 23, and Manchester and Beaver from 10 to 35. Bear Lake was the only one showing significant vertical differences in color. Although the surface waters ranged from 5 to 20, the lowermost water sample ranged from 5 to 65, the latter figure being reached during late summer stagnation.

TRANSPARENCY

As measured with the Secchi disc, the eight lakes showed a surprising range of transparency and an unexpected summer variation within single bodies of water (Table II). As a matter of fact, the variations were generally greater than those found during a year-round study of Colorado plains reservoirs (Pennak, 1949). Usually the lakes were least transparent during periods of greatest plankton development, which varied considerably from lake to lake.

Mountain lakes not fed by glaciers often are said to be exceptionally transparent, and there are many general (but often unsubstantiated) statements in the literature to that effect. Of the eight Colorado lakes studied, however, the greatest transparency was only 5.0 meters (for Bear Lake on August 4). Even Summit Lake, the most "typical" mountain lake of them all, had disc readings ranging from 3.2 to 4.9 meters. The greatest variation (1.2 to 4.6 meters) was found in Grand Lake, and the least in Estes (0.9 to 2.0 meters). Lake Estes was also the least transparent of all the lakes, since it was the only one containing appreciable quantities of finely divided inorganic silt in suspension, most of which originated from the eroding north shoreline during hard winds.

Grand Lake was studied on September 6, 1941, when a disc reading of 9.2 meters was found. In 1953, however, the greatest reading was only 4.6 meters. Undoubtedly this striking change is an indication of the rapid approach of eutrophy in Grand Lake since its recent incorporation in the Colorado-Big Thompson project and the reversal of water flow through the lake during most of the year.

TABLE II. *Open-season Secchi disc readings for eight Colorado mountain lakes*

Lake	Disc reading, meters	
	Range	Mean
Estes	0.9–2.0	1.4
Copeland	2.4 (bottom)	
Grand	1.2–4.6	3.1
Manchester	1.1–3.2	2.2
Beaver	0.8–3.5	2.1
Bear	2.6–5.0	4.1
Brainard	3.3 (bottom)	
Summit	3.2–4.9	4.0

This contention is strengthened by the recent radical changes in the phytoplankton populations (see below).

Mean summer disc readings ranged from 1.4 meters for Lake Estes to 4.0 meters for Summit Lake and 4.1 meters for Bear Lake. Copeland and Brainard lakes are so shallow that the disc could still be seen when it rested on the bottom. The water of Brainard Lake is exceptionally clear, and, if it were deeper, the disc readings would undoubtedly be higher than those obtained for Bear and Summit lakes.

Chemical Conditions

DISSOLVED OXYGEN

Four lakes (Copeland, Manchester, Brainard, and Summit) showed no appreciable stratification in the dissolved oxygen content of their waters, and data for them are summarized in Table III. Conditions in the first three of these lakes were similar to those found in exposed shallow ponds and reservoirs everywhere in temperate latitudes. In general, the dissolved oxygen concentrations seldom fell below 85 or rose above 105 per cent saturation. None of these lakes had a sufficient abundance of rooted aquatics and phytoplankton to produce an appreciable supersaturation, and none of them had sufficient respiration and bacterial action in the bottom waters to show any significant depletion of dissolved oxygen. The only noteworthy exception occurred in Copeland Lake on June 30, when the bottom waters showed 50.3 per cent saturation.

Although Summit Lake is much deeper (17.2 meters) than the other three lakes shown in Table III, it also showed no appreciable oxygen depletion in the bottom waters. The greatest difference between determinations for surface and bottom waters was found on August 30, when 108.4 and 100.5 per cent saturation, respectively, were found. The general oligotrophic nature of Summit Lake along

TABLE III. *Warm-season dissolved oxygen conditions in four lakes showing little or no oxygen stratification*

Lake	Depth	Oxygen concentration, per cent saturation	
		Range	Mean
Copeland	Surface	95.5–108.5	101.9
	Bottom	50.3–105.3	92.7
Manchester	Surface	83.3– 98.5	91.0
	Bottom	81.7– 90.1	90.1
Brainard	Surface	95.7–103.9	100.5
	Bottom	97.0–101.8	99.6
Summit	Surface	85.8–106.0	101.1
	Bottom	86.2–102.2	98.1

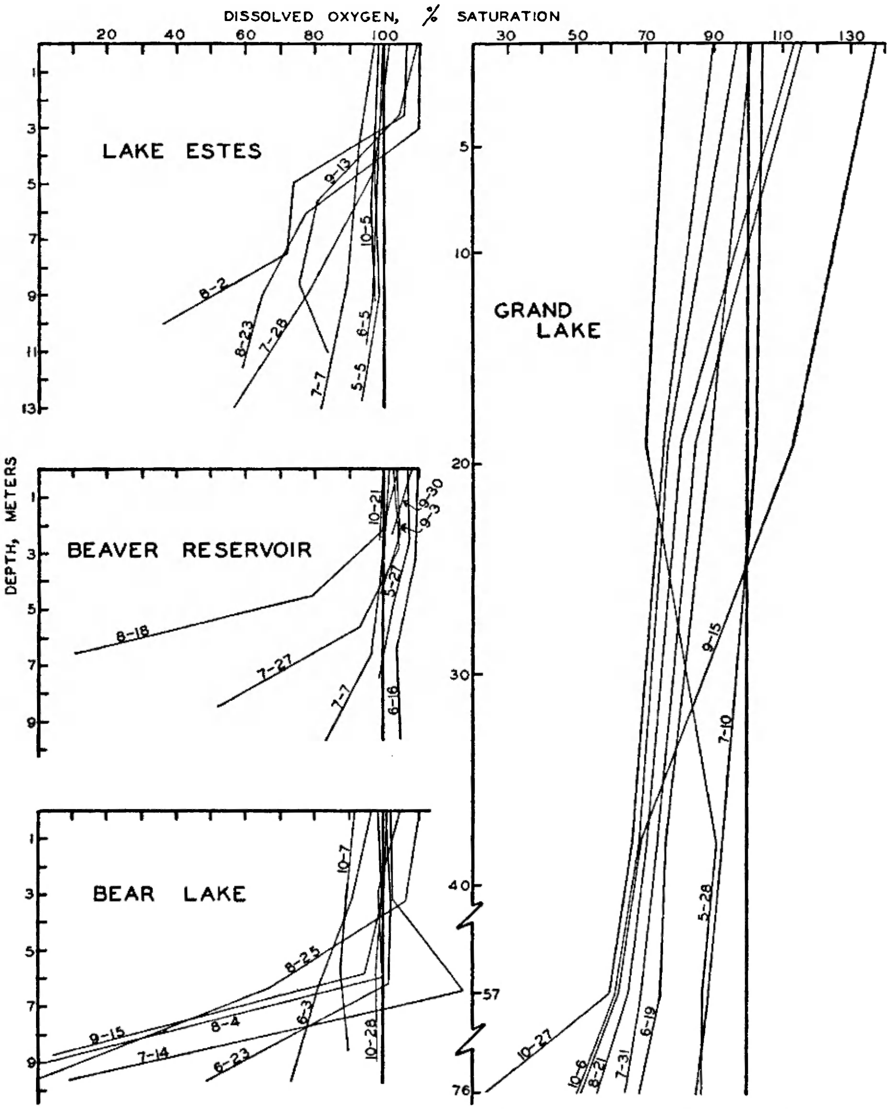

FIG. 19. Dissolved oxygen conditions in four Colorado mountain lakes. Month and day of month indicated on each curve. Note breaks in vertical depth scale for Grand Lake.

with its low temperatures and poor plankton population are undoubtedly responsible for the abundance of oxygen found at all depths. Although midwinter conditions are unknown, it is presumed that oxygen exhaustion does not occur in the lower waters in spite of the very thick and persistent ice and snow cover. When Summit Lake was visited on July 14, for example, it was still covered with 40 to 60 cm. of ice, but there was a newly formed crack running from shore to shore and traversing the regular sampling area. Water samples taken from the edge of this crack showed 85.5 per cent saturation at the surface and 86.2 per cent saturation at a depth of 9.6 meters. It is very likely that these determinations were reasonably indicative of conditions under the ice cover at the close of the long winter.

Oxygen conditions in Estes, Beaver, Bear, and Grand lakes (Fig. 19) were considerably different from those just discussed. The epilimnetic regions of the first three of these lakes usually showed saturations ranging between 95 and 110 per cent, but, beginning at a depth of about 5 meters, the oxygen content fell progressively with increasing depth, so that the hypolimnetic water showed a pronounced oxygen deficit during July, August, and September. The lowermost 5 meters of Beaver and Bear lakes showed this progressive summer hypolimnetic oxygen depletion in a particularly striking fashion, and by the end of the stagnation period the bottom samples for these two lakes showed 10.1 per cent saturation and complete exhaustion, respectively. Oxygen stratification was much less pronounced in Lake Estes, and the lowest figure found was 36.3 per cent saturation at a depth of 10 meters. Judging from the depth and plankton population of this lake, a much lower figure would be expected, but it is probable that the wind, large inflow, and currents (mentioned previously) had much to do with maintaining a partial circulation in the hypolimnion. Hutchinson (1937) found eutrophic oxygen conditions in certain shallow, alkaline, high-altitude lakes in Tibet that were similar to those occurring in Estes, Beaver, and Bear lakes.

In spite of frequent stocking, fishing in Bear Lake does not come up to expectations, and there are frequent and bitter complaints from fishermen. At least a partial explanation may lie in the fact that the lowermost one-quarter of this body of water has insufficient oxygen to maintain a trout population during a large part of the summer, and a considerable portion of the bottom is inaccessible for foraging for bottom food organisms. In addition, the competition for food afforded by the large sucker population undoubtedly makes the situation much worse.

It is interesting to speculate on midwinter oxygen conditions in Bear Lake. In view of its long snow and ice cover (as long as seven months), it appears likely that a partial winter kill of the trout population enters into the picture. Since there is a good and continuous inflow and outflow for this lake, however, it is doubtful if a winter kill accounts for a large part of the trout population. In general, winter kills are uncommon in Colorado mountain lakes and are mostly restricted to very shallow lakes and ponds with no winter inlet.

Perhaps the most striking feature of summer oxygen conditions in Grand Lake was the progressive and gradual decrease in dissolved oxygen between surface and bottom on most of the sampling dates (Fig. 19). There were, in other words, no depths at which the oxygen curves "broke" and showed a comparatively rapid decrease in deeper waters. This situation has been reported for certain other very deep lakes. Below a depth of 38 meters the waters of Grand Lake showed a regular and progressive decrease in their dissolved oxygen, as shown by the curves for June through October. Near the bottom, at a depth of 76 meters, the dissolved oxygen fell to 23.7 per cent saturation by October 23. On the same date, the determination for 57 meters was 59.8 per cent. During July, August, and September the surface waters showed unusually large quantities of dissolved oxygen, with a maximum of 137.4 per cent saturation on September 15. This condition was undoubtedly produced by a very dense algal population (see below).

A subsurface oxygen maximum, indicating an optimum depth for photosynthesis in the epilimnion or thermocline was seldom encountered, though one reason may be the fact that samples were not taken at sufficient depth intervals to demonstrate it. Two slight maxima were found at a depth of 3 meters in May and September for Beaver Reservoir, and a pronounced maximum (123.0 per cent saturation) was found at a depth of 6.4 meters in Bear Lake on July 14.

COMPENSATION POINT

With respect to natural plankton populations, "compensation point" has been defined as that depth in a lake at which oxygen production by photosynthesis balances the sum of algal respiration plus zooplankton respiration plus bacterial decomposition processes. By implication, this definition is usually meant to apply to a typical 24-hour period in midsummer. Yoshimura (1938) and Winberg and Ivanova (1935) concluded that the compensation point averages 1.2 times the maximum Secchi disc reading during the summer months. Thienemann (1928) uses a factor of 2.0 for the Baltic lakes. Other investigators, including the present author (Pennak, 1949), maintain that the compensation point for shallow lakes (less than 15 meters deep) is 1.5 or more times the maximum summer Secchi disc reading. It has also been suggested that for lakes deeper than 15 meters a factor of 1.2 should be used, apparently on the assumption that deeper lakes are more transparent. This contention does not seem logical, however, since the depth of a lake is not necessarily an indication of its transparency. Obviously, deep lakes may have low transparencies under many circumstances, and the compensation point is a measure of the thickness of the primary production zone regardless of how much water may lie below this stratum. For this reason the present author prefers to use a single factor (1.5 times the maximum June-September disc reading) for all lakes, regardless of depth. According to this criterion, the compensation point for the six deepest mountain lakes ranged as follows: Estes, 3.0; Manchester, 3.6; Grand, 4.8; Beaver, 5.0; Bear, 7.2; Summit, 7.4. It is significant that with the exception of the reversed positions of Manchester and Grand, all of these lakes are arranged in order of increasing altitude.

FREE CARBON DIOXIDE

Free carbon dioxide readings are summarized in Table IV. Surface waters generally contained small amounts, determined chiefly by the partial pressure of carbon dioxide in air. Estes, Copeland, and Grand lakes showed slight negative readings a few times, produced by increased photosynthetic activity. One surface reading at Grand Lake was 8.0 ppm. on October 6 about 10 A.M. A flat calm prevailed at that time, and a dense growth of *Aphanizomenon* filaments was rapidly disintegrating. Grand Lake had the highest average reading for the surface water, 4.2 ppm., and Lake Estes had the lowest, 1.4 ppm.

TABLE IV. *Free and bound carbon dioxide content of eight Colorado mountain lakes during the open season*

Lake	Depth	Free carbon dioxide, ppm.		Bound carbon dioxide, ppm.	
		Range	Mean	Range	Mean
Estes	surface	−0.7– 2.5	1.4	5.5–10.0	8.5
	bottom	2.0– 6.0	3.8	7.3–10.2	8.2
Copeland	surface	−0.2– 2.6	1.8	4.9–13.5	7.1
	bottom	0.5– 4.2	2.2	4.5–10.0	6.5
Grand	surface	−0.7– 8.0	3.1	5.8–26.6	12.5
	bottom	4.2–32.2	13.0	8.0–10.9	9.1
Manchester	surface	1.7– 7.1	3.4	23.0–32.0	28.7
	bottom	1.7– 8.6	3.7	23.0–31.8	28.6
Beaver	surface	1.4– 3.0	2.3	5.0–12.0	8.1
	bottom	1.5–10.1	4.1	5.5–12.5	8.3
Bear	surface	1.8– 3.5	2.3	4.1– 7.6	5.9
	bottom	2.6–17.5	8.8	5.0– 8.0	6.2
Brainard	surface	1.1– 1.8	1.5	3.2– 5.3	4.6
	bottom	1.1– 3.5	2.0	3.2– 5.5	4.6
Summit	surface	1.1– 2.1	1.7	4.5– 5.6	5.1
	bottom	1.5– 2.5	2.0	4.6– 6.4	5.2

Free carbon dioxide was always more abundant in the bottom waters, ranging from an average of 2.0 ppm. in Brainard and Summit lakes to 8.8 ppm. for Bear Lake and 13.0 for Grand Lake. Estes, Copeland, Brainard, and Summit lakes showed no special concentrations of free carbon dioxide in the bottom waters, but the other four lakes exhibited varying degrees of stratification. On September 24 the bottom waters of Manchester Lake reached 8.6 ppm., and on August 18, before autumn cooling, the bottom waters of Beaver Reservoir showed 10.1 ppm. Bear Lake showed a progressive summer increase in the free carbon dioxide content of the lowermost three meters of water, and the bottom sample reached a maximum of 17.5 ppm. by August 25. Grand Lake, with its great depth, had by far the largest accumulation of free carbon dioxide, and by October 6 the bottom waters reached a maximum of 32.2 ppm.

BOUND CARBON DIOXIDE

According to the bound carbon dioxide hardness classification adopted by the present writer (Pennak, 1945b), Grand Lake, with an average surface reading of 12.5 ppm., is a lake of medium hardness, being slightly above the lower limit of that category. Manchester Lake, with an average of 28.7 ppm., is also a medium lake. The other six, however, are clearly soft-water lakes, ranging from 4.6 ppm. for Brainard Lake to 8.5 ppm. bound carbon dioxide for Lake Estes.

On September 15 the surface of Grand Lake contained 26.6 ppm. bound carbon dioxide, and the bottom sample (76 meters) 9.4 ppm. Otherwise surface to bottom differences seldom exceeded 3 ppm.

Seasonal differences in the bound carbon dioxide content of the surface waters were largely a reflection of the vagaries of snow-melt intensity and the relative volume of inflow and outflow. Such seasonal differences were only slight (Table IV) for Beaver, Bear, Brainard, and Summit lakes, but the other four lakes, lying at lower altitudes, had considerably greater variations, ranging from 5.5 to 10.0 ppm. for Lake Estes to 5.8 to 26.6 ppm. for Grand Lake. Undoubtedly the unusual latter case was caused by a large inflow of the harder waters of Shadow Mountain Reservoir during the later summer.

HYDROGEN-ION CONCENTRATION

In view of their relatively small quantities of dissolved salts and their general location in a granitic area, the surface waters of all eight of the lakes showed pH readings clustered about neutrality, with a majority slightly below the neutral point (Table V). Manchester Lake, with medium-hard water, had a mode of pH 7.5 for both surface and bottom waters, but the next highest mode was pH 7.1 for Grand Lake. Bear Lake, with a mode of pH 6.6, was at the other extreme.

Photosynthesis and variable water chemistry were responsible for some seasonal changes in the hydrogen-ion concentration of the surface waters of the individual lakes, but these were of a magnitude generally encountered in the surface waters of soft to medium-hard lakes everywhere. The widest range, pH 6.5 to pH 8.5, was found for Grand Lake, the latter reading being found during a time of exceptional

TABLE V. *Summary of hydrogen-ion concentration determinations for eight northern Colorado mountain lakes during the open season*

Lake	Depth	Range	Mode
Estes	surface	6.6–7.9	6.9
	bottom	6.3–7.0	6.5
Copeland	surface	6.3–7.5	6.7
	bottom	6.2–7.3	6.7
Grand	surface	6.5–8.5	7.1
	bottom	6.4–6.6	6.5
Manchester	surface	7.3–7.7	7.5
	bottom	7.3–7.7	7.5
Beaver	surface	6.6–7.3	6.9
	bottom	6.2–7.1	6.8
Bear	surface	6.3–6.7	6.6
	bottom	6.0–6.7	6.2
Brainard	surface	6.3–7.1	6.8
	bottom	6.3–7.1	6.8
Summit	surface	6.3–7.1	6.9
	bottom	6.4–7.0	6.7

algal development and photosynthesis. Lake Estes had the next highest seasonal variation in its surface waters, pH 6.6 to pH 7.9, while both Bear and Manchester exhibited the other extreme, with a range of only 0.4 of a pH unit.

Differences between surface and bottom readings for a particular date were sometimes moderate but usually small or negligible. Such differences were, of course, most pronounced for the deeper lakes and those showing the greatest degree of summer stratification. On August 21, for example, the surface and bottom determinations for Grand Lake were pH 8.5 and pH 6.4, respectively, and for Lake Estes on September 13 the corresponding figures were pH 7.9 and pH 6.8. Beaver Reservoir showed a difference of 0.6 of a pH unit, and Bear and Summit lakes 0.5 of a pH unit. Copeland, Manchester, and Brainard showed maximum differences of only 0.2 or 0.1 of a pH unit.

SESTON

In view of the fact that some investigators are according increasing significance to seston determinations as a relatively accurate and critical measure of the standing crop of plankton and an important index to productivity, a rather thorough study of seston was made for the eight lakes. As used in the present investigation, seston includes *all* particulate organic matter, both living and dead, (expressed as milligrams per liter, ash-free dry weight) suspended in the water, and ranging in size from macroplankton to bacteria and colloidal aggregates.

From the standpoint of comparative limnology, it is most unfortunate that so few investigators have made use of seston determinations in their studies. Furthermore, a good deal of the existing information is of only limited use, since it is often based on surface samples only and does not consider seasonal or annual variations.

Sixty-seven vertical series of samples were taken from the eight lakes, and each series consisted of two to six individual determinations, depending on lake depth. In general, the vertical distribution of seston at any one time was found to be somewhat variable, depending chiefly on the abundance and distribution of the plankton and the speed of settling of tripton. (The term "tripton" is used to include all non-living particles suspended in the water, such as dead and disintegrating organisms, detritus of all kinds, and colloidal materials.) In 12 series the seston maximum was found in the surface sample; in 32 series the maximum occurred in the lowermost water sample; and in 23 series the maximum occurred in some intermediate sample. For all 67 series of samples it was found that the first subsurface sample contained, on the average, 11 per cent more seston than the surface sample. Such conditions are comparable with those found in an earlier study on plains reservoirs (Pennak, 1949) and also in 19 large New York lakes by Tressler and Bere (1936, 1937, 1938). Thus, although a surface sample is adequate for determinations of dissolved organic materials, a subsurface sample is more nearly accurate for the estimation of the seston picture as a whole.

In a few cases there were exceptionally wide differences in seston determinations within single series. At Beaver Reservoir on July 7, for example, the surface water had 0.56 mg. per liter, while at 6.4 meters the figure was 2.58 mg. per liter. At Bear Lake on July 14, the surface water contained 0.36 mg. per liter, and at a depth of 6.4 meters the result was 5.08 mg. per liter. At Grand Lake on July 31, on the other hand, the surface water contained 1.33 mg. per liter, and at a depth of 38 meters the figure was only 0.30 mg. per liter. Undoubtedly the latter instance was produced by an unusually heavy crop of algae in the surface waters.

Figure 20 shows the variations in seston during the open season for the eight lakes. Each point on these curves represents an average of two to six determinations, depending on lake depth, for a particular sampling date. It is abundantly evident that, as a whole, these lakes supported a medium to poor crop of seston, since the great majority of determinations were below 2.0 mg. per liter. The curves for Grand and Brainard lakes are remarkably flat and similar, none of the points exceeding 0.93 mg. per liter.

Beaver Reservoir was characterized by a surprisingly high seston on September 20 (7.14 mg. per liter) when the water level was very low and when there was a very large burst of phytoplankton, the latter perhaps being caused by a mixing and re-utilization of nutrients which had been adsorbed by the bottom during the previous summer months, when the water was deeper. Bear Lake likewise had a

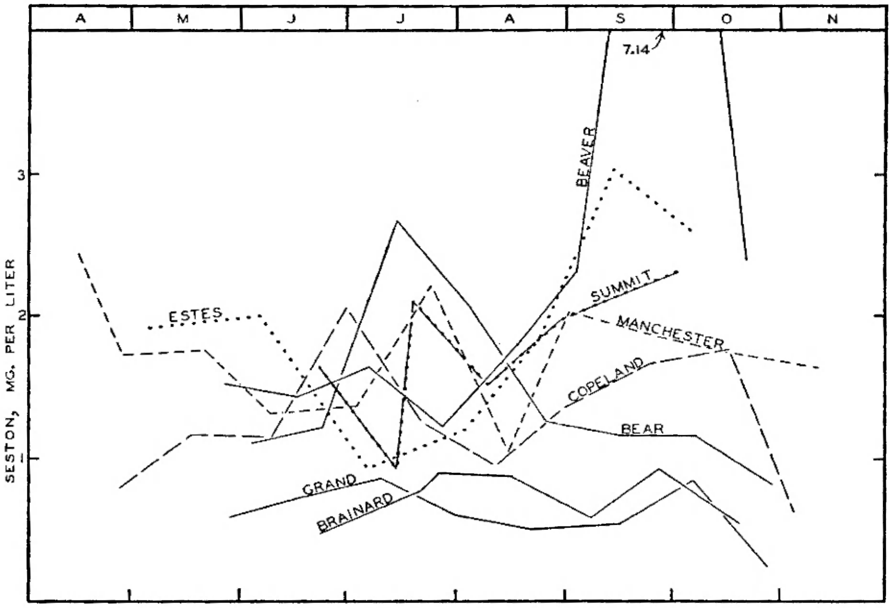

FIG. 20. Open-season seston conditions in eight Colorado mountain lakes. Each point on the curves represents an average of two to six evenly spaced samples taken between the surface and bottom on a particular date.

single prominent maximum on July 14, when the water contained 2.67 mg. per liter.

Both Estes and Copeland lakes had poorly defined seston maxima in late spring and autumn, the former in May-June and September-October and the latter in June-July and September-October. Manchester Lake had three slight maxima — in April, July, and September. The curve for Summit Lake is short and irregular, and cannot be easily interpreted, although a maximum of 2.30 mg. per liter occurred on September 30.

In general, it can be seen that, with the possible exception of Estes and Copeland lakes, none of these bodies of water exhibited the "typical" seston curve of large lakes, which is said to include a primary spring maximum and a secondary autumn maximum. Rawson (1942) found that the summer curves of "net plankton" for six large Canadian alpine lakes were also without a consistent and definite pattern. It must be emphasized that the data shown in Figure 20 represent only *one* open season for each lake. Presumably the year-to-year variations in these curves are considerable.

Seasonal variations are but transient phenomena, and the mean annual standing crop of seston has much greater significance as a rough index of productivity, since it is generally considered to be much less variable than the vagaries of month-to-month seston determinations. Unfortunately, however, it was impossible to obtain year-round seston determinations for these mountain lakes because of their general inaccessibility and other factors. Nevertheless, a hypothetical, but reliable, mean annual seston calculation may be derived from the spring, summer, and autumn determinations, provided the proper correction factors are applied. Work on northern Colorado plains lakes and occasional winter samples from certain mountain lakes have shown that, in general, the mean standing crops of seston for the six coldest months of the year amount to 75 per cent of the mean standing crops for the six warmest months of the year. By means of this factor, properly weighted, mean annual standing crops may be postulated.

TABLE VI. *Seston determinations for 15 northern Colorado lakes and reservoirs; ash-free dry weight. Data for first seven lakes in this list are from Pennak, 1949*

Lake	Altitudinal zone	Mean for period of field work, mg. per liter	Annual mean, mg. per liter	Kg. per hectare
Baseline	Plains		1.74	72.1
Hayden's	"		1.78	64.6
Allens	"		1.91	124.6
Beasley	"		2.35	38.7
Boulder	"		4.66	171.3
Gaynor	"		13.64	252.1
Kossler	Foothills		1.19	43.5
Estes	"	1.84	1.57	84.8
Copeland	Montane	1.28	1.13	15.8
Grand	"	0.62	0.54	270.0(?)
Manchester	"	1.77	1.55	40.0
Beaver	"	2.44	2.08	104.0
Bear	"	1.43	1.33	47.9
Brainard	"	0.73	0.65	10.5
Summit	Alpine	1.77	1.49	104.3

These estimates, along with those for seven reservoir lakes studied earlier, are shown in Table VI. Mean annual seston for the eight "mountain lakes" covered the narrow range of 0.54 mg. per liter for Grand Lake to 2.08 mg. per liter for Beaver Reservoir. Furthermore, it is quite striking to note that, of the nine foothills-montane-alpine lakes listed, the seston of only one (Beaver) falls within the range for the first six (plains) lakes listed. If these data are averaged, it is seen that the lakes of the foothills, montane, and alpine zones contain only about 29 per cent as much seston as the plains reservoirs. If, however, the abnormally high seston for

Gaynor Lake is omitted, the corresponding figure is about 51 per cent, which is probably the more reasonable one to use. In using such comparative data, one should bear it in mind that *both* the plains and high-altitude lakes were selected for study with the idea of including a *wide* representation of types. The selection of a group of rock-basin lakes restricted to the upper montane and alpine zone, for example, would have given a lower mean seston.

The paper of Birge and Juday (1934) contains extensive seston data for 529 northern Wisconsin lakes. These figures are not directly comparable with those obtained for the Colorado lakes, because (1) the Wisconsin samples were taken only from the surface waters, (2) they were taken mostly during midsummer, and (3) the results are expressed in terms of Foerst centrifuge seston without taking into account the necessary 25 per cent correction factor used in the Colorado work. Discrepancies (1) and (2) roughly cancel each other out, as compared with the year-round, top-to-bottom results for the Colorado lakes. The third discrepancy may be rectified by adding a factor of 25 per cent to the results of Birge and Juday. As a result, the range of seston for the Wisconsin lakes becomes 0.29 to 11.50 mg. per liter as compared with 0.54 to 13.64 mg. per liter for the 15 Colorado lakes. The mean for the 529 northern Wisconsin lakes was 1.70 in contrast to 2.51 for all 15 northern Colorado lakes and 1.28 for the nine Colorado lakes above the plains zone.

The paper of Birge and Juday also gives a small amount of seston data for the hard-water lakes of southern Wisconsin. The annual mean (also adjusted) for Lake Mendota was about 2.00 mg. per liter, and for 23 other lakes in southeastern Wisconsin it was about 1.39 mg. per liter. Thus, on the basis of unit volume, it is seen that the hard-water lakes do not have a markedly higher standing crop of seston than the Colorado mountain lakes.

Table VI also shows the total standing crop of seston expressed as kilograms per hectare. The results cover such a wide range (10.5 to 270.0 kg. per hectare for mountain lakes) because of the great range in depth represented by these lakes. The former figure is for Brainard Lake, which had a mean seston of 0.65 mg. per liter but a mean depth of only 1.6 meters. The latter figure is for Grand Lake, which had an even lower seston (0.54 mg. per liter) but which had an assumed mean depth of 50 meters. Except for Brainard and Copeland lakes, these data on standing crops in terms of lake area compare favorably with those for the plains lakes. In general, the deeper, hard-water lakes of southern Wisconsin show standing crops, in terms of kg. per hectare, of the same general magnitude as those for Grand Lake and Gaynor Lake (a highly alkaline, shallow body of water on the plains).

Several investigators have attempted, usually with little success, to correlate seston with certain physical and chemical features of lakes. Mean depth, total residues, temperature conditions, oxygen conditions, hardness of water, transparency, climate, and the like have all been suggested. None of these factors, however, appear to have any obvious or simple relationships to the standing crop of seston for the 15 lakes listed in Table VI. If these lakes were more homogeneous in their physical and chemical features, it is quite probable that certain correlations with seston could be shown. But in view of their highly diverse nature such relationships are not apparent.

COMPARISON OF CHEMICAL AND PHYSICAL CONDITIONS IN PLAINS AND MOUNTAIN LAKES

At the beginning of the present study it was anticipated that field and laboratory work would show numerous chemical and physical features of these Colorado mountain lakes which would distinguish them clearly and consistently from the plains lakes. The more the work progressed, however, the more apparent it became that there were relatively few fundamental and important differences between these two groups of lakes, and in view of the frequent sterotyped impression of "mountain lakes", it might be well to review these differences and similarities.

From the standpoint of physical features, the plains and mountain lakes were generally similar in the following respects: size, depth (except for Grand Lake), morphometry, hydrography, and color. As would be expected, the chief physical difference was in the annual temperature cycles. Mountain lakes had a much shorter open season (only 10 to 12 weeks for Summit Lake) and considerably lower maximum summer temperatures. The average maximum summer surface temperature for six plains lakes was 26.4°, while that for nine lakes of the foothills, montane, and alpine zones was only 16.1°. It seems very likely that these marked temperature differences were at least in part responsible for the much more dense algal populations in the plains lakes, but on the other hand it would seem that the temperature differences should produce greater differences in the zooplankton than was actually the case in these two groups of lakes. The temperature stratification picture was not markedly different. In both groups of lakes the presence or absence of a thermocline and its configuration were similarly modified by depth, wind action, currents, and draw-down of water for irrigation. In addition to differences of summer temperature, the two kinds of lakes differed slightly in their transparencies. The mean Secchi disc reading for seven mountain lakes was 2.7 meters as compared with 1.6 meters for six plains lakes. Lower transparencies in the plains lakes were mostly produced by higher turbidities.

From the standpoint of water chemistry, the plains and mountain lakes were generally similar in their dissolved oxygen conditions (in lakes of comparable depths) and in their free carbon dioxide. Since the basins of the high lakes contain more "youthful" water in contact with relatively insoluble rocks, their waters had lower bound carbon dixoide readings and much lower total solids. And as a reflection of these features, the high lakes had pH values clustered more closely about neutrality than was true for the plains lakes. For the former, the surface water had a pH mode of 6.6 to 7.5; for the latter it ranged from 7.3 to 8.6. Seston determinations did not differ as much as was anticipated. For five plains lakes (omitting Gaynor Lake) the mean annual seston average 2.49 mg. per liter and for nine foothills, montane, and alpine lakes it averaged 1.28 mg. per liter.

PHYTOPLANKTON POPULATIONS

Two hundred forty-one quantitative samples of algae were taken, but because the emphasis was mainly on gross population trends, the algae were identified only to genus. A small percentage of the cells could not be identified definitely and were sometimes placed in certain generic categories more or less arbitrarily. The list which follows, however, accounts for more than 99 per cent of the cells enumerated from the eight lakes.

Bacillarieae

Amphora
Asterionella
Ceratoneis
Cocconeis
Cyclotella
Cymbella
Fragilaria
Gomphonema
Gyrosigma
Melosira
Navicula
Pinnularia
Stauroneis
Surirella
Synedra
Tabellaria

Chlorophyceae

Ankistrodesmus
Closterium
Coelastrum
Cosmarium
Crucigenia
Elaktothrix
Golenkinia
Kirchneriella
Oocystis
Pediastrum
Scenedesmus
Schroederia
Spondylosium
Staurastrum
Tetraedron

Myxophyceae

Anabaena
Aphanizomenon
Chroococcus > 70%
Dactylococcopsis
Lyngbya
Oscillatoria

"small green flagellates"

Dinobryon
Eudorina
Euglena
Glenodinium
Phacus
encysted flagellates
unidentifiable flagellates

This list of genera is strikingly similar to that already published for Colorado plains lakes, the most notable difference being the occurrence of only about half as many genera of limnetic Myxophyceae in the mountain lakes as were found in the plains lakes. The great majority of Bacillarieae were *Asterionella*, *Melosira*, and *Fragilaria*. Though abundant in plains lakes, *Synedra* was seldom present in the mountain lakes, and this situation may be correlated with the fact that *Synedra* populations are well developed only where calcium is abundant (Patrick, 1948).

The most common diatom genera in the Colorado lakes were also found by Hustedt (1943) to be the most common ones in a group of lakes in the Swiss Alps.

More than 90 per cent of the Myxophyceae were *Chroococcus; Aphanizomenon* was found only in Grand Lake and *Lyngbya* only in Lake Estes, but *Anabaena* was found in both Grand and Manchester lakes. *Coelosphaerium*, *Microcystis*, *Gloeotrichia*, and *Merismopedia*, which are common phytoplankters in midwestern and eastern lakes, were not found.

The Chlorophyceae were variously represented by numerous genera, especially non-filamentous forms, but usually by only small numbers of individuals.

"Small green flagellates" is a heterogeneous category including several major taxonomic groups which are included together merely for the sake of convenience. *Dinobryon* was by far the most abundant form. In this category are also included certain flagellates which were contracted and unidentifiable owing to the alcoholic fixation in the field. In addition, this category includes the encysted stages of certain flagellates.

The great similarity in species composition of the phytoplankton in all these Colorado lakes strengthens the argument for tabulating results in terms of "cells per liter". If one or more of the lakes had a phytoplankton composed of cells belonging to species and genera of greatly different size from those in the other lakes, "cells per liter" would be a much less desirable criterion to use.

Like the plains lakes, the mountain lakes were characterized by diatom and blue-green floras which exhibited much greater seasonal fluctuations than the corresponding seston determinations.

BACILLARIEAE

Because of the wide seasonal variations in the standing crop and because of the great differences in diatom populations from one lake to another, it was found necessary to summarize the data on semi-logarithmic paper (Fig. 21). Each point on these curves represents the average population on one day for samples taken at two to six different depths between surface and bottom, depending on the depth of the lake.

The precise factors responsible for the occurrence of diatom pulses are still not definitely known, but turbidity, wind, precipitation, light conditions, and dissolved salts have all been suggested by various investigators. Nevertheless, two general theories have been advanced, especially for deeper lakes than those considered in the present report. The more popular theory maintains that the diatom population is greatest in late winter and early spring when the overturn enriches the water with phosphates, nitrates, and silicon compounds. Certain other investigators emphasize the frequent possibility of a second pulse at the time of the autumn overturn. McCombie (1953), for example, generalizes as follows: "In each case the seasonal distribution of phytoplankton is bimodal, with minimum numbers in winter and maxima in spring and autumn." Judging from the data available, however, the eight mountain lakes do not fit into either of these patterns with any consistency.

Beaver Reservoir had an enormous diatom pulse lasting from August to October, with a peak of 31,440,000 cells per liter in late September. *Asterionella* accounted for most of this pulse, *Melosira* being second in abundance. Pulses of such great magnitude do not appear to have been reported previously in the literature for mountain lakes, and only seldom do lakes at lower elevations develop such dense diatom populations. While there is no obvious explanation for this pulse, it appears logical to assume that it was associated in some way with the extensive draw-down of water in the reservoir between August and October. A secondary pulse, chiefly *Melosira*, was found on May 27; it amounted to 5,105,000 cells per liter.

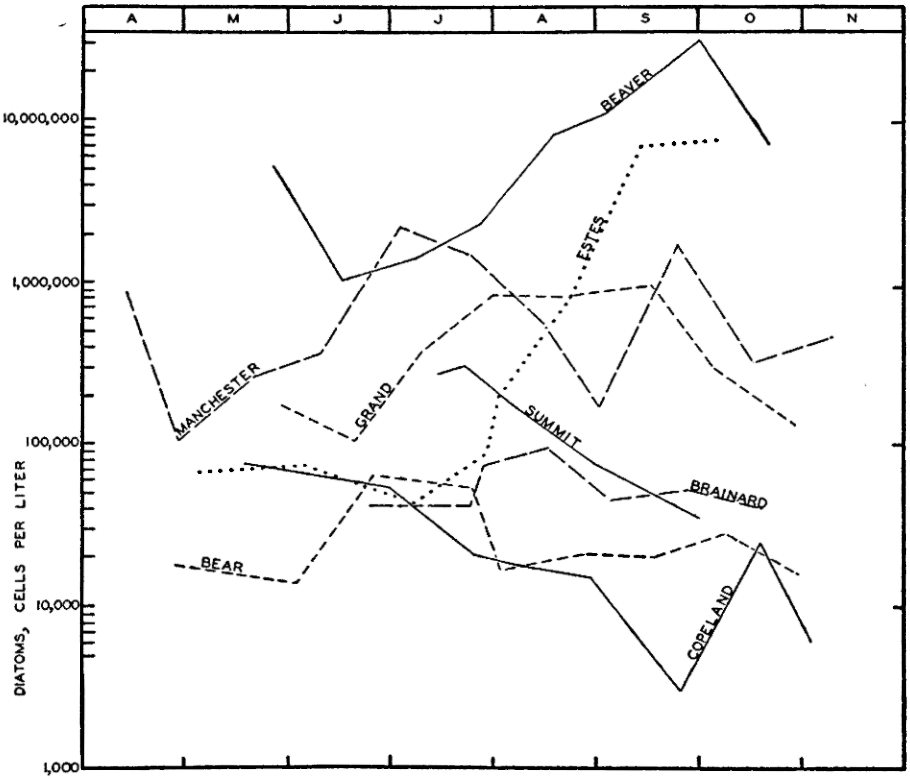

FIG. 21. Semilogarithmic curves of diatom abundance for the open season in eight Colorado mountain lakes. Each point on the curves represents an average of two to six evenly spaced samples taken between the surface and bottom on a particular date.

The diatom population in Manchester Lake was highly irregular, with some evidence of two pulses, one during summer and another in autumn. The former reached a maximum of 2,162,000 cells per liter on July 3 and the latter 1,688,000 cells per liter on September 24. *Asterionella*, *Fragilaria*, and *Melosira* were all exceptionally abundant during both these pulses. Manchester Lake was also sampled through the ice on January 3 and a population of *Asterionella* amounting to 1,656,000 cells per liter was found. Only 106,000 cells per liter were found on April 28.

Grand Lake exhibited a single pulse which lasted from late July to mid-September. A maximum of 955,200 cells per liter (chiefly *Melosira* and *Asterionella*) was found on September 15. Minimal numbers occurred in June.

Lake Estes also had a single very large *Melosira* pulse, but it reached its peak in September and October with a maximum of 7,450,000 cells per liter on October 5. Since sampling stopped on that date, it is not known how long it persisted. Populations were relatively small during May, June, and July.

Summit Lake had its greatest diatom population (303,000 *Asterionella* cells per liter) on July 19, when there was still a partial ice cover. Thereafter the population decreased throughout the open season and had dropped to 35,400 cells per liter when the last series was taken on September 30.

No definite pulses were found for Brainard, Copeland, or Bear lakes. Maximum populations were 95,000 in August, 77,000 in May, and 66,000 in June, respectively.

Chandler (1940, 1942, 1944) and Pearsall (1932) have discussed the spring or autumn dominance of certain genera, presumably as determined by certain physical-chemical conditions (Chandler) and by "toxicity" and "stimulating" substances secreted into the water (Pearsall), but no such seasonal occurrence or dominance of any particular genus or species was found for the Colorado lakes. The same diatom might be numerically dominant in spring, summer, or autumn, or in any one or two of these seasons. These results are also in contrast to the results shown by the careful studies of Lund (1950) which demonstrated a regular spring pulse of *Asterionella* in several English lakes. The disappearance of this pulse is thought to have been caused chiefly by the depletion of available silica, especially when it dropped below 0.5 mg. per liter. Chu (1942), on the other hand, maintains that diatoms are inhibited when the silicon dioxide content of water exceeds 54 mg. per liter.

MYXOPHYCEAE

Open season Myxophyceae populations for the eight mountain lakes are shown in Figure 22, and again, because of the very wide range in numbers, the data are plotted on a semilogarithmic basis. According to the literature, these algae are usually said to exhibit a pronounced late summer or autumn pulse with the occasional addition of a spring pulse of small magnitude. None of these bodies of water had the "typical" single autumnal pulse, but three of them had both spring and autumn pulses during varying months. Copeland Lake, for example, had its chief pulse (mostly *Chroococcus*) from late August to mid-October, with a maximum of 4,590,000 cells per liter on October 16; the secondary pulse reached 2,085,000 cells per liter on June 30. Beaver Reservoir had slight spring and autumn pulses, with a negligible population in mid-August; the autumn pulse was the more pronounced, with a maximum of 264,000 cells per liter on October 21; the spring pulse of 162,000 cells per liter occurred on June 16. Manchester Lake also had spring and autumn pulses, but the former reached a much greater density than the latter; populations were 7,760,000 cells per liter on April 13 and 1,314,000 cells per liter on September 1.

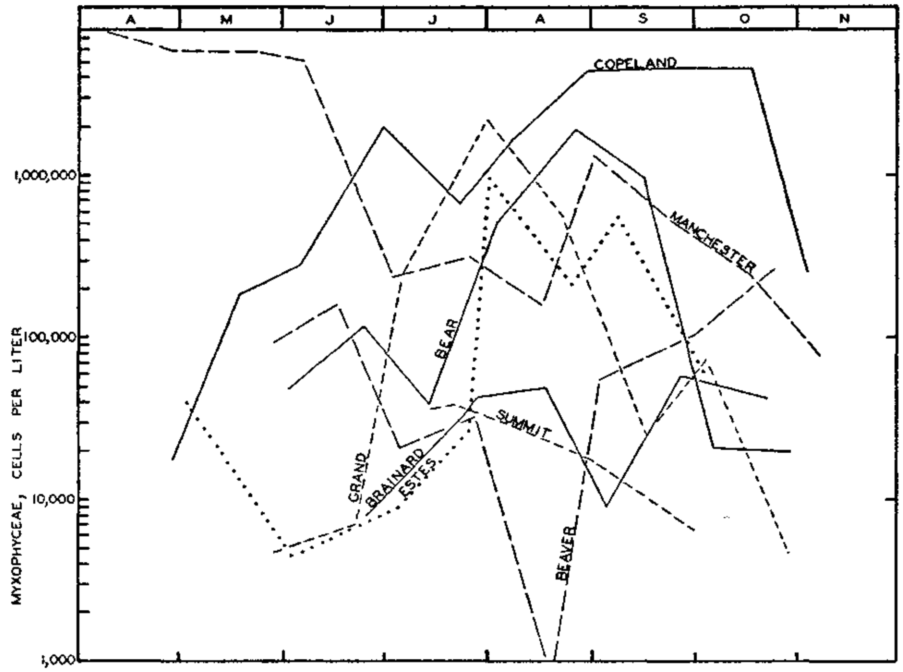

FIG. 22. Semilogarithmic curves of abundance for blue-green algae during the open season in eight Colorado mountain lakes. Each point on the curves represents an average of two to six evenly spaced samples taken between the surface and bottom on a particular date.

Three lakes had single blue-green pulses. The one for Bear Lake extended through August and September and reached a maximum of 1,929,000 cells per liter on August 25. For Lake Estes the pulse also extended through August and September, but the maximum was only 984,600 on August 2. The Grand Lake pulse, on the other hand, was a clearly defined summer pulse extending through July and August, with a pronounced maximum of 2,283,000 cells per liter (mostly *Anabaena* and *Aphanizomenon*) on July 31. The local residents of the Grand Lake area spoke of a "nuisance bloom" in the summer of 1954, but the algal density was very much below those attained during blooms in midwestern states. There was no unusual algal odor, nor were any windrows of dead algae found along the shore of Grand Lake. Before 10 A.M. on exceptionally calm and sunny mornings, however, temporary floating masses of *Anabaena* and *Aphanizomenon* would form. These were in the magnitude of 2 x 3 x 15 cm. With the coming of the wind they would disintegrate and the individual filaments would disperse from the surface and into the top few meters of water.

The remaining lakes, Brainard and Summit, had small numbers of blue-green algae, and true pulses did not occur. The former had a maximum population of 58,000 cells per liter on September 26, and the latter 39,000 on July 19. These were the two highest lakes studied, and since they are characterized by low temperatures and rock and gravel basins with limited surrounding drainage areas, large populations of Myxophyceae were not to be expected.

Pearsall (1932) contends that blue-green blooms develop in late summer (McCombie, 1953, says mid-summer) when inorganic nutrients are practically exhausted, and the work of Hutchinson (1944) strengthens the former contention. On the basis of the present data, however, it is doubtful if this generalization is of broad importance. Only Copeland and Bear lakes had "late summer" blue-green pulses. Grand and Estes lakes had midsummer pulses, but all the other lakes had pulses at various other times in spring and autumn. Undoubtedly the shallowness, greater circulation, and more frequent availability of nutrients in the Colorado lakes had much to do with this discrepancy.

CHLOROPHYCEAE

Compared with diatoms and blue-green algae, only small numbers of green algae were found in the plankton, and populations were generally much too thin to speculate concerning any supposed seasonal "nutritional antagonism" between them and the other two groups of algae, as has been tentatively suggested by several investigators.

By far the largest population of green algae was found in Manchester Lake where *Pediastrum* and *Scenedesmus* were usually the most abundant forms. A maximum of 576,000 Chlorophyceae cells per liter was found on June 9, and a secondary maximum of 416,000 cells per liter on August 15. Beaver Reservoir had a maximum of 216,000 cells per liter on September 30, but during other months fewer than 30,000 cells per liter were found. Copeland Lake had a maximum of 114,000 cells per liter on May 18, but fewer than 60,000 cells per liter during other months. The other five lakes all had negligible populations.

"SMALL GREEN FLAGELLATES"

Small flagellates were abundant only in Manchester Lake. The dominant form, *Dinobryon*, reached its maximum in September and October. In Beaver Reservoir *Dinobryon* was most abundant in May, June, and July. In large temperate lakes this genus is usually said to be most abundant in spring and autumn. Bear Lake had a small pulse of *Glenodinium* in June and July. Mixed populations of *Dinobryon*, *Glenodinium*, and other forms were found in small numbers at various times in most of the other lakes.

VERTICAL DISTRIBUTION

As a whole, the vertical distribution of the algae varied widely, without consistent seasonal patterns. Of the 67 series of phytoplankton samples, the maximum populations of diatoms were found in the surface waters in 26 series, in the bottom sample in 19 series, and in an intermediate sample in 22 series. For the blue-greens the corresponding figures were 25, 20, and 22 series. In Estes and Grand lakes the maximum population was never found in the bottom sample, but this fact is to be expected since these were the two deepest lakes studied, and in deep lakes it is usual to find few algae in the lower hypolimnetic water. Green flagellates were generally most abundant in the uppermost three meters of water during the late morning hours when sampling was done.

Grim (1950) has shown that a large fraction of the algal cells, especially those below the photosynthetic zone, are "inactive", moribund, or dead. In a lake ten meters deep he found that 15 to 60 per cent of the *Cyclotella* cells were dead at depths of 1 to 3 meters, and that 30 to 100 per cent were dead at depths of 7 to 9 meters. When phytoplankton counts were made in the present study a large number of cells were seen to be dead and were not tallied, but undoubtedly an important fraction of the tallied cells were actually dead but could not be distinguished as such. For this reason the present phytoplankton estimates are undoubtedly a little high, but for that matter they are too high in all similar studies.

MEAN ANNUAL STANDING CROP

In view of the extreme seasonal variations from one lake to another and from one species to another, it is felt that the most dependable method of comparing the plankton of the various lakes is that one based on the mean annual standing crop. For purposes of comparison, some earler materials for seven lakes at lower elevations (Pennak, 1949) are included with the summarized data for the eight mountain lakes in Table VII. It is indeed unfortunate that so few comparable studies have been carried out in other parts of the world. Most "quantitative" plankton studies suffer from one or more of the following difficulties which make them unsuited for comparison with the present investigation: (1) Samples are taken only during two or three months of the the year (and are thus scarcely "typical" for the whole year-round growing season). (2) Samples are taken at insufficient depth intervals and cannot possibly be interpreted as an accurate estimate of the momentary standing crop; some investigators have even been satisfied with taking only surface samples, which are completely worthless for quantitative work. (3) Samples are taken with an ordinary plankton net — a procedure which is by no means a quantitative method for phytoplankton.

TABLE VII. *Mean annual phytoplankton populations for 15 northern Colorado lakes. Data for the first seven lakes in this table are from Pennak (1949). A dash signifies fewer than 50 cells per liter*

Lake	Altitudinal zone	Mean annual phytoplankton, cells per liter				Ratio of Bacillarieae: Myxophyceae
		"Small green flagellates"	Chlorophyceae	Bacillarieae	Myxophyceae	
Baseline..........	Plains		16,600	118,100	719,800	.16
Hayden's.........	"		11,300	102,100	488,600	.21
Allens............	"		30,200	309,400	269,500	1.15
Beasley..........	"		115,000	857,600	990,000	.87
Boulder..........	"		1,154,700	824,800	6,468,800	.13
Gaynor..........	"		3,600,500	3,615,100	20,191,200	.16
Kossler...........	Foothills		300	871,100	37,500	23.23
Estes............	"	—	100	905,900	130,400	6.94
Copeland.........	Montane	1,000	22,400	22,700	1,167,600	.02
Grand...........	"	7,900	700	299,200	190,700	1.57
Manchester.......	"	436,600	154,500	852,800	2,558,800	.33
Beaver...........	"	25,000	22,000	7,426,000	79,000	94.00
Bear.............	"	42,300	1,400	20,100	234,700	.09
Brainard.........	"	—	2,300	47,900	29,500	1.62
Summit..........	Alpine	47,100	9,000	154,700	23,200	6.66

Although actual collections were made in the mountain lakes only during the open months of the year, a somewhat arbitrary system was adopted in order to derive hypothetical means on a 12-months' basis. For each lake the phytoplankton population found for the first spring visit and the phytoplankton population found for the last autumn visit were averaged. This figure was used as the mean population for the whole of the unsampled portion of the year. Year-round sampling on numerous lakes not included in the present investigation has shown that such an average gives a surprisingly good indication of the general size of the mean population for the winter months. In addition, several of the more accessible of the eight mountain lakes were visited in midwinter, and these phytoplankton counts have been suitably incorporated into the results in Table VII. Furthermore, the annual means have been properly weighted in accordance with the relative length of the sampling periods.

To many hydrobiologists, the expression "mountain lake" is automatically associated with "poor plankton", and while "poor plankton" is true of certain bodies of water indicated in Table VII, it is by no means true of the whole group of nine high-altitude lakes. The Table emphasizes this heterogeneity of phytoplankton conditions in the 15 lakes. Among the nine mountain lakes, a curious mixture of correlations (or lack of correlations) is apparent. Manchester Lake, for example, had the largest blue-green population and the fourth largest diatom population, but Copeland Lake, with the second largest blue-green population, had the second smallest diatom population. Beaver Reservoir, on the other hand, with the fourth smallest blue-green population, had the largest diatom population, while Lake Estes with a blue-green population at about the midpoint had the second largest diatom population.

In general, the Myxophyceae populations of the nine high lakes were far below those for the six plains lakes, the former having only 10.2 per cent as many cells as the latter. But if the abnormally high population for Gaynor Lake is omitted from the calculations, the ratio is 27.7 per cent. The situation was just the reverse with respect to diatoms, since the high lakes contained 27.8 per cent more diatoms than the plains lakes. If the unusually large populations for both Gaynor and Beaver lakes are omitted from consideration, however, the remaining five plains lakes are seen to have had 11.1 per cent more diatoms than the remaining eight high lakes.

Green algae were markedly more abundant in the plains lakes. Even if the very high population for Gaynor Lake is omitted from consideration, the high lakes contained only 8.9 per cent as many green algae as the plains lakes.

Only a few scattered small green flagellates were found in Estes and Brainard lakes, and Copeland Lake had a mean annual population of only about 1,000 cells per liter. For the other five high lakes the mean annual population ranged from 7,900 cells per liter for Grand Lake to 436,600 cells per liter for Manchester Lake. Comparable "small green flagellate" data are not available for the first seven lakes listed in Table VII because of different methods of tabulating. On a very rough basis, however, it may be said that small green flagellates were about three times as abundant in plains lakes as they were in lakes at high elevations.

Bear, Brainard, and Summit lakes had general algal populations that were markedly lower than those for any of the other 12 lakes listed in Table VII. These three bodies of water were at the top of the altitudinal range and had the lowest summer maximum temperatures in the photosynthetic zone, as well as the shortest growing season. In addition, all three have rocky basins, small surrounding drainage areas, and stable water levels. They are, in other words, the most "typical" mountain lakes and are characterized by "low productivity".

Some textbooks and many research papers state that "characteristically" the lakes of the North Temperate Zone have a numerically dominant diatom phytoplankton. Although this statement may be true for large deep lakes which usually have spring and autumn phytoplankton pulses, it is by no means true for small and/or shallow lakes of these general latitudes. The weakness of this generalization is shown by the last column in Table VII, which gives the mean annual ratios of diatoms to blue-green algae for the 15 Colorado plains and mountain lakes. (For all practical purposes, perhaps all but the last two lakes listed are "North Temperate Zone" lakes; Brainard and Summit are more nearly "Subarctic".) Only seven of these bodies of water had more diatoms than Myxophyceae, with ratios ranging from 1.15 (Allens Lake) to 94.00 (Beaver Reservoir). The ratios for the other eight lakes ranged from 0.02 (Copeland Lake) to 0.87 (Beasley Reservoir). It is notable that the mountain lakes had a much wider range in these ratios than was true for the plains lakes.

It should be borne in mind that the "mean annual populations" discussed in this section are derived from collections taken only for one year, and that they are undoubtedly subject to considerable year-to-year variation within each lake. Nevertheless, it is felt that "mean annual populations" are subject to a much smaller degree of variation than is indicated, for example, by data gathered in many types of limnological investigations only in July and August. In view of the very wide seasonal variations in the algal populations of single lakes as well as from one lake to another, the "averages" calculated above are of considerably less significance than is desirable.

Since about 1938 a good many investigators of both marine and fresh-water phytoplankton have been making quantitative estimates of the chlorophyll in plankton samples with extraction and photoelectric procedures. Some of these workers are firmly convinced of the quantitative accuracy of such measurements for the determination of the standing crop of phytoplankton, but a number of serious shortcomings for this method have been pointed out by Manning and Juday (1941), Rodhe (1948), Tucker (1949), Berardi and Tonolli (1953), and others. In view of these opinions, the present writer prefers to continue using the "physiological unit" (cell) in making estimates of the standing crop of phytoplankton for lakes having generic similarities in their algal populations.

ZOOPLANKTON POPULATIONS

PROTOZOA

The species represented in this category are large and relatively sparse motile forms that could be quantitatively sampled with the ten-liter plankton trap more satisfactorily than with a Kemmerer water sampler. These are *Ceratium hirundinella*, *Peridinium*, *Difflugia*, and unidentifiable ciliates.

Ceratium hirundinella was the most common species. Small numbers were found throughout the sampling period in Estes, Grand, Manchester, Beaver, Brainard, and Summit lakes. Beaver Reservoir had maximum populations of 640 per liter on August 21 and 663 per liter on September 15, while Manchester had enormous populations of 5273 per liter on August 15 and 4017 per liter on September 1. The other four lakes, on the other hand, usually had only one to five individuals per liter.

Peridinium was found only in Copeland and Beaver lakes, usually in densities of less than five per liter.

A very large burst of *Difflugia* was found in Manchester Lake between September and November, with a maximum of 531 individuals per liter on November 10. Although *Difflugia* is usually considered a substrate species, it sometimes becomes a pseudoplankter by altering its specific gravity and becoming suspended in the water at all depths.

Several contracted ciliates were found in the lowermost samples of Lake Estes during June and July when the dissolved oxygen content was low.

ROTATORIA

Most of the rotifers were easily identifiable to species and are therefore treated in detail. Table VIII is a summary of their abundance in the eight lakes. Most of these species are common and widely distributed limnetic plankters. So far as most published lists of plankton rotifers are concerned, this group of species is unusual in that it includes only one record for *Brachionus,* a very common and cosmopolitan genus. This is, however, a genus that has alkaline-water affinities and consequently has become established in very few mountain lakes. Another unusual feature of this list is the fact that *Kellicottia,* also a common and cosmopolitan genus, occurred in only one of the eight lakes.

Eight of the 26 species listed occurred in four or more of the lakes. *Polyarthra vulgaris* was found in all eight lakes, and *Keratella cochlearis* and *Synchaeta pectinata* in seven lakes. Fifteen species, on the other hand, were found in only one or two lakes; some of these were represented by only a very few individuals in a single sample. The annual means indicated in Table VIII are only rough approximations, since some of the species listed were abundant for only short periods of the year and since the data are weighted averages to take into consideration the cold months of the year when no samples were usually taken. Procedures used were the same as those used for calculating mean annual phytoplankton populations. There is a considerable but scattered literature on the seasonal periodicity of rotifers (partly summarized by Rylov, 1935), and for this reason most of the species listed in Table VIII are treated individually.

Asplanchna priodonta Gosse. This carnivorous species was found in four lakes but never in abundance. It is usually considered a late spring and early summer

TABLE VIII. *Mean annual standing crop of plankton Rotatoria in eight Colorado mountain lakes. Expressed as numbers of individuals per liter; a dash indicates less than 0.1 individual per liter*

Species	Lake							
	Estes	Copeland	Grand	Manchester	Beaver	Bear	Brainard	Summit
Asplanchna priodonta	—		7.4	4.2	0.4			
Brachionus calyciflorus				—				
Cephalodella gibba		0.1						
Conochilus unicornis		124.9	2.6		17.7	42.8	—	
Conochiloides dossuarius					0.4			11.9
Diurella sp.		—						
Filinia longiseta			6.4	—		34.9		
Filinia terminalis	1.5				5.1			2.2
Kellicottia longispina			44.0					
Keratella cochlearis	13.3	4.2	9.1	285.4	57.8	0.3		0.1
Keratella quadrata	3.1		2.6	16.7	1.9	40.3	—	
Keratella serrulata		—						
Lecane luna	0.2	0.2				—		
Lepadella patella	—							
Monostyla lunaris		0.6	—	—		—		
Notholca acuminata	0.7			0.1				
Notholca striata					0.3			
Notommata sp.		—						
Pedalia sp.	—							
Ploesoma hudsoni						1.7		
Polyarthra vulgaris	31.5	33.4	18.3	274.6	60.1	20.5	0.4	6.2
Pompholyx sp.			—	9.6				—
Synchaeta pectinata	1.2		2.5	1.4	2.5	32.9	0.8	3.9
Testudinella patina		0.1					0.2	
Trichocerca spp.	—			1.8				
Trichotria tetractis		0.3						
Miscellaneous	6.5	1.3			3.6		0.1	

form, but it reached a peak of 22 per liter in Grand Lake on October 27 and 37 per liter in Manchester Lake on July 24.

Brachionus calyciflorus Pallas is an alkaline-water form which is abundant in many plains reservoirs. A few specimens were found in Manchester Lake, the most alkaline of all eight lakes (28.7 ppm. bound carbon dioxide).

Cephalodella gibba (Ehrenberg) is a species usually associated with rooted aquatic vegetation. It was found only in Copeland Lake on August 11, when it was taken in the bottom sample in the immediate vicinity of the carpet of *Chara*.

Conochilus unicornis Rousselet. This species is said to be more common in larger lakes, but the largest population was found in Copeland Lake, the smallest of the eight Colorado lakes. The most dense population was 676 per liter on June

30, with a second peak of 309 per liter on August 11 (Fig. 23). Grand Lake had 41 per liter on July 10 but very few individuals during other months. Beaver Reservoir had a single maximum of 104 individuals per liter on July 27, and Bear Lake a single maximum of 455 per liter on July 14. This is a year-round species, usually abundant only during midsummer, and its occurrence in four mountain lakes is in agreement with this generalization.

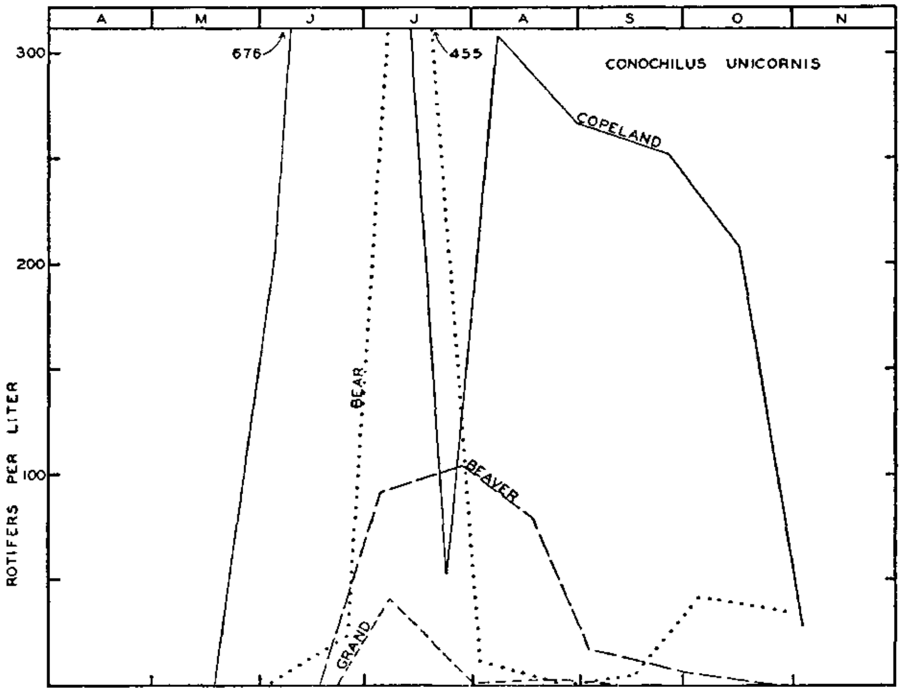

FIG. 23. Abundance of the rotifer, *Conochilus unicornis*, during the open season in four Colorado mountain lakes. Each point on the curves represents an average of two to six evenly spaced samples taken between the surface and bottom on a particular date.

Conochiloides dossuarius (Hudson) is a monocyclic summer or early autumn species characteristic of smaller bodies of water. A few specimens were found only in Beaver Reservoir in June and July.

Filinia longiseta (Ehrenberg). This common species is said to be dicyclic, with summer and autumn maxima, or monocyclic, with only one of these maxima. It was found in Grand Lake on all sampling dates, and a maximum of about 10 per liter was found from August through early October. In Bear Lake, however, it was much more abundant and reached a peak of 260 per liter on July 23. *F. longiseta* was found to be similarly irregular in its seasonal occurrence in four plains lakes (Pennak, 1949).

Filinia terminalis (Plate). This form is much less common than the preceding species, and its periodicity is poorly known. Small numbers were found in Estes, Beaver, and Summit lakes, where poorly defined maxima were attained in September, July, and July, respectively.

Kellicottia longispina (Kellicott), usually called *Notholca longispina* in the literature, is one of the most characteristic limnetic rotifers in larger lakes, and, significantly, it was found only in Grand Lake, the largest body of water studied. A primary maximum of 84 per liter was found on September 15 and a secondary maximum of 45 per liter on July 10. Other investigators state that it usually becomes most abundant in spring or summer.

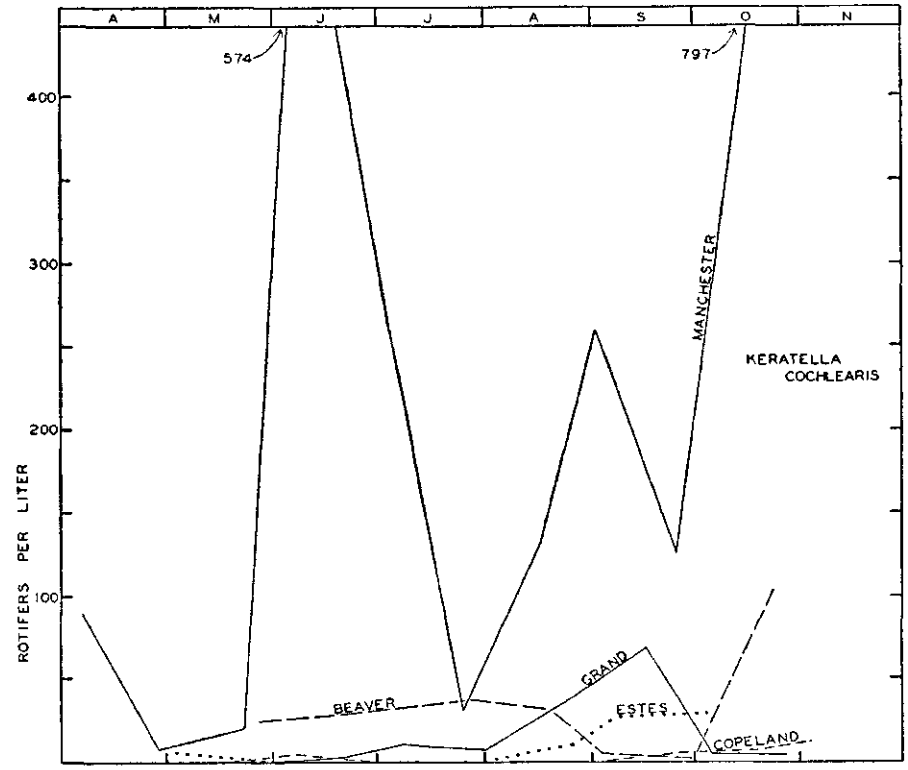

FIG. 24. Abundance of the rotifer, *Keratella cochlearis*, during the open season in five Colorado mountain lakes. Each point on the curves represents an average of two to six evenly spaced samples taken between the surface and bottom on a particular date.

Keratella cochlearis (Gosse). This common and cosmopolitan species (often called *Anuraea cochlearis*) was found in all lakes except Brainard, although only negligible numbers were found in Bear and Summit lakes (Fig. 24). Small population peaks occurred during September and October for Beaver, Grand, Estes, and Cope and lakes, but Manchester Lake had two pronounced pulses, one of 574 per liter on June 9 and a larger one of 797 per liter on November 10. In general, these spring and autumn pulses conform with the results obtained for this species in plains lakes. Most published literature, however, mentions this species as a warm-season form.

Keratella quadrata (Müller). This common species is highly variable in its seasonal occurrence but is sometimes described as a summer form. It was found in six of the mountain lakes, but in four of these the populations were negligible. In Manchester Lake *K. quadrata* was dicyclic, with peaks of 91 per liter on June 9 and 99 per liter on September 1. In Bear Lake there was a single maximum of 151 per liter on June 23.

Keratella serrulata (Ehrenberg) is uncommon in Colorado and is usually found in small weedy ponds. A few specimens were collected in Copeland Lake on June 30 in the bottom sample, where the rotifers were undoubtedly associated with the carpet of *Chara* in this small lake.

Lepadella patella (Müller) is an occasional and uncommon plankter. Several specimens were found in Lake Estes on June 5.

Monostyla lunaris (Ehrenberg) is also an occasional plankter. A few specimens were found in Copeland, Grand, Manchester, and Bear lakes.

Notholca acuminata (Ehrenberg) is said to be a monocyclic cold-water species occurring in a variety of waters (including brackish) but it rarely becomes abundant. A few specimens were collected from Estes and Manchester lakes in April and May.

Notholca striata (Ehrenberg). The ecological characteristics of this species are similar to those of the foregoing species. Several specimens were taken in Beaver Reservoir.

Ploesoma hudsoni (Imhof) is a monocyclic summer species occurring in lakes of medium to large size. It was found from July to October in Bear Lake and attained a peak of 21 per liter on August 4.

Polyarthra vulgaris Carlin. This is the species referred to as *P. trigla* by the present writer (Pennak, 1949) and by many other authors. It is a common cosmopolitan and was the only species found in all eight lakes. *P. vulgaris* is said to be a perennial form, often with two or three peaks of abundance during the year. The open-season distribution in the mountain lakes, however, was just as variable and unpredictable (Fig. 25) as it was in the plains lakes. Manchester Lake had by far the most dense population with three sharply alternating peaks of abundance, one

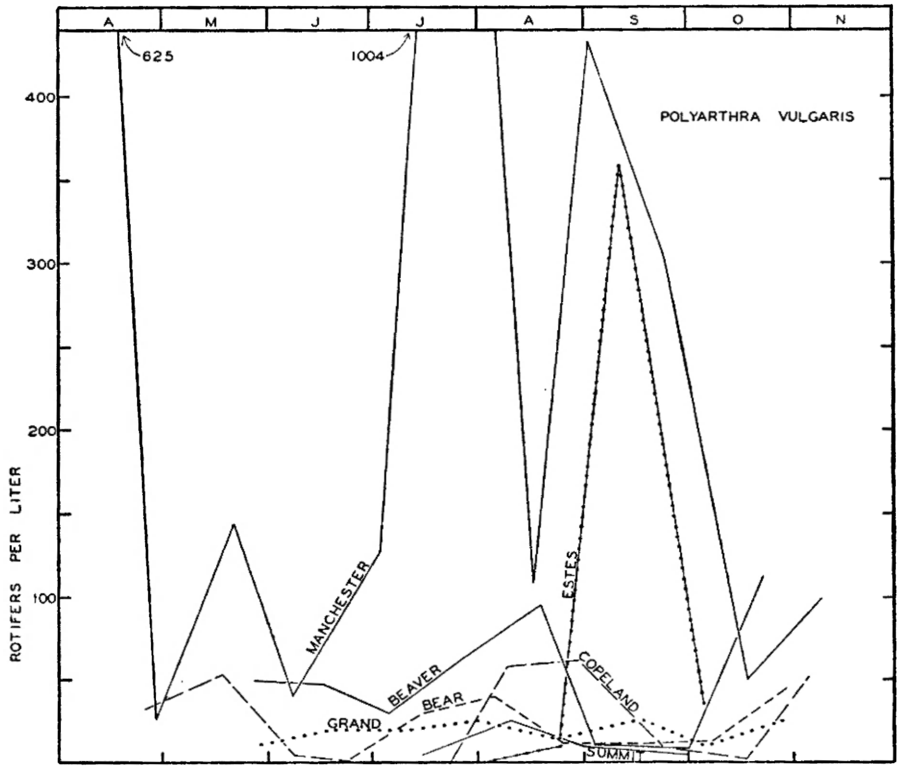

FIG. 25. Abundance of the rotifer, *Polyarthra vulgaris*, during the open season in seven Colorado mountain lakes. Each point on the curves represents an average of two to six evenly spaced samples taken between the surface and bottom on a particular date.

of 625 per liter on April 13, a second of 1004 per liter on July 24, and a third of 434 on September 1. Copeland Lake also had three maxima, but they were all relatively slight. One attained 56 per liter on May 18, a second reached 62 per liter on August 29, and the third 51 per liter on November 4. Two maxima were found in Beaver Reservoir, one of 93 per liter on August 18 and one of 113 per liter on October 21. Bear Lake had two similar pulses but they were even less pronounced; one reached 40 per liter on August 4 and the second was 44 per liter on October 28. Very few *P. vulgaris* were found in the spring and summer in Lake Estes, but on September 13 a very large burst of 357 per liter was counted. Summit and Grand lakes had only negligible numbers of this species, and no definite pulses were detected.

Synchaeta pectinata Ehrenberg is usually characterized as dicyclic, with summer and autumn maxima. Although it was found in seven of the mountain lakes, it was abundant only in Bear Lake, where it was collected in June, July, and October. Here it did have two maxima, one of 59 per liter on June 23 and another of 50 per liter on October 28. Although *S. pectinata* was found on most sampling dates in the other lakes, it was seldom more abundant than five specimens per liter.

Testudinella patina (Hermann) is a species usually associated with a substrate. Several specimens were found fortuitously in the plankton of the shallow Copeland and Brainard lakes.

Trichotria tetractis (Ehrenberg) is also a species of the substrate. A few examples were taken in Estes and Manchester lakes.

Judging from the foregoing remarks, Table VIII, and Figures 23 to 25, it is obvious that the only valid conclusion to be drawn is one of inconsistency. These lakes differed widely in the number of species found in each, from six species in Brainard and Summit lakes to 12 species in Estes and Copeland lakes. Even some of the most common species were unaccountably absent from one or more lakes. The numerical abundance of several of the species varied remarkably from one lake to another, ranging from negligible numbers to dense concentrations, especially for such common species as *Conochilus unicornis*, *Keratella cochlearis*, *K. quadrata*, *Polyarthra vulgaris*, and *Synchaeta pectinata*. And perhaps most striking of all, these species showed no consistency in their seasonal population curves. A single species, for example, might have one, two, or three population pulses, or no pulses at all, varying with the particular lake and the season. Thus, while certain limnetic species may be characterized as "spring", "summer", or "autumn" species, or as "monocyclic" or "dicyclic" with reference to larger lakes, such generalizations should not be used in dealing with plankton populations of smaller lakes, such as have been studied in Colorado. It should also be remembered that the nature of the seasonal curves for individual species undoubtedly varies from year to year within a single lake.

When the data for the individual species are combined, the resulting open-season population curves appear as shown in Figure 26. In general, the pronounced peaks were produced by one or two species that happened to be especially and momentarily abundant. The three maxima for Manchester Lake, for example, were produced by large populations of both *Polyarthra vulgaris* and *Keratella cochlearis*. Copeland and Beaver lakes showed two pulses; Bear and Estes lakes, a single pulse; and Grand and Summit lakes had no special pulses. The curve for Brainard Lake is not included in Figure 26 because it had such small rotifer populations that they could not be shown on the scale used.

Obviously, then, there was no seasonal "pattern" of rotifer abundance in these mountain lakes. The early spring and late autumn populations were usually small, but the intervening maximal populations (if present) occurred variously

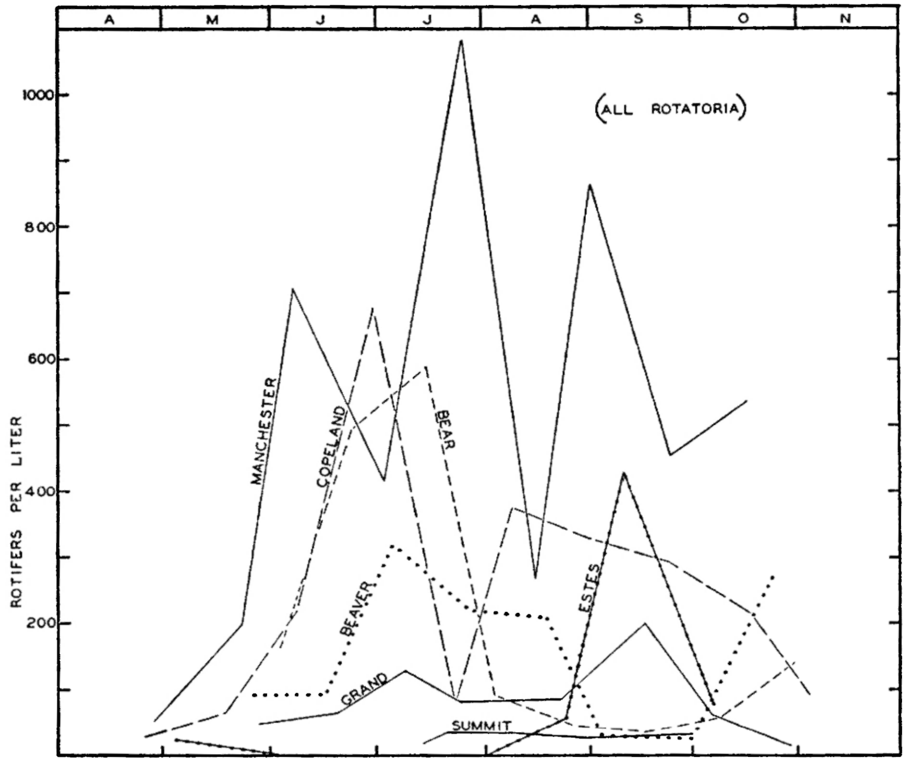

FIG. 26. Open-season abundance for all rotifers in seven Colorado mountain lakes. Each point on the curves represents an average of two to six evenly spaced samples taken between surface and bottom on a particular date.

between June and September. This irregular (and somewhat puzzling) situation is fundamentally similar to the conditions found in plains lakes.

COPEPODA

Cyclops bicuspidatus Claus was the only limnetic copepod found in seven of the lakes. This fact was one of the most striking features of the zooplankton of the mountain lakes, since limnetic populations everywhere are almost invariably characterized by a dominant calanoid species in addition to a cyclopoid species. *C. bicuspidatus* was absent from the Copeland Lake samples, but very small numbers of three other species were found: *Diaptomus leptopus* Forbes, *Macrocyclops albidus* (Jurine), and *Eucyclops agilis* (Koch). The latter two species are bottom-inhabiting forms often closely associated with rooted aquatics and were thus merely fortuitous individuals taken by the plankton trap just off the bottom of Copeland Lake.

Data for *Cyclops bicuspidatus* are summarized in Figure 27. These curves include nauplius stages and copepodids as well as adults. Although the nauplii are considerably smaller than the adults and copepodids, they are very active in feeding, and it is felt that their ecological role in consumption of food materials is roughly similar to that of the more advanced instars.

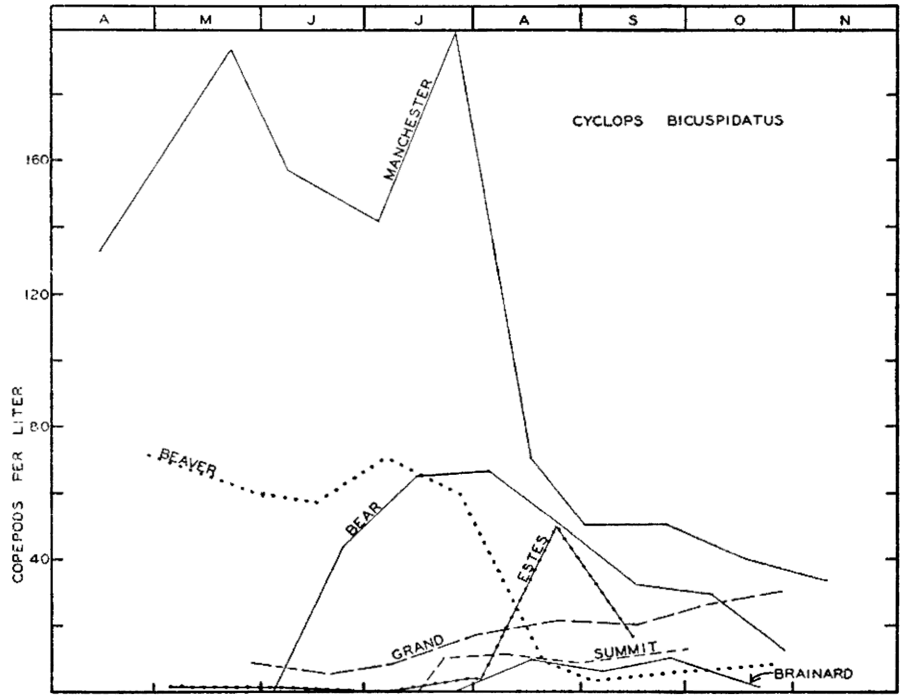

FIG. 27. Open-season abundance of *Cyclops bicuspidatus* in seven Colorado mountain lakes. Each point on the curves represents an average of two to six evenly spaced samples taken between the surface and bottom on a particular date.

Manchester Lake had by far the largest numbers of *C. bicuspidatus*, the maximum population extending from May through July and a peak of 200 individuals per liter being found on July 24. Beaver Reservoir likewise had a long maximum extending from April through July and a peak of 71 per liter on July 7. Both of these bodies of water had rather large populations beginning with the first spring collections. Although the magnitude of the late winter populations is not known, a visit to Manchester Lake on January 3 showed a population of 75 per liter.

The maximum numbers in Estes and Bear lakes were attained well after sampling began in the spring, and the most dense populations were 50 per liter on

August 23 and 67 per liter on August 4, respectively. Grand Lake had a small population which increased gradually through the warm months to a maximum of 30 per liter on October 27, when the lake was last visited. Both Brainard and Summit lakes had very small populations with no pronounced peaks. Maxima were only 10 and 13 per liter, respectively.

The general nature of the curves in Figure 27 shows that *C. bicuspidatus* was either monocyclic or acyclic in these seven lakes and that the time of the maximum varied from early spring to late autumn. In seven plains lakes this same species was shown to be dicyclic, monocyclic, or acyclic, with maxima at various times of the year (Pennak, 1949). It is possible that the sudden appearance of large limnetic populations is produced by the emergence of many individuals from an inactive cocoon or resting stage in the surface of the bottom mud, but this possibility was not investigated during the present study.

The mean annual ratios of nauplii : copepodids plus adults show some interesting variations in the seven mountain lakes containing *C. bicuspidatus*. Nauplii were relatively most abundant in Bear Lake, where the ratio was 7.1:1, and second most abundant in Brainard Lake with a ratio of 5.5:1. The lowest ratio, 1.3:1, occurred in Summit Lake; the second lowest, 1.5:1, in Beaver Reservoir. These ratios had no apparent relationship to seston, temperatures, or algal populations.

CLADOCERA

As is usual in limnetic plankton communities, the cladoceran populations were more varied than the copepod populations, and six species were found which covered a wide range of numerical abundance.

Bosmina longirostris Müller was found in seven lakes, being absent only from Bear Lake. Negligible numbers were found in Copeland and Brainard lakes, where the mean annual population for this species was only 0.1 individual per liter. Population curves for the other five lakes are shown in Figure 28. (Data in Figures 28 to 30 include both immature and mature individuals.) In all of these lakes the populations developed rather late in the season. In Manchester Lake peaks were reached in August and October, the latter amounting to 39 individuals per liter. Grand Lake also had a dicyclic curve, with the first maximum of 30 per liter on July 2 and a second of 16 per liter on October 27, the date of the last field trip of the year. Beaver, Estes, and Summit lakes all had monocyclic curves. The population for Beaver Reservoir increased slowly to 13 individuals per liter on July 27, and thereafter decreased to a minimum toward the end of October. *B. longirostris* was collected from Lake Estes only on September 13 (10 per liter) and October 5 (5 per liter). Summit Lake had a very large population, which developed rapidly during August to a peak of 83 specimens per liter on August 30 followed by a decrease to 20 per liter on September 30. Although *B. longirostris* is usually con-

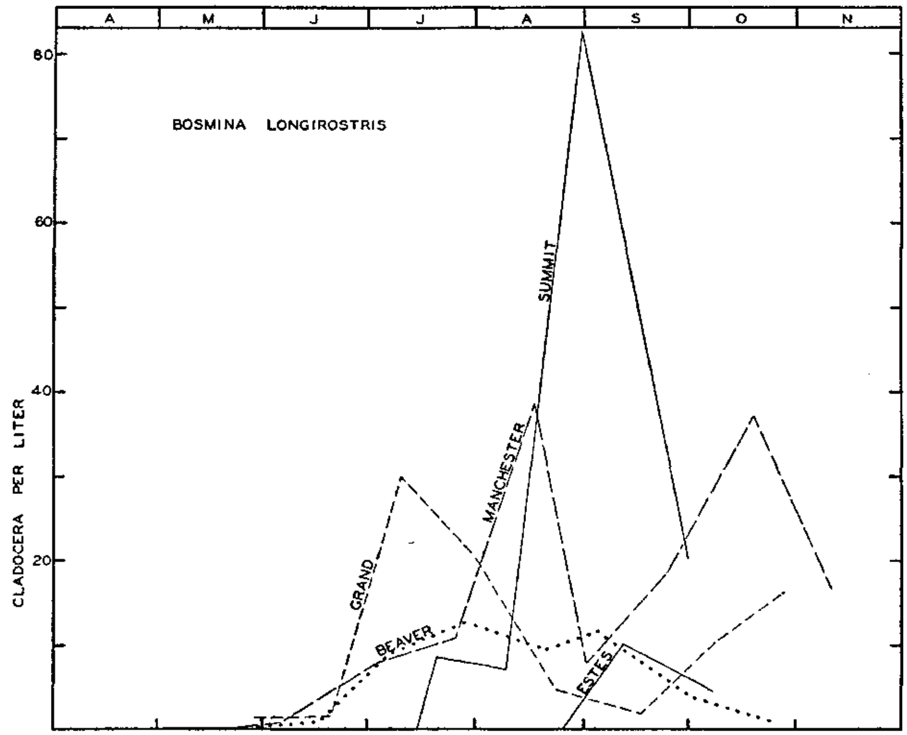

FIG. 28. Open-season abundance of *Bosmina longirostris* in five Colorado mountain lakes Each point on the curves represents an average of two to six evenly spaced samples taken between the surface and bottom on a particular date.

sidered a spring and early summer species, these Colorado results seem to indicate late summer and early autumn tendencies.

Ceriodaphnia reticulata (Jurine) was found in very small numbers in Estes and Grand lakes, and its periodicity could not be ascertained.

Chydorus sphaericus (Müller) occurred in similar small numbers in Estes, Copeland, Bear, and Brainard lakes.

Daphnia longispina (Müller), the most common of all plankton cladocerans, was found in Copeland, Grand, Manchester, Beaver, and Bear lakes. Three years after actual field work for the present investigation was carried out, however, it was found to have become abundant also in Summit Lake (Pennak, 1955). Most writers consider this species to have two or three population maxima during the year. In view of the highly variable results found for a group of plains lakes and five of the mountain lakes (Fig. 29), it might be much more accurate to characterize

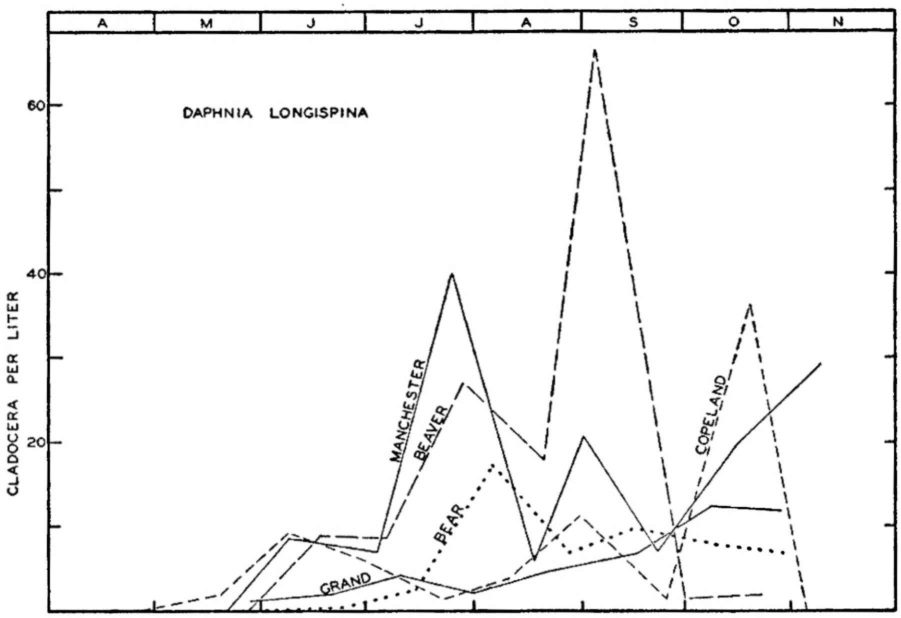

FIG. 29. Open-season abundance of *Daphnia longispina* in five Colorado mountain lakes. Each point on the curves represents an average of two to six evenly spaced samples taken between the surface and bottom on a particular date.

D. longispina as a species of "irregular" occurrence. Manchester Lake exhibited what were probably three maxima, with peaks in July, late August, and November; the most dense population was 40 per liter on July 24. Beaver Reservoir had the greatest density, 67 per liter, on September 3, with a suggestion of a second small peak in late July. Copeland Lake had an irregular population with a maximum of 36 per liter on October 16, after which time the population declined rapidly. Bear Lake had a small midseason maximum of 17 per liter on August 4, but in Grand Lake the population built up very slowly to 13 per liter on October 6. Ziegelmeier (1940), working on six small ponds, found that *D. longispina* had from none to four low maxima during the summer months, depending on the particular pond.

Daphnia pulex (DeGeer) is also an extremely common plankton cladoceran, but of the group of eight mountain lakes, it was found only in Estes and Brainard. A single pronounced peak population of 58 per liter was found in the former on September 13; a very few individuals were found in the latter on August 16. This is another species having a peculiar, intermittent occurrence in Summit Lake. Although it could not be found during the regular period of field work in 1950–1951, it was abundant in 1940, and a few specimens were found in 1954.

Diaphanosoma brachyurum (Liéven) is a common limnetic species, but it was found only in Copeland Lake in very small numbers.

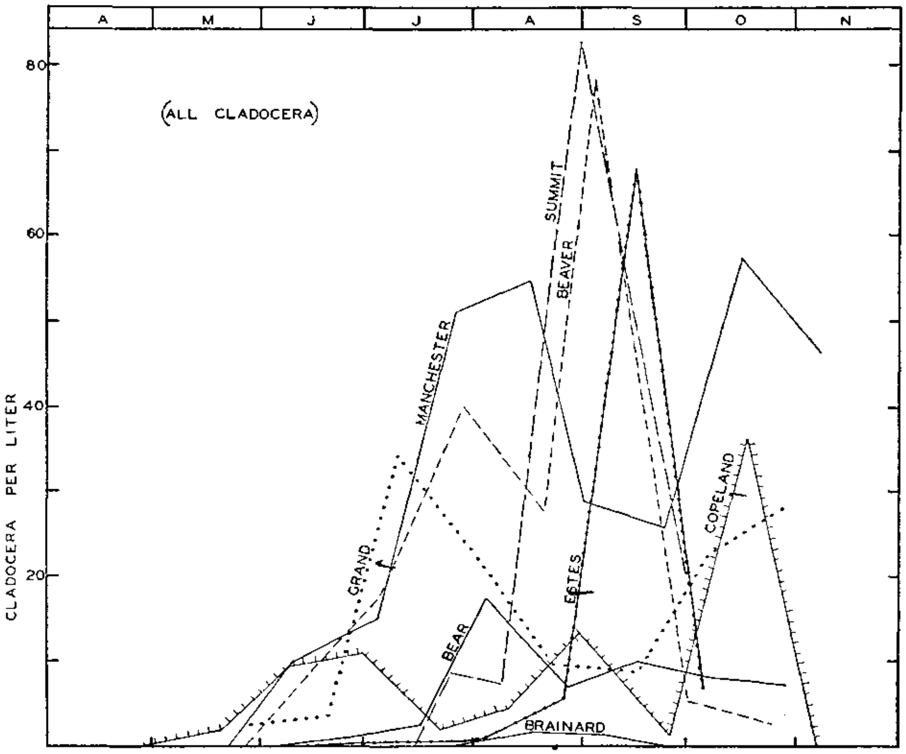

FIG. 30. Open-season abundance of all cladocerans in eight Colorado mountain lakes. Each point on the curves represents an average of two to six evenly spaced samples taken between the surface and bottom on a particular date.

Like the curves for total rotifer populations, those for total cladoceran populations (Fig. 30) are irregular and somewhat confusing, and there is no evidence whatever for the "typical" spring and autumn maxima said to be characteristic of lakes of the temperate zone. All eight lakes were similar in that the cladoceran populations were negligible early in the open season and developed relatively late, maxima being attained sometime between July and October. Much of the irregularity of these curves is produced by the staggered or cumulative pulses of the several species occurring in each lake. Copeland Lake had three maxima, but only the last of these, in October, was well defined. Both Grand and Manchester lakes had two maxima. Bear, Estes, Beaver, and Summit lakes all had a single maximum, the one for Bear Lake being poorly defined. Brainard Lake had only a negligible summer cladoceran population.

Mean annual cladoceran populations, as shown in Table IX, were all small — considerably smaller than similar populations in most plains lakes. The largest

TABLE IX. *Mean annual populations of the various species of plankton Cladocera in eight Colorado mountain lakes. A dash signifies less than 0.1 individual per liter*

Lake	*Bosmina longirostris*	*Cerio-daphnia reticulata*	*Chydorus sphaericus*	*Daphnia longispina*	*Daphnia pulex*	*Diapha-nosoma brachyurum*
Estes	2.2	0.1	—		4.0	
Copeland	0.1		0.1	4.2		0.3
Grand	9.7	—		6.2		
Manchester	11.2			11.7		
Beaver	3.1			8.4		
Bear			0.2	4.9		
Brainard	0.1		0.1		0.1	
Summit	15.0					

single population was that for *Bosmina longirostris*, only 15.0 per liter, in Summit Lake. The same species averaged 11.2 per liter for Manchester Lake and 9.7 per liter for Grand Lake. *Daphnia longispina* was most abundant in Manchester (11.7 per liter), and second most abundant in Beaver Reservoir (8.4 per liter). Table IX emphasizes the simple species composition for these lakes. Only one or two species clearly dominated the cladoceran plankton. Third and fourth species, when present, occurred in very small numbers.

MEAN ANNUAL STANDING CROP

Mean annual standing crops of zooplankton are summarized in Table X for both mountain and plains lakes. Theoretical means for the former were derived in the same fashion as those for the phytoplankton. Presumably these mean values undergo considerable variation from year to year within the same lake, just as is true for the phytoplankton. Such variations have been adequately demonstrated by several workers investigating the plankton of Lake Erie, but little reliable year-to-year quantitative information has been gathered for small lakes. Nevertheless, an important paper by Tonolli (1954) emphasizes a surprising year-to-year constancy in the entomostracan populations of a group of tarns in the Italian Alps.

Since rotifer populations in the mountain lakes were generally lower than those in the plains lakes, it is indeed anomalous to find the very large population of 594 per liter in Manchester Lake, in the montane zone. This density was exceeded only by that for Gaynor Lake, with 774 per liter, in the plains zone. Average figures, however, were 345 per liter for the plains lakes and 144 per liter for the foothills, montane, and alpine lakes.

With the exception of Manchester Lake, all of the high-altitude lakes had lower copepod populations than any of the plains lakes, and even when the exceptionally dense population in Gaynor Lake is omitted from consideration the five plains

TABLE X. *Mean annual standing crop of zooplankton in 15 northern Colorado lakes. Data for the first seven lakes in this list are from Pennak (1949). Zooplankton is expressed as organisms per liter; a dash signifies less than 0.5 organism per liter*

Lake	Altitudinal zone	Rotatoria	Copepoda	Cladocera	"Protozoa"
Baseline.........	Plains	479	45	58	
Hayden's........	“	158	43	73	
Allens...........	“	169	94	16	
Beasley..........	“	324	137	59	
Boulder..........	“	163	74	67	
Gaynor..........	“	774	602	60	
Kossler..........	Foothills	30	20	2	
Estes............	“	58	6	6	2
Copeland........	Montane	165	14	5	1
Grand...........	“	93	18	16	82
Manchester......	“	594	98	23	888
Beaver..........	“	152	35	12	81
Bear............	“	173	20	5	—
Brainard.........	“	2	3	—	—
Summit..........	Alpine	24	8	15	2

lakes averaged 79 copepods per liter as compared with only 25 per liter for the nine mountain lakes.

Perhaps the most reliable criterion of a basic plankton difference between the plains and mountain lakes is the cladoceran population. Although Manchester Lake had 23 per liter, all of the other mountain lakes had very sparse populations. Averages were 56 per liter for the plains lakes and 9 for the foothills, montane, and alpine lakes.

Five of the high lakes had only negligible numbers of protozoans in the plankton, but the enormous pulses of *Ceratium* in Manchester Lake were chiefly responsible for a mean annual population of 888 individuals per liter in that body of water.

In general terms, it thus appears that an "average" mountain lake has about 20 to 35 per cent as many zooplankters (grazers) as an "average" plains lake. This ratio is in contrast with that of the phytoplankters, since an "average" mountain lake has about 30 to 80 per cent as many algal cells as an "average" plains lake.

Considering the mountain lake plankton picture as a whole, as shown in Tables VII to X, the only really sound generalization that can be drawn is the fact that both Brainard and Summit lakes had exceptionally poor populations. In a sense, both of these bodies of water, in the alpine and high montane zones, are close to the popular conception of a "mountain lake". Their basins and shorelines are largely composed of gravel and boulders, their summer maximum temperatures are low, there is little (Brainard) or no (Summit) growth of shrubs and trees around the immediate periphery, their ice-free season is very short, and their supply of plant nutrients is very low. On the other hand, these characteristics are also applicable to a greater or lesser degree to the seven foothills and other montane lakes.

Although there is a considerable difference in many ecological conditions between the lowest foothills lake on the one hand and the highest alpine lake on the other, these conditions do not form graded series through all nine of these lakes, but many factors (such as size, depth, and nutrients) vary in a heterogeneous fashion. This irregularity in the relative effectiveness and intensity of ecological factors is probably in large measure responsible for the lack of correlation between plankton and altitude *per se*.

Some Plankton Correlations

In quantitative plankton work of all kinds, the investigator usually has the impulse to look for numerical correlations between the density of algae on the one hand and the density of zooplankton grazers (rotifers, copepods, cladocerans) on the other. Often, by inference or otherwise, the development of a large population of algae is presumed to act as an abundant food source which is responsible for a marked increase in the grazer population. It is further supposed that when the algae decrease (either by grazing or otherwise) there is often insufficient food to support the existing zooplankton population level and that the latter therefore have a slower rate of feeding and reproduction, which is soon responsible for a marked decrease in numbers of individuals.

This concept has been discussed by the present writer (Pennak, 1946) at some length, and by detailed statistical analysis it was shown (1) that there was no *momentary* correlation between phytoplankton populations and zooplankton grazers, (2) that low to medium phytoplankton populations may support populations of grazers which range from very low to dense, (3) that dense phytoplankton populations are not necessarily associated with dense zooplankton, and (4) that there are seldom obvious numerical relationships between pulses of zooplankton and pulses of algae. A statistical analysis of the data in the present paper supports these contentions, and even a superficial examination of Tables VII to X and Figures 22 to 30 will corroborate them. As pointed out in the author's 1946 and 1949 papers, there is increasing evidence that the grazers in natural limnetic plankton communities rely heavily on fine particulate detritus and bacteria for food rather than on intact algal cells and that these materials seldom appear to constitute a serious limiting factor. This contention is supported by the work of Järnefelt (1940). Anyone who has counted plankton samples prepared with a Foerst centrifuge is well aware of the preponderance of microscopic organic debris and detritus (tripton) in them. At this point it seems pertinent to emphasize caution in translating to natural environments the results obtained by feeding laboratory entomostracan populations with pure cultures of algae.

A few authors have discussed probable direct numerical relationships between plankton entomostraca and the abundance of diatoms. Marine investigators, especially, have attempted to show reduction of diatom populations by the grazing activities of large copepods, notably Harvey (1937), Fleming (1939), and Gauld (1950). The latter admits, however, that other factors, in addition to grazing, are operative. A few other marine investigators maintain that this "grazing effect" is unimportant (Fuller and Clarke, 1936; Fuller, 1937; Riley, 1941). In the opinion of the present writer, speculation about a relationship between diatoms and entomostraca in *fresh waters* is fruitless for the very obvious reason that the usual plankton diatom cells and colonies (*Asterionella*, *Synedra*, *Melosira*, *Fragilaria*, and so on) are often too large to be ingested intact by cladocerans and the small calanoid and cyclopoid copepods! Certainly this fact is invariably true of the nauplius stages. Lund (1950), incidentally, found that zooplankton grazing on *Asterionella* was "negligible" in fresh water. If there is any grazing effect or direct numerical relationship between fresh-water zooplankton and phytoplankton, it is in all likelihood dependent upon the Myxophyceae and Chlorophyceae fractions of the photosynthetic phytoplankton.

In spite of the fact that the plankton work on Colorado lakes shows no *momentary* phytoplankton-zooplankton correlations, there remains one further important aspect of this general problem to be discussed — namely, the question of probable correlations between the elements of the mean annual phytoplankton and the elements of the mean annual zooplankton for the 15 lakes for which data have been collected. In other words, is there a significant correlation between numbers of Myxophyceae cells and zooplankton, and the like, *on a mean annual basis?* Or, to put it another way, do lakes with large (or small) Myxophyceae populations have large (or small) zooplankton populations, and so on? A considerable variety of

TABLE XI. *Some correlation coefficients* (r) *between the mean annual standing crop of plankton, seston, and bound carbon dioxide for 14 northern Colorado lakes of the plains and mountains. Significance of* r *has been derived from the "t" test in each case*

	Correlation coefficient, *r*		
	Mean annual Myxophyceae population	Mean annual seston	Mean annual bound carbon dioxide
Rotatoria......	.30 (not significant)	.18 (not significant)	.56 (probably not significant)
Copepoda......	.42 (not significant)	.51 (not significant)	.45 (not significant)
Cladocera......	.52 (not significant)	.64 (significant)	.95 (very significant)
total Algae.....	.70 (significant)	.77 (significant)	.36 (not significant)
bound CO_2.....	.62 (probably significant)	.41 (not significant)	
seston.........	.82 (significant)		

these correlation coefficients have therefore been calculated, as shown in Table XI, in an attempt to answer this question. In order to obtain more significant results, the extremely high seston, bound carbon dioxide, and Myxophyceae population for Gaynor Lake have not been included in Table XI.

The usual correlation coefficient, *r*, has been calculated and the "t" test applied in establishing the relative significance of *r*. The use of *r* for biological correlations has been discouraged by some biometricians, but it appears to be the least unreliable mathematical treatment for the available data in the present study. The first column of *r* values in Table XI shows the relationships between the mean annual Myxophyceae populations and the various components of the plankton, as well as bound carbon dioxide. Among the zooplankters, it is seen that neither rotifers, copepods, nor cladocerans have a significant numerical relationship to numbers of Myxophyceae cells. Since the blue-greens constitute the most abundant and readily available algal food source for zooplankters, the lack of correlation may be taken as at least partial evidence for (1) the fact that the phytoplankton, as a food element, is not a limiting factor and (2) the fact that tripton is an important (or chief) food.

In spite of the fact that several of the lakes had a dominant diatom flora, it is important to note that there was a significant relationship ($r = .70$) between the Myxophyceae and the total algae. To be sure, "total algae" is a very rough measure of the total standing crop of algae since it includes a mere summation of Myxophyceae, Bacillarieae, and Chlorophyceae. On the other hand, these 14 lakes had such a striking similarity in the genera and species make-up of their phytoplankton that the usage of "total algae" *for this particular group of lakes* does not seem altogether unreasonable.

Studies on lakes in the midwestern United States and in Europe have emphasized a general relationship between the Myxophyceae and hardness of water. Those lakes, for example, having a great abundance of blue-greens and true summer "nuisance blooms" are almost invariably "hard" to "very hard" lakes. Over the entire range of 14 "soft" to "hard" lakes in northern Colorado, however, there was a questionable correlation ($r = .62$).

On the other hand, the correlation coefficient between Myxophyceae and seston was found to be quite significant ($r = .82$). This correlation occurred in spite of numerically predominant diatom populations in several of the lakes and is perhaps indicative of the relatively small percentage of organic matter in a diatom cell as compared with a blue-green cell.

Mean annual seston is often considered one of the most reliable indicators of productivity on a standing crop basis. Certainly it is subject to far less seasonal fluctuation than any single element of the plankton. In the third column of Table XI *r* values are calculated for mean annual seston, plankton, and bound carbon dioxide. It is rather striking to note the complete lack of correlation between rotifers and seston, the lowest value ($r = .18$) being found between these two elements. Copepods similarly had no significant correlation with seston, but cladocerans showed a significant correlation ($r = .64$). Perhaps this situation is associated with the differing food habits of cladocerans and copepods. The former are more or less random filterers which utilize a wide variety of bacteria and detritus particles. Cyclopoid copepods, on the other hand, are more specific in their habits and have the mouth parts modified for seizing and grasping particles of a larger size. It is logical to presuppose the significant correlation ($r = .77$) between algae and seston, since the former, both living and dead, contribute significantly to the latter. Bound carbon dioxide, on the other hand, had no significant correlation with seston throughout the range of conditions found. A similar lack of correlation was found for the soft-water lakes of northern Wisconsin by Birge and Juday (1934). In the high carbonate lake areas of the midwest, however, there often does seem to be a correlation between these two variables.

The last column in Table XI shows some r values for bound carbon dioxide and elements of the plankton. Limnological literature contains frequent statements and implications about the relatively dense plankton produced by hard-water lakes, but, while such statements may be generally valid, it does not necessarily follow that medium-hard and soft lakes necessarily contain small plankton populations. This point is shown especially for the Colorado lakes by the lack of correlation between bound carbon dioxide on the one hand and rotifers, copepods, and total algae on the other. Cladocerans and bound carbon dioxide, however, showed an exceptionally high correlation coefficient ($r = .95$).

As a whole, then, Table XI appears to emphasize the following fundamental close relationships and interdependence: algae (especially blue-greens) — seston — cladocerans — bound carbon dioxide.

Most of the foregoing data have re-emphasized the variability of plankton population composition in small Colorado lakes seasonally within a single body of water and from one lake to another. As compared with conditions in large lakes, it seems logical to suspect that such irregularity is associated with the less stable and less predictable ecological conditions characteristic of small water masses. Unquestionably, the explanation of complicated plankton interrelationships lies in multiple-factor analyses that can be solved only through carefully controlled laboratory studies in conjunction with field studies. The past few years, especially, have indicated the probable fundamental significance of such obscure factors as species antagonism, competition, and growth-promoting and growth-inhibiting substances (Ryther, 1954; Lefèvre, Jakob, and Nisbet, 1951; Lucas, 1947; Pratt and Fong, 1944; Rice, 1954). These new concepts must of course be added to the influences exerted by light, temperature, depth, water circulation, turbidity, size and activity of the bacterial population, and variations in the quality and quantity of numerous dissolved nutrients, especially phosphates, nitrates, manganese, and iron compounds.

DISSOLVED AND PARTICULATE MATERIALS IN LAKE WATERS

Most of the previous discussion is centered around phytoplankton and zooplankton, and the fact that these living organisms represent only a small fraction of the total mass of material suspended (and dissolved) in lake waters is often forgotten. Figure 31 serves to emphasize some of these gravimetric relationships of phytoplankton and zooplankton biomass, tripton (suspended dead materials), and dissolved substances. The data represent average conditions for 14 northern Colorado plains and mountain lakes ("alkalitrophic" Gaynor Lake omitted), but this diagram would hold true, in general, for any "typical" body of water. When individual bodies of water are considered, the relative areas of the various segments of the circle shown in Figure 31 are subject to considerable variation. A highly alkaline lake, for example, would have a much larger relative area for "dissolved salts" (perhaps 90 per cent), and certain alpine lakes would have a much smaller relative area for "dissolved salts" (perhaps 30 per cent). Similar variations apply for the other segments.

Dissolved salts, dissolved organic matter, and seston are easily and accurately determined for lake waters, but the relative proportions of zooplankton and phytoplankton are very difficult to establish, since there is no quantitative laboratory or field method of separating these two kinds of organisms. A few investigators have used a number 10 net to separate zooplankton from tripton and phytoplankton, but this method is uncertain because it allows many rotifers and nauplii to escape and holds back a varying amount of phytoplankton and tripton, depending on the particular species present and their abundance.

There is, furthermore, no known method of separating the living plankton organisms from the (usually) much larger bulk of tripton. The latter includes all sizes and aggregations of organized and unorganized particles in suspension, from dead macroplankters to finely divided colloids. Estimates of living plankters: tripton range from about 1:20 to 1:0.25.

Nevertheless, by various combinations of nets, centrifugation, weighing, displacement, calculation of volumes of the various plankton species present, and by inspection of plankton samples under the microscope, it has been possible for a few investigators to arrive at tentative gravimetric values for zooplankton, phytoplankton, and tripton. Birge and Juday (1934) estimated that 50 per cent of the seston of Trout Lake consisted of dead material (tripton). This estimate was based on uncorrected Foerst-centrifuge determinations and, if the 25 per cent centrifuge correction factor is taken into consideration (Pennak, 1949), should

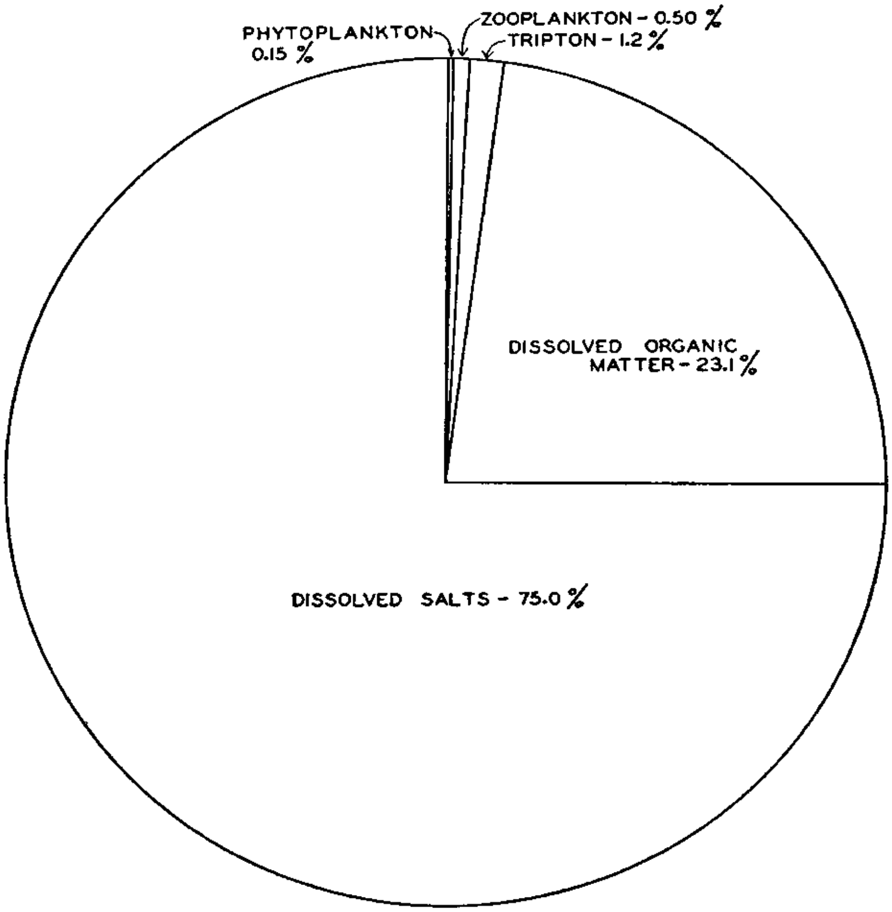

FIG. 31. Percentage composition of dissolved materials, tripton, and plankton components in the waters of a "typical" lake.

be revised to about 60 per cent. In the present investigation it is estimated that 65 per cent of the seston consists of tripton. This figure is derived from rough measurements of the size and volume of many plankton organisms as compared with the total seston determinations. According to Grim (1950, discussed above), a large percentage of phytoplankton cells in any population are moribund and non-functional, or dead, and it is therefore extremely difficult to estimate the necessary correction factor, since such cells, strictly speaking, are properly included with the tripton fraction of seston determinations. The present author took this factor also into consideration in arriving at the 65 per cent fraction.

A wide variety of phytoplankton:zooplankton ratios (dry weight) have been suggested in the literature. Riley (1940) found a P:Z ratio of 1:0.22 for Linsley Pond, Connecticut. Birge and Juday (1934) suggest a ratio of 1:1.20 for Trout Lake and 1:0.50 for Lake Mendota (1922). In a later paper (1940), Juday suggests that zooplankton accounted for 6 per cent and phytoplankton for 94 per cent of the "total plankton". Undoubtedly, however, this was a tabulating error, since this author almost invariably used "total plankton" as the equivalent of "centrifuge plankton" and "seston". Presumably he meant that the zooplankton for Lake Mendota amounted to 6 per cent of the centrifuge plankton, with a P:Z ratio in the general magnitude of 1:0.70 to 1:0.30. Ruttner (1937) suggests ratios of 1:2.00 to 1:15.00 for European alpine lakes, and Rawson (1953b) comments, "While the data are scanty, it seems probable that in alpine and other oligotrophic lakes the zooplankton is often greatly in excess of the phytoplankton, while in eutrophic lakes the reverse is usually true."

The calculated phytoplankton:zooplankton ratios for the 15 Colorado lakes are given in Table XII, where, contrary to the concept previously held by the author, the gravimetric (or volumetric) determinations show that the zooplankton biomass was larger than the phytoplankton biomass in 11 of the 15 lakes. In the four lakes having a greater amount of phytoplankton, the P:Z ratios varied from 1:0.36 for Beaver Reservoir to 1:0.83 for Gaynor Lake. Two of these four lakes are in the plains zone, one in the foothills, and one in the montane zone. The greatest preponderance of zooplankton was found in Allens Lake (plains zone) where the

TABLE XII. *Mean annual phytoplankton:zooplankton ratios (gravimetric) for 15 northern Colorado lakes*

Lake	Altitudinal zone	Ratio of phytoplankton to zooplankton, (P:Z)
Baseline	Plains	1:8.62
Hayden's	"	1:7.81
Allens	"	1:9.90
Beasley	"	1:4.08
Boulder	"	1:0.55
Gaynor	"	1:0.83
Kossler	Foothills	1:1.76
Estes	"	1:0.78
Copeland	Montane	1:2.08
Grand	"	1:2.74
Manchester	"	1:1.66
Beaver	"	1:0.36
Bear	"	1:5.10
Brainard	"	1:1.57
Summit	Alpine	1:2.00

P:Z ratio was 1:9.90, and the second greatest relative zooplankton was found in Baseline Lake, where the P:Z ratio was 1:8.62. The mean P:Z ratio was 1:3.32, which was used in constructing Figure 31.

Although the P:Z range found for Colorado lakes resembles the range suggested by Ruttner (1937), there is no indication that the lakes with eutrophic tendencies necessarily showed the higher P:Z ratios, as suggested by Rawson (1953b). Brainard Lake, for example, is definitely not eutrophic, yet it had a P:Z ratio of 1:1.57; neither is Lake Estes with a ratio of 1:0.78 nor Kossler Lake with a ratio of 1:1.76. Bear Lake, on the other hand, has some eutrophic characteristics, but had a P:Z ratio of 1:5.10, and the first three lakes listed in Table XII all have certain eutrophic characteristics (Pennak, 1949), yet they had the three lowest P:Z ratios.

In view of these results, it appears that a reassessment of quantitative relationships in the trophic levels of certain aquatic communities and in the Eltonian pyramid is in order (Lindeman, 1942). In addition, it is now very apparent that the generally larger amounts of zooplankton biomass than of phytoplankton biomass is further evidence of the primary importance of tripton as a food source for rotifers, copepods, and cladocerans in natural habitats.

It should be emphasized that the derivation of P:Z biomass ratios is an uncertain procedure and fraught with errors, and the figures given in Table XII should be considered subject to an error of ±20 per cent. The bacterial populations have not been considered in this treatment of the data, but, in spite of their relatively large numbers, it is well established that their total bulk is less than 5 per cent of the algal phytoplankton.

Classification of the Mountain Lakes

Just as the majority of plains lakes do not fit clearly into either of the basic "oligotrophic" or "eutrophic" categories, it is also true that the majority of mountain lakes do not fit clearly into either of these categories, and for all practical purposes the oligotrophic-eutrophic series is of little use for these lakes.

Of the group of eight mountain lakes considered here (plus Kossler Lake, which was covered in the earlier "plains lakes" study), only two could be called truly oligotrophic. Summit Lake, with its very cold waters, maximum depth of 17.2 meters, poor plankton, and abundance of oxygen at all depths is a striking example of an oligotrophic mountain lake. In the sense of Lundbeck (1934) it embodies both "primary (edaphic) oligotrophy" (poor in nutrient salts) and "thermal oligotrophy". In the sense of Thomasson (1952) Summit Lake is a typical ultra-oligotrophic lake; and according to the criteria of Pesta (1929) it is panoligotrophic.

Grand Lake is also an oligotrophic lake, but to a less striking degree. Its oligotrophy is both "primary" and "secondary" (owing to its maximum depth of 80.8

meters). In spite of these features, however, the summer oxygen conditions tended toward eutrophy, since the bottom waters were less than 30 per cent saturated by the end of summer stagnation. It is undoubtedly true that Grand Lake is rapidly losing its oligotrophic identity. The writer has made observations on the lake since 1938, and the reversed flow of water (now from west to east for most of the year) as the result of the Big Thompson Reclamation Project, has brought about striking changes, especially since 1951. A new, large, shallow lake (Shadow Mountain Reservoir) has been constructed immediately to the southwest of Grand Lake, and from this fertile reservoir water flows into the west end of Grand Lake. Such water, being relatively warm, remains at the surface of Grand Lake for much of the year and is mostly responsible for the eutrophication tendencies of the entire water mass of Grand Lake. As emphasized in the foregoing sections, these evidences of eutrophication are the following: greatly decreasing transparency, less oxygen in the deep waters, greater algal and zooplankton populations, and higher water color.

Both Brainard and Kossler lakes are quite shallow (3.3 and 6.8 meters, respectively) but otherwise they have general oligotrophic characteristics. Both have a large inflow and outflow.

Lake Estes, though very recently formed, showed certain eutrophic (or mesotrophic) features, but fundamentally it is probably in the oligotrophic category. The bottom waters contained less than 40 per cent dissolved oxygen, the mean summer Secchi disc reading was only 1.4 meters, and the mean annual seston exceeded the seston found in seven of the other eight mountain lakes. Large numbers of diatoms and medium numbers of Myxophyceae were characteristic, but the zooplankton was relatively scanty. No rooted aquatic vegetation has appeared. It is possible that a more distinctive oligotrophic nature may be restored when the readily available nutrients in the basin (flooded range land) are leached out during the next few years. Some of the residents in the area of Lake Estes maintain that the Big Thompson River inflow becomes polluted as it traverses the village of Estes Park just above the lake, but it is the author's observation that such pollution is negligible.

Beaver and Bear lakes, in spite of their relatively low temperatures, are probably more eutrophic than oligotrophic. Both had little oxygen in the hypolimnion, but Beaver Reservoir had the greater plankton populations, greater seston, and lower transparency. Bear Lake had a sparse growth of potamogetons at the west end, but Beaver Reservoir had no rooted aquatics (presumably because of the fluctuating water level).

Copeland Lake is small, shallow (2.4 meters), and pondlike, and does not fit into any special category. It had low seston, high transparency, a high population of blue-green algae, a poor diatom population, a medium zooplankton, and a mat of *Chara* over most of the bottom.

In spite of its shallowness (4.5 meters), Manchester is probably more nearly eutrophic than anything else. It had a high seston, low transparency, and exceptionally high zooplankton and phytoplankton populations.

SUMMARY

Eight northern Colorado mountain lakes, exhibiting a wide variety of ecological conditions, were studied during an entire open season from early spring to late autumn. Of these lakes, the altitudes range from 2277 to 3884 meters; areas, from 1.5 to 205.2 hectares; maximum depths, from 2.4 to 80.8 meters; total residues, from 17.38 to 102.74 mg. per liter. Five lakes are artificial; three are natural.

Maximum summer water temperatures were correlated with altitude. The surface waters of the lowest lake in the foothills zone reached 21.6°; Summit Lake reached only 10.0°. The three shallowest lakes (Brainard, Copeland, and Manchester) were essentially homothermous throughout the open season, but the other five lakes showed varying degrees of temperature stratification. Temporary "surface thermoclines" were common.

Mean Secchi disc readings ranged from 1.4 to 4.1 meters, and calculated compensation points ranged from 3.0 to 7.4 meters.

All chemical, seston, and plankton determinations were made from quantitative samples taken at two to six evenly spaced depths between surface and bottom, depending on the depth of the lake at the regular deep-water sampling station.

The three shallowest lakes and Summit Lake (the highest body of water, with a maximum depth of 17.2 meters) showed no appreciable oxygen stratification. Estes, Beaver, Grand (80.8 meters), and Bear lakes all showed hypolimnetic oxygen depletion in varying degrees. Bear Lake had complete oxygen exhaustion in the bottom waters in August and September.

Grand, Bear, and Beaver lakes showed midsummer accumulations of free carbon dioxide in the bottom waters which reached 32.2, 17.5, and 10.1 ppm., respectively. Bottom waters of the other five lakes and the surface waters of all eight lakes seldom contained more than 3.0 ppm. of free carbon dioxide.

Bound carbon dioxide exhibited no significant stratification. Determinations ranged from 3.2 to 32.0 ppm.

The great majority of hydrogen-ion determinations ranged between pH 6.5 and 7.5. In the stratified lakes a few readings as low as pH 6.2 were found in the bottom waters.

Subsurface and mid-depth samples showed the highest seston. None of the lakes showed "typical" spring and autumn maxima. Theoretical mean annual seston ranged from 0.54 mg. per liter for Grand Lake to 2.08 mg. per liter for Beaver Reservoir (both in the montane zone). There was no correlation between seston and altitude.

As compared with northern Colorado lakes of the plains zone, the following were the chief distinguishing chemical and physical features of the foothills, montane, and alpine lakes: lower temperatures, shorter open seasons, higher Secchi disc readings, lower bound carbon dioxide, less alkaline waters, lower seston, and smaller amounts of dissolved materials.

Phytoplankton samples were prepared with the Foerst centrifuge. They were dominated by Myxophyceae and Bacillarieae, and the generic composition of the mountain lake phytoplankton was remarkably similar to that of the plains lakes. Most of the Bacillarieae population consisted of *Asterionella*, *Melosira*, *Fragilaria*, and *Synedra*. The seasonal pattern of diatom populations varied widely among the eight lakes, with three, two, one, or no pulses. Mean annual diatom populations ranged from 22,700 to 7,426,000 cells per liter, the latter figure being exceptionally high for mountain lakes.

Myxophyceae populations consisted mostly of *Chroococcus* and were also highly variable in the seasonal occurrence of pulses. Only two lakes showed "typical" late summer blue-green pulses. Mean annual populations ranged from 23,200 to 2,558,800 cells per liter, the latter figure being exceptionally high for mountain lakes.

The eight lakes differed widely in the relative density of their diatom and blue-green phytoplankton. Bacillarieae: Myxophyceae ratios ranged from 0.02 (Copeland Lake) to 94.00 (Beaver Reservoir). In spite of the wide range in phytoplankton densities, a "typical" mountain lake may be said to have only 25 per cent as much blue-green phytoplankton and 89 per cent as much diatom phytoplankton as a "typical" plains lake.

Small populations of Chlorophyceae were found. Manchester Lake had the most dense population, with an annual mean of 154,000 cells per liter.

Twenty-six plankton species of rotifers were identified, of which the following were most abundant and of general occurrence: *Conochilus unicornis*, *Keratella cochlearis*, and *Polyarthra vulgaris*. The relative abundance and seasonal maxima of these and other species were completely inconsistent from one lake to another. With respect to total rotifer populations, only two lakes (Copeland and Beaver) showed the so-called "typical" spring and autumn pulses. Mean annual rotifer populations ranged from 2 per liter (Brainard Lake) to 594 per liter (Manchester Lake). In general, the mountain lakes contained rotifer populations which were only 42 per cent as dense as those found for Colorado plains lakes in a previous study.

Cyclops bicuspidatus was the only common copepod, and it occurred in all lakes except Copeland. Populations were generally low in all lakes in the autumn, but varied irregularly during spring and summer. Mean annual populations ranged from 3 individuals per liter (Brainard Lake) to 98 per liter (Manchester Lake). On the average, the mountain lakes contained copepod populations that were only 15 per cent as dense as those in typical plains lakes.

Bosmina longirostris and *Daphnia longispina* were the only cladocerans of general occurrence and the only abundant forms. Numbers were generally low in spring and variable in summer and autumn. Some lakes had three pulses for one of these species; others had two, one, or no special pulses. Mean annual cladoceran densities ranged from less than 1 individual per liter (Brainard Lake) to 23 per liter (Manchester Lake). Mountain lakes averaged only 16 per cent as many cladocerans as Colorado plains lakes.

By use of mean annual standing crops of Rotatoria, Copepoda, Cladocera, "total algae", seston, and mean annual bound carbon dioxide for five plains, two foothills, six montane lakes, and one alpine lake, correlation coefficients (*r*) were calculated for these data against mean annual Myxophyceae, seston, and bound carbon dioxide. By means of the "t" test, the following pairs of variables were found to have significant correlation coefficients: "total algae" and Myxophyceae, bound carbon dioxide and Myxophyceae, Cladocera and seston, "total algae" and seston, and Cladocera and bound carbon dioxide.

By measuring the volumes of many plankton organisms and by the use of appropriate correction factors, mean annual gravimetric phytoplankton:zooplankton ratios (P:Z ratios) were calculated for 15 plains and mountain lakes. These ratios ranged from 1:0.36 (Beaver Reservoir, in the montane zone) to 1:9.90 (for a plains reservoir); the average P:Z ratio for all 15 lakes was 1:3.32. Contrary to the prevailing opinion, it thus appears that the phytoplankton biomass is usually much smaller than the zooplankton biomass. This generalization is accepted as strong evidence for the fact that tripton is an essential and most important portion of the diet of zooplankton grazers.

Total dissolved and particulate matter in the waters of a typical northern Colorado lake are apportioned as follows: dissolved salts 75.0 per cent, dissolved organic matter 23.1 per cent, tripton 1.2 per cent, zooplankton 0.50 per cent, and phytoplankton 0.15 per cent.

The classification of the eight mountain lakes is evaluated and compared. Summit Lake, the highest in altitude, is clearly an oligotrophic (or ultraoligotrophic) lake. Grand Lake was formerly oligotrophic but is now rapidly developing eutrophic features. Brainard Lake is very shallow but has certain oligotrophic features. Lake Estes, though only about six years old, shows some eutrophic features. Beaver and Bear lakes are eutrophic. Copeland Lake is pondlike and does not fit into any special category, while Manchester Lake is also shallow but more eutrophic. P:Z ratios showed no correlation with the degree of eutrophy.

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