# ORGANIC CONTENT OF LAKE WATER

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## INTRODUCTION

For many years the Wisconsin Geological and Natural History Survey has been engaged in studies on the inland lakes of the State. These have received aid from the University of Wisconsin and the United States Bureau of Fisheries, whose assistance is gratefully acknowledged.

This paper brings together the results of several investigations on the quantity and kinds of organic matter found in lake water. In these, as in earlier studies, by far the largest amount of attention has been given to Lake Mendota, on whose shore the University of Wisconsin is situated. The study has been extended to other lakes, in as great number and variety of type as practicable, in order to ascertain how far the conditions found in Mendota are present elsewhere.

The present paper reports results from 14 waters other than Lake Mendota, including 12 lakes and 2 rivers. It shows the total amount of organic matter contained in the water and gives some idea of the nature of the organic compounds. Thus it furnishes the beginnings of an inventory of the primary food supply of the inland lakes. The results from the lakes other than Mendota are such as to show that this may be regarded as a typical Wisconsin lake.

## I. DATA

The data of this paper came from five sources:

1. An elaborate study of the quantity and chemical composition of the plankton of Lake Mendota and the other Madison lakes. This was made by Birge and Juday (1922) from 1911 to 1917. The results of this work are used in this paper to furnish data regarding the average amount of plankton from Lake Mendota and also to give its composition. This paper is cited as the "plankton report."

2. A study of the quantity and the forms of nitrogen found in lake waters, made primarily by Dr. B. P. Domogalla (Domogalla, Juday, and Peterson, 1925). This study was based on the same samples as those employed in the present paper; it is the source of the nitrogen determinations of plankton and residues given in the present paper. It is cited as the "nitrogen report."

3. A more complete study of the forms of nitrogen found in a small number of these waters, made primarily by Prof. W. H. Peterson (Peterson, Fred, and Domogalla, 1925). This is used only in some of the final conclusions of the present paper.

4. A determination of the organic carbon contained in some of the residues originally prepared for the work of Doctor Domogalla. These results are published for the first time in the present paper. The determinations were made by Dr. C. R. Wise, of the department of chemistry, University of Wisconsin.

5. Determinations of the ether extract made by Doctor Domogalla on a number of the same samples. These also are reported here for the first time.

### DISSOLVED ORGANIC NITROGEN AND ORGANIC CARBON

The figures for organic nitrogen in this section of the paper are taken from the nitrogen report (Domogalla, Juday, and Peterson, 1925), for which all of the samples originally were secured.

The methods of collecting and handling the samples of lake water are reported fully in this paper (p. 270); they contained from 50 liters to 525 liters of water. The plankton was extracted by a Sharples centrifuge running at a speed of 40,000 revolutions per minute, which removed the plankton, including about 70 per cent of the bacteria. The centrifuged water was evaporated in a copper vacuum pan at a temperature of about 60° C. The plankton nitrogen was determined from the dried material extracted by the centrifuge, and six forms of nitrogen were regularly determined from the dry residues resulting from evaporation. For the inorganic nitrogen these were free ammonia, nitrate, and nitrite; and for the organic nitrogen there were determined the free-amino nitrogen, peptide, and nonamino nitrogen.

All of this nitrogen from the residues is called "dissolved," and the same term is applied to the organic carbon from the same source. In the use of this word the present paper follows the terminology of the nitrogen report, which considers nitrogen under two categories—plankton nitrogen and soluble nitrogen. It is not intended that inference should be made from the use of either word as to the exact condition in which organic substances, other than plankton, exist in the water. No doubt they are present in various forms, including (*a*) that part of the plankton and the organic débris that escapes the centrifuge, (*b*) colloids of different kinds, and (*c*) true solutions. These necessarily are treated together as they are mingled in the dry residues, and at present there is no way of distinguishing them. Probably by far the greater portion of the "soluble nitrogen" or the "dissolved carbon" is dissolved only as egg albumen or starch may be said to be dissolved in water.

The organic carbon was determined by Doctor Wise, who had for his examination 31 specimens of dry residues; 14 of these were from Lake Mendota, 14 from 12 other lakes, and 3 from 2 rivers. They represented the larger samples prepared by Doctor Domogalla, the material of which had not been used up in the study of the nitrogen.

The specimens for determination of organic carbon were dried carefully to constant weight, over concentrated $H_2SO_4$, in a vacuum. The temperature was kept at 46 to 47° by an electrically heated nichrome wire, and a pressure of 60 to 70 millimeters of mercury was maintained. Under these conditions the organic matter should not be decomposed and the water mechanically held should be dissipated. Most of the air-dry specimens lost 4 to 5 per cent in this process.

The total carbon dioxide was determined by the ordinary methods of organic combustion. The evolved (carbonate) carbon dioxide was determined by a method almost identical with that of Hillebrand (1919). Two soda-lime tubes, however, were found to be more satisfactory than one.

All determinations were made in duplicate and checked closely. Two examples are given; these are Nos. 21 and 42, each the residue from the evaporation of 100 liters of water from Lake Mendota. No. 21 came from surface water; No. 42 was a bottom sample; both were collected on July 24, 1923.

TABLE 1.—*Determination of carbon dioxide in dry residue from water of Lake Mendota*

| | No. 21 | | No. 42 | |
|---|---|---|---|---|
| | A | B | A | B |
| | *Per cent* | *Per cent* | *Per cent* | *Per cent* |
| Total $CO_2$ | 47.75 | 47.77 | 44.45 | 44.89 |
| Evolved $CO_2$ | 27.65 | 27.83 | 27.99 | 28.21 |
| Difference | 20.10 | 19.94 | 16.46 | 16.68 |

The results show 20.02 per cent of organic $CO_2$ in the surface sample and 16.57 per cent in the bottom sample, corresponding, respectively, to 5.45 and 4.53 per cent of organic carbon. The surface yielded 135 milligrams of dry residue per liter of lake water, and the bottom 129.2 milligrams. The organic carbon, therefore, was 7.36 milligrams per liter in surface water and 5.85 milligrams in water at 20 meters. Already there had been found 0.407 milligram per liter of soluble organic nitrogen in the surface sample and 0.404 milligram in the water from the bottom. These figures are reached by adding the amounts of nitrogen given (nitrogen report, p. 274) under the heads of free-amino, peptide, and nonamino nitrogen.

The following table gives the amounts of dissolved organic nitrogen and carbon found in the several waters:

TABLE 2.—*Dissolved organic nitrogen and carbon in lake water*

[In milligrams per liter of lake water]

| | Depth, in meters | Date | Residue | N | C | Ratio, N:C |
|---|---|---|---|---|---|---|
| LAKES | | | | | | |
| Mendota | 0 | Oct. 18, 1922 | 152.0 | 0.438 | 4.00 | 1: 9.1 |
| Do | 0 | Dec. 5, 1922 | 176.2 | .484 | 7.95 | 1:16.4 |
| Do | 0 | Feb. 28, 1923 | 183.0 | .554 | 6.31 | 1:11.4 |
| Do | 0 | July 24, 1923 | 135.0 | .407 | 7.36 | 1:18.1 |
| Do | 0 | Sept. 21, 1923 | 129.1 | .372 | 4.48 | 1:12.1 |
| Do | 0 | Oct. 24, 1923 | 126.3 | .289 | 5.96 | 1:20.6 |
| Do | 0 | Apr. 23, 1924 | 119.5 | .335 | 5.89 | 1:17.6 |
| Do | 0 | June 18, 1924 | 169.0 | .307 | 5.58 | 1:18.2 |
| Do | 20 | July 21, 1922 | 136.7 | .314 | 4.84 | 1:15.7 |
| Do | 20 | Sept. 26, 1922 | 162.8 | .304 | 4.69 | 1:15.4 |
| Do | 20 | Feb. 28, 1923 | 166.5 | .559 | 6.14 | 1:11.0 |
| Do | 20 | July 24, 1923 | 129.2 | .404 | 5.85 | 1:14.5 |
| Do | 20 | Sept. 21, 1923 | 131.0 | .376 | 5.72 | 1:15.2 |
| Do | 20 | June 25, 1924 | 172.1 | .357 | 6.37 | 1:17.8 |
| Mean | | | | .393 | 5.80 | 1:15.2 |
| Bass | 0 | Dec. 20, 1923 | 30.8 | .426 | 9.41 | 1:22.1 |
| Devils | 0 | July 11, 1923 | 46.6 | .219 | 3.02 | 1:14.0 |
| Do | 0 | Oct. 27, 1923 | 33.3 | .302 | 4.02 | 1:13.3 |
| Geneva | 0 | July 16, 1923 | 114.0 | .337 | 4.52 | 1:13.4 |
| Green | 0 | July 18, 1923 | 143.7 | .310 | 3.95 | 1:12.8 |
| Do | 0 | Oct. 16, 1923 | 138.0 | .296 | 6.51 | 1:22.0 |
| Kegonsa | 0 | July 20, 1923 | 101.4 | .730 | 7.33 | 1:10.0 |
| Madeline | 0 | Dec. 12, 1923 | 59.5 | .455 | 5.26 | 1:11.6 |
| Michigan | 0 | Feb. 28, 1924 | 96.4 | .143 | 3.24 | 1:22.7 |
| Monona | 0 | June 28, 1923 | 141.9 | .712 | 7.92 | 1:11.1 |
| Rock | 0 | July 6, 1923 | 132.6 | .550 | 8.20 | 1:14.9 |
| Turtle | 0 | Jan. 18, 1924 | 66.3 | .490 | 13.22 | 1:27.0 |
| Waubesa | 0 | July 20, 1923 | 107.2 | .744 | 7.11 | 1: 9.6 |
| Wingra | 0 | June 26, 1923 | 199.9 | .722 | 9.52 | 1:13.2 |
| RIVERS | | | | | | |
| Wisconsin [1] | 0 | July 30, 1923 | 82.9 | .487 | 15.23 | 1:31.3 |
| Do | 0 | Nov. 21, 1923 | 85.1 | .394 | 9.85 | 1:25.0 |
| Yahara [2] | 0 | July 6, 1922 | 684.0 | .372 | 9.58 | 1:25.8 |

[1] At Prairie du Sac Dam. [2] Above Lake Mendota.

Of the lakes listed in the table, Monona, Waubesa, and Kegonsa are in the same chain as Mendota. Wingra is a small and shallow lake about 1 mile south of Mendota. It is largely surrounded by marsh. Rock Lake is about 22 miles east of Madison, Green Lake is about 55 miles north, and Geneva Lake is about 57 miles southeast of Madison. All these are typical hard-water lakes of southeastern Wisconsin, ranging in depth from Wingra (3 meters) and Kegonsa (12 meters) to Mendota (24 meters), Geneva (43 meters), and Green (68 meters). Wingra is the smallest of this group (about 1 square mile); Geneva has an area of 8.8 square miles; Green has 11.5 square miles; and Mendota has 15.2. Devils Lake (360 acres) is the only soft-water lake in southeastern Wisconsin, occupying a drift basin in the gorge of the quartzites of the Baraboo Range, about 30 miles northwest of Madison. Bass, Turtle, and Madeline Lakes are small soft-water lakes or lakelets of northeastern Wisconsin. Full statistics for all of these lakes may be found in Bulletin XXVII of the Wisconsin Geological Survey (Juday, 1914). The Wisconsin River traverses the State from north to south, carrying a high-colored water with low mineral content; the Yahara is the stream connecting the Madison lakes, and its water is much like that of the lakes. The sample was taken just above the entrance of the stream into Lake Mendota, the upper lake of the series.

The data of the table disclose no difference in the content of dissolved organic matter between hard-water lakes with large amounts of carbonates in solution and soft-water lakes with little mineral matter. Lake Wingra, with the highest dry residue, has also the second highest figure for organic carbon; while Bass Lake, whose organic carbon is nearly as great, has by far the smallest amount of dry residue. In Bass Lake the total carbon dioxide was 112.9 per cent of the weight of the dry residue, while the evolved carbon dioxide was only 2.51 per cent of the same weight. The five waters in the list (omitting Mendota) whose dry residue is smallest have an average of 6.99 milligrams per liter of organic carbon; the nine others average 6.48 milligrams.

The nature of the drainage basin of the lakes and the resulting character of the inflowing water seem also to make no noteworthy differences. Turtle Lake has the greatest amount of organic carbon and its water is very high colored, derived through streams from the drainage of marshes. On the other hand, Bass Lake, a lakelet with no affluent and with very clear water, stands very high in organic carbon. The area and volume of Lake Michigan are so enormous in relation to its margin and the small amount of water brought in by affluents that its organic carbon must come almost entirely from its inner resources. The 14 observations on Lake Mendota show no clear relation between depth or season in the amount of organic carbon.

The nitrogen-carbon ratio has a wide range in these observations. The minimum ratio is 1 to 27; the maximum 1 to 9.1; and the range is nearly as great in the series from Lake Mendota—minimum 1 to 20.6, maximum 1 to 9.1. If, however, the observations are grouped and the mean nitrogen-carbon ratio is computed the results are singularly uniform. The computation may be made in two ways—the mean of the single ratios may be found, or the quantity of carbon and nitrogen in the observations may be added and the ratio of their sums computed. The result will differ somewhat according to the method employed.

TABLE 3.—*Nitrogen-carbon ratios*

| | Mean of ratios | | Mean of observations | |
|---|---|---|---|---|
| | N | C | N | C |
| Mendota, surface, 8 cases | 1 | 15.4 | 1 | 14.9 |
| Mendota, bottom, 6 cases | 1 | 14.9 | 1 | 14.5 |
| Mendota, all cases | 1 | 15.2 | 1 | 14.8 |
| Other lakes, 14 cases | 1 | 15.5 | 1 | 14.5 |
| All cases, 28 | 1 | 15.4 | 1 | 14.6 |

The average yield from all observations, 28 in number from 13 different lakes and aggregating 3,495 liters of water, is as follows:

Organic nitrogen ........ 0.426 milligram per liter
Organic carbon ........ 6.230 milligrams per liter
Ratio—N:C::1:14.6

Thus, in spite of the wide range of the single ratios and the small number of observations, there is a close correspondence of average results in five different combinations. We are warranted in believing that the average nitrogen-carbon ratio is about 1 to 15.

The organic carbon and nitrogen must be derived from (*a*) the plankton, (*b*) the higher plants growing from the bottom, (*c*) matter derived from the land and ultimately from the higher plants of dry land or marsh or from the fauna and flora of the soil. Thus the sources are similar, whether in water or on land. The proportion from each source must differ in different lakes and in the same lake at different times; but on the whole the plankton must be much the largest contributor.

Birge and Juday's plankton report (p. 215) furnishes data from which may be computed the nitrogen-carbon ratio in plankton algæ, higher water plants, and plankton. The figures used for the percentage of carbon in crude protein, fats, and carbohydrates are the same as those employed later in the present paper (p. 199). The ratio of nitrogen to carbon was determined directly in 11 samples of plankton from Lake Mendota and was found to average 1 to 6.3, a sufficiently close agreement with the ratios given in the table as the result of computation from a much larger number.

TABLE 4.—*Ratio of nitrogen to carbon in algæ, water plants, and plankton*

| | N | C | | N | C |
|---|---|---|---|---|---|
| Blue-green algæ (11 analyses) | 1 | 5.5 | Vallisneria (1 analysis) | 1 | 13.5 |
| Diatoms (1 analysis) | 1 | 9.0 | Plankton, Mendota (87 analyses) | 1 | 7.1 |
| Potamogeton, mature (1 analysis) | 1 | 24.0 | Plankton, Monona (21 analyses) | 1 | 5.6 |
| Potamogeton, green (1 analysis) | 1 | 19.2 | Plankton, Waubesa (16 analyses) | 1 | 6.5 |
| Myriophyllum (1 analysis) | 1 | 11.8 | | | |

We have no knowledge of the composition of the extractives from soil or from marshes, which are always present in lakes in some quantity and which give a high color to some waters. Russell (1923, p. 172) remarks on "the slow rate of disappearance of complex nitrogenous compounds in soil as compared with the rate of oxidation of carbon." In land plants the ratio of nitrogen to carbon may be 1 to 40; in the soil it is rapidly raised to 1 to 10. But we do not know at what point in this process these substances get into the lake.

We are not able at present to show how the nitrogen-carbon ratio is established in the lakes. It is plain that the nitrogen of the dissolved matter is much smaller, relatively to the carbon, than it is in the plankton. It is plain also that the average ratio—1 to 15, in round numbers—is not far from the ratio of 1 to 17 that comes from the four analyses of higher plants, as given in Table 4. The three general there analyzed yield about 88 per cent of the crop of aquatic plants in Lake Mendota. (Rickett, 1922, p. 525.)

One might be tempted to infer that the low ratio of nitrogen to carbon is due to extractives from these plants, but such a conclusion would be wrong. The average standing crop of organic carbon in Lake Mendota is nearly 6.0 grams per cubic meter of water; the volume of the lake is 478,370,000 cubic meters. The lake, therefore, contains nearly 2,900 metric tons of organic carbon. Rickett's study of the larger aquatic plants (1922, p. 527) assigns to the annual crop for the entire lake a dry weight of 2,100 metric tons, of which less than one-half would be organic carbon. Thus, the *annual* carbon crop of the higher plants of Lake Mendota is hardly more than one-third of the average *standing* crop of dissolved organic carbon.

The situation in Green Lake is even more unfavorable to large contributions from the higher plants. The smaller figure in Table 2 for organic carbon in this lake is 3.95 grams per cubic meter; the volume of the lake is 973,000,000 cubic meters; and on this basis the lake would contain more than 3,800 metric tons of organic carbon. Rickett (1924) found in Green Lake an annual crop of higher plants, yielding about 1,528 metric tons of dry matter; but almost exactly half of this is in the form of Chara, which contains more than 50 per cent of ash. An outside estimate of the annual crop of organic carbon from the higher plants of this lake would be 500 to 600 metric tons.

It is equally clear that inflowing water brings only relatively small quantities of organic matter into the lakes, and the plankton necessarily is left as by far the chief source of the dissolved matter. Other facts of secondary importance look the same way. If extractives from the higher plants were influential in controlling the amount of organic carbon and nitrogen, then the spread between these substances ought to be greater in late fall and winter than in spring and early summer; but this is not the case. Again, the centrifuge plankton ought to show the influence of vegetable débris at the same seasons; but this also is not the case. The small and shallow lakes should show a larger proportion of carbon than the larger and deeper bodies. This also does not appear; on the contrary, in Lake Michigan, whose water must receive only minimal supplies of organic matter from affluents and from plants of shallow water, the carbon is twenty-two and seven-tenths times the nitrogen, being exceeded in this respect by only one lake.

Much further study will be needed before the intricate story of the organic matter of lakes is finally unraveled. But at present we may conclude that the plankton is the chief source of the dissolved organic matter, and that its nitrogen compounds disappear more rapidly than its nonnitrogenous substances, thus reversing the situation as stated by Russell for the land. This conclusion might be expected in view of the rapid accumulation of carbohydrates in peat under water, as compared with the very slow growth of humus under subaerial conditions.

## ETHER EXTRACT

The ether extract from several of these samples was determined by Dr. B. P. Domogalla in 1925 and 1926. Six samples of single residues were treated; of these, four were from Mendota—two surface and two bottom water—one sample was from Green Lake, and one from Lake Geneva. Ether extracts also were made from 2 large composite samples from Lake Mendota; 10 residues taken from the surface water at various dates were combined into 1 sample, and 6 residues from the bottom water made up the other. In the composite sample from surface water 2 specimens were taken in February; 2 others, April and November, during the homothermous period; the other 6 were taken during the period of summer stratification—2 in July, 2 in early October, and 1 each in August and September. The 6 bottom samples included in the composite came 1 in February, 2 in July, 2 in September, and 1 in early October; all but the first were in the period of summer stratification of water.

TABLE 5.—*Ether extract, milligrams per liter*

| Lake | Depth, meters | Date | Dry matter | Ether extract |
|---|---|---|---|---|
| | | | | *Single samples* |
| Mendota | 0 | June 7, 1922 | 167.8 | 0.323 |
| Do | 0 | Sept. 18, 1924 | 169.0 | .380 |
| Do | 20 | Sept. 26, 1922 | 162.8 | .488 |
| Do | 20 | June 25, 1924 | 172.1 | .688 |
| Green | 0 | July 18, 1923 | 143.7 | .352 |
| Geneva | 0 | July 16, 1923 | 114.0 | .217 |
| | | | | *Composite samples* |
| Mendota | 0 | 10 samples | 164.3 | 0.482 |
| Do | 20 | 6 samples | 149.7 | .765 |

The range of ether extract, as shown from these specimens, is from about 0.2 milligram per liter to nearly 0.8 milligram. No doubt a larger series would show a greater range. The quantities obtained were not large enough to permit further chemical study, but under the microscope they were seen to be made up of clear droplets of oil.

This ether extract must have its main source in the plankton, just as the nitrogenous substances of the dissolved matter come from similar substances in the plankton. The ether extract has been determined for many samples of the plankton from the Madison lakes (plankton report, pp. 196, 202–209). In Lake Mendota the average amount is 0.149 milligram per liter, or 7.53 per cent of the ash-free organic matter. This may be compared with the average result of the 20 samples of residues from Lake Mendota, which yield 0.564 milligram of fat per liter, or 4.4 per cent of the total organic matter as computed.

The range of ether extract in plankton is great. It extends from 0.004 milligram per liter of lake water to 0.136 milligram in the case of the net plankton, and from 0.018 milligram to 0.356 milligram in the case of the centrifuge plankton. Thus, the fats of the dissolved organic matter found in a unit of volume of water are much greater than those in the plankton from the same amount of water. However, they constitute a smaller per cent of the dissolved matter than of the plankton.

The nitrogen and carbon were determined for the two composite samples from Lake Mendota. The results, stated in milligrams per liter, are as follows:

| | Surface | Bottom |
|---|---|---|
| Nitrogen | 0.457 | 0.452 |
| Carbon | 5.580 | 6.360 |
| Ratio, nitrogen to carbon | 1 : 13.1 | 1 : 14.0 |

## PLANKTON

In the study of the forms of soluble nitrogen the plankton was extracted from the water by the centrifuge; it was dried and weighed, and the organic matter and nitrogen were determined. The quantities were too small to permit other determinations, such as ether extract. The amounts of nitrogen from these samples already have been published (nitrogen report, pp. 273, 282), but the other data appear here for the first time. The "ash" of these specimens ought rather to be called "total inorganic matter," for it is composed in large part of minute particles of silt that remain suspended in the water and are removed by the centrifuge. This subject is discussed in the plankton report, page 80.

TABLE 6.—*Plankton, milligrams per liter*

| | Date | Depth, meters | Total plankton | Ash | Total organic | Nitrogen |
|---|---|---|---|---|---|---|
| LAKES | | | | | | |
| Mendota | Oct. 18, 1922 | 0 | 3.23 | 1.98 | 1.25 | 0.105 |
| Do | Dec. 5, 1922 | 0 | 3.20 | 1.47 | 1.73 | .144 |
| Do | Feb. 28, 1923 | 0 | 1.62 | .74 | .88 | .052 |
| Do | July 24, 1923 | 0 | 4.60 | 1.23 | 3.37 | .113 |
| Do | Sept. 21, 1923 | 0 | 4.06 | 2.00 | 2.06 | .091 |
| Do | Oct. 24, 1923 | 0 | 3.90 | 2.08 | 1.82 | .045 |
| Do | Apr. 23, 1924 | 0 | 1.96 | 1.01 | .95 | .080 |
| Do | June 18, 1924 | 0 | 2.12 | .80 | 1.32 | .092 |
| Do | July 21, 1922 | 20 | 2.12 | 1.43 | .69 | .050 |
| Do | Sept. 26, 1922 | 20 | 3.60 | 2.75 | .85 | .047 |
| Do | Feb. 28, 1923 | 20 | 2.45 | 1.68 | .78 | .057 |
| Do | July 24, 1923 | 20 | 3.42 | 1.93 | 1.49 | .058 |
| Do | Sept. 21, 1923 | 20 | 4.62 | 2.34 | 2.28 | .098 |
| Do | June 25, 1924 | 20 | 1.84 | 1.00 | .84 | .045 |
| Mean | | | 3.05 | 1.60 | 1.45 | .077 |
| Bass | Dec. 20, 1923 | 0 | 1.08 | .51 | .57 | .034 |
| Devils | July 11, 1923 | 0 | 1.30 | .88 | .42 | .016 |
| Do | Oct. 27, 1922 | 0 | .86 | .47 | .39 | .038 |
| Geneva | July 16, 1923 | 0 | 2.18 | .93 | 1.25 | .051 |
| Green | July 18, 1923 | 0 | 2.18 | 1.25 | .93 | .042 |
| Do | Oct. 16, 1923 | 0 | 2.05 | 1.16 | .89 | .049 |
| Kegonsa | July 20, 1923 | 0 | 22.30 | 3.02 | 19.28 | .697 |
| Madeline | Dec. 12, 1923 | 0 | 2.26 | .52 | 1.74 | .096 |
| Michigan | Feb. 28, 1923 | 0 | 4.38 | 2.76 | 1.62 | .020 |
| Monona | June 28, 1923 | 0 | 7.20 | 2.00 | 5.20 | .389 |
| Rock | July 6, 1923 | 0 | 1.66 | .64 | 1.02 | .073 |
| Turtle | Jan. 18, 1924 | 0 | 1.40 | .66 | .74 | .030 |
| Waubesa | July 20, 1923 | 0 | 10.12 | 1.97 | 8.15 | .299 |
| Wingra | June 26, 1923 | 0 | 25.72 | 8.51 | 17.21 | .882 |
| RIVERS | | | | | | |
| Wisconsin | July 30, 1923 | 0 | 7.95 | 5.38 | 2.57 | .161 |
| Do | Nov. 21, 1923 | 0 | 2.26 | 1.25 | 1.01 | .053 |
| Yahara | July 6, 1922 | 0 | 20.12 | (1) | (1) | .609 |

[1] Not determined.

The average amount of organic matter in the specimens from Lake Mendota is small, as is also the percentage of nitrogen in it. In 87 large samples that were analyzed during the years 1915–1917 for the plankton report, the organic matter averaged 1.974 milligrams per liter and the nitrogen was 0.140 milligram. The specimens in the plankton report were taken, meter by meter, through the whole depth of the lake and therefore represent average conditions; also, they were far larger than those employed for evaporation, each sample analyzed representing about 2,000 liters of water, as compared with 50 to 100 liters, the ordinary sample for evaporation.

In the case of the other lakes there is no such opportunity for comparison, as the analyses are not so numerous. In general, the cases reported are fairly representative. The total plankton reported from Lakes Kegonsa and Wingra is very large, aggregating more than 60 per cent of the total organic matter from the 14 specimens. Large amounts, but less noticeable, also are found in Lake Monona and Lake Waubesa. In the first two cases the water was collected close to the surface at the time of great growths of blue-green algæ, and the collection was made at this time in order to note the effect of these growths on the dissolved organic matter. The samples from the other two lakes also were taken at a time of maximum abundance of plankton. It will be noted that the "ash" is relatively low in these specimens, especially in the first two cases. The ash of the blue-green algæ is low; in 11 analyses (plankton report, p. 215) it ranged from 4.3 per cent to 7.8 per cent, and the presence of many milligrams per liter of this material greatly reduces the percentage of total inorganic matter.

The ratio of the nitrogen to the total organic matter of the plankton in Lake Mendota is 1 to 20.1, a ratio that is much lower than the average for the catches analyzed in the plankton report. In these the ratio was 1 to 14.1. The ratio of the average from the other lakes, as given in Table 6, is 1 to 21.8, or 1 to 20.2 if Lakes Kengosa and Waubesa are omitted as being exceptional cases.

## II. DISCUSSION OF THE DATA

### ORGANIC NITROGEN AND ORGANIC CARBON

Table 2 states the amount of organic nitrogen and organic carbon found in the residues from the water of the several lakes. They represent what is usually called "dissolved" or "soluble" carbon or nitrogen, as the water has been passed through a supercentrifuge to remove the plankton.

It should be noted that the lake water received a different treatment from that given to sea water by Raben (1910) and by Moore (Moore, et al., 1912); for example, in determining the dissolved carbon. In their experiments a small amount of water was employed, which had been passed through a Berkefeld filter. In studies on lake water the plankton was extracted from large quantities of water—50 to 575 liters—by means of the centrifuge. It is not probable that the two methods yield identical results. Both leave the water far from optically pure, and both undoubtedly remove substances that are neither living cells nor organic débris that exists in a particulate form—to employ Moore's useful word. In either case the weight of the matter left in particulate form probably is very small.

Two classes of experiments were made in the course of our studies that give some idea of the percentage of the particulate organic matter that was removed by the centrifuge. The first gave an indirect answer, based on the percentage of bacteria removed from the water by the centrifuge.

It is difficult to imagine that particles of organic débris suspended in water should be free from bacteria, and if they have bacteria adherent to them or colonized in them, a rough measure of the efficiency of any process in removing these particles of débris may be found in its efficiency in removing bacteria.

We found that the De Laval centrifuge, employed in the extraction of the plankton for the plankton report, removed 35 to 50 per cent of the bacteria. The Sharples supercentrifuge, used by Domogalla, Juday, and Peterson, removed about 70 per cent of the bacteria (p. 270). It is a fair conclusion that about the same percentage of the particles of débris also was removed, at least down to the size of the bacteria.

It is a fair conclusion also that the weight of the very numerous particles left in the water by the centrifuge is only a small fraction of the amount extracted by the centrifuge. In the plankton report (p. 89) there was computed the weight of the bacteria of Lake Mendota. At the summer maximum of 30,000 per cubic centimeter there were about 20,000 rods averaging 2.5$\mu$ long and 0.9$\mu$ in diameter, and about 10,000 cocci averaging 0.44$\mu$ in diameter. Such a crop would yield 0.0048 milligram of dry organic matter per liter, which would represent about one-half that weight of organic carbon. Such an amount is almost infinitesimal when compared with the average of nearly 6.0 milligrams per liter of dissolved organic carbon found in the water of Lake Mendota.

We may conclude, therefore, that only a small part of the organic material found in the evaporated residues is in the particles left behind by the centrifuge. The nitrogen and carbon of Table 2 may be called "dissolved" in any sense of that word in which it is properly applicable to colloids.

The same conclusion was reached directly by filtration experiments. In two cases 100 liters of water from Lake Mendota were divided into two parts after centrifuging. One-half was evaporated at once and the other was passed through a Berkefeld filter before evaporation. In both cases the nitrogen was determined both as to amount and kinds. The filtered water yielded slightly less organic nitrogen than did the unfiltered.

TABLE 7.—*Organic nitrogen in filtered and unfiltered water, milligrams per liter*

| Date | Filtered | Unfiltered |
|---|---|---|
| Dec. 16, 1924 | 0.306 | 0.319 |
| Feb. 19, 1925 | .341 | .351 |

These specimens were used in the study of the nitrogenous compounds, which agreed in detail as closely as in the total.

As some part of any colloids in the water would adhere to the filter and thus reduce the total nitrogen, it does not seem probable that any considerable part of the weight of the organic substances left in the water by the centrifuge exists in the form of particles. It is certain that very little is left that is removed by a Berkefeld filter.

Those who have studied the organic content of sea water (Henze, 1908; Raben, 1910; Moore et al., 1912) have left the subject with the statement of the amount of organic nitrogen and carbon. Table 2, therefore, gives a basis of direct comparison between the conditions existing in fresh and in salt water. If comparisons regarding nonorganic nitrogen are desired also, the data may be found in the paper on the forms of nitrogen (p. 273).

Thus the facts presented in Table 2 complete the proof, if such were needed that the fresh-water lake offers an unrivaled opportunity for the study of plankton in its relations to the fundamental food supply of water animals. The lake contains not only a complex association of living organisms, each group existing in numerous representatives and forms and in quantities great enough for study, but it contains also a great amount of organic material not removable by centrifuge and apparently not existing in particulate form. In this matter of quantity the fresh water has a great advantage over the sea. Studies on the water of the Mediterranean (Henze, 1908), the Baltic (Raben, 1910), and the Irish Sea (Moore et al., 1912) agree in finding that the total amount of organic carbon in the water of the open sea is so small that it lies "at the limits of detectability by the best known methods" (Moore et al., p. 269). The difficulty of studying this minute amount is increased further by the great quantity of salts dissolved in the water.

The water of lakes, on the other hand, contains organic matter, extractable by the centrifuge, in quantities ordinarily present to the amount of 1 milligram per liter; often as great as 5 to 7 milligrams per liter; and sometimes much greater. It contains, also, organic matter not thus extractable, whose quantity is ordinarily five to ten times as great. The dissolved salts of fresh water are small in amount, and there are many lakes whose dissolved organic content is larger than that of the dissolved salts. Thus, the fresh water far exceeds the salt in its opportunities for the study of the numerous and complex problems offered by its organic content.

As yet the science of limnology hardly has begun to deal with these problems. For years there has been an active discussion of the question whether the organized plankton is distributed to the two classes of eaters and eaten so as to make them into a self-sustaining community. But as yet there is no agreement on the quantity of organic matter contained in either group, on the rate of its renewal, or on the amount, kinds, and availability of organic matter in the water but outside of organized beings.

## TOTAL ORGANIC CONTENT

In this section the organic content of lake water is discussed without taking into account the ether extract. The amount of this and the effect on the statement of total content are discussed in the next section.

The data for the plankton content of the water are given in Table 6, which gives total content and nitrogen. The "crude protein," the nitrogenous part of the plankton, may be computed from the nitrogen by employing the standard factor—6.25. The nonnitrogenous part is the remainder of the organic matter after the crude protein has been subtracted. The samples of plankton were too small to permit the determination of the ether extract, and therefore the nonnitrogenous substance can not be subdivided further into fats and carbohydrates. The plankton of the Madison lakes has been so analyzed in the tables of the plankton report.

In the study of the dissolved organic matter it is not possible to separate this from the relatively large quantities of inorganic salts that make up the bulk of the residues from evaporated lake water. Recourse must be had to indirect methods, based on the data of Table 2, which states the nitrogen and the organic carbon.

The nitrogenous part of the dissolved matter—the crude protein—is computed as in the case of the plankton by multiplying the amount of nitrogen by 6.25. The proteins contain 50 to 55 per cent of carbon, and an average amount of 53 per cent may be assigned to them. Thus, the organic carbon may be divided at once into two parts, one belonging to the nitrogenous substances and the other to nonnitrogenous compounds. The first part equals 53 per cent of the weight of the crude protein and the remainder goes to nonnitrogenous substances. If the ether extract has not been determined (and this is true for most of the residues here considered), the nonnitrogenous substance must be computed as carbohydrate. This method involves an overestimate of the total amount of organic matter, proportional to the quantity of fat that is present; in the present cases the excess is about 3 per cent.

The carbohydrates contain only a negligible amount of sugars, as is the case also with the water plants and plankton. They may be computed as starch or cellulose, containing an average of about 45 per cent of carbon. The "crude fiber," so far as it contributes to the dissolved matter, comes either from plankton or higher water plants, and this also would have about the same composition.

If, then, the organic carbon is distributed to proteins on the basis that 53 per cent of these consists of carbon, and to nonnitrogenous organic substances on the basis of 45 per cent of carbon, the following table will result:

TABLE 8.—*Total organic matter, milligrams per liter*

[D.=depth. N.=nitrogen×6.25, or crude protein. Nonn.=nonnitrogenous matter computed as carbohydrate. Pkn.=plankton. Dis.=dissolved organic matter.]

| | Date | Plankton | | | | Dissolved | | | Total organic | | | Per cent | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | D. | N. | Nonn. | Total | N. | Nonn. | Total | N. | Nonn. | Total | Pkn. | Dis. |
| LAKES | | | | | | | | | | | | | |
| Mendota | Oct. 18, 1922 | 0 | 0.66 | 0.59 | 1.25 | 2.74 | 5.67 | 8.41 | 3.40 | 6.26 | 9.66 | 12.9 | 87.1 |
| Do | Dec. 5, 1922 | 0 | .90 | .83 | 1.73 | 3.02 | 14.10 | 17.12 | 3.92 | 14.93 | 18.85 | 9.2 | 90.8 |
| Do | Feb. 28, 1923 | 0 | .32 | .56 | .88 | 3.46 | 9.95 | 13.41 | 3.78 | 10.51 | 14.29 | 6.2 | 93.8 |
| Do | July 24, 1923 | 0 | .70 | 2.67 | 3.37 | 2.44 | 13.48 | 15.92 | 3.14 | 16.15 | 19.29 | 17.5 | 82.5 |
| Do | Sept. 21, 1923 | 0 | .57 | 1.49 | 2.06 | 2.32 | 7.22 | 9.54 | 2.89 | 8.71 | 11.60 | 17.8 | 82.2 |
| Do | Oct. 24, 1923 | 0 | .28 | 1.54 | 1.82 | 1.81 | 11.10 | 12.91 | 2.09 | 12.64 | 14.73 | 12.4 | 87.6 |
| Do | Apr. 23, 1924 | 0 | .50 | .45 | .95 | 2.10 | 10.61 | 12.71 | 2.60 | 11.06 | 13.66 | 7.0 | 93.0 |
| Do | June 18, 1924 | 0 | .58 | .74 | 1.32 | 1.92 | 10.12 | 12.04 | 2.50 | 10.84 | 13.34 | 9.7 | 90.3 |
| Do | July 21, 1922 | 20 | .31 | .38 | .69 | 1.96 | 8.44 | 10.40 | 2.27 | 8.82 | 11.09 | 6.3 | 93.7 |
| Do | Sept. 26, 1922 | 20 | .30 | .55 | .85 | 1.90 | 8.17 | 10.07 | 2.20 | 8.72 | 10.92 | 8.7 | 91.3 |
| Do | Feb. 28, 1923 | 20 | .36 | .42 | .78 | 3.50 | 9.50 | 13.00 | 3.86 | 9.92 | 13.78 | 5.7 | 94.3 |
| Do | July 24, 1923 | 20 | .36 | 1.13 | 1.49 | 2.52 | 10.01 | 12.53 | 2.88 | 11.14 | 14.02 | 7.8 | 92.2 |
| Do | Sept. 21, 1923 | 20 | .62 | 1.66 | 2.28 | 2.35 | 9.92 | 12.27 | 2.97 | 11.58 | 14.55 | 15.7 | 84.3 |
| Do | June 25, 1924 | 20 | .28 | .56 | .84 | 2.23 | 12.65 | 14.88 | 2.51 | 13.21 | 15.72 | 6.0 | 94.0 |
| Mean | | | .48 | .97 | 1.45 | 2.45 | 10.07 | 12.52 | 2.93 | 11.03 | 13.96 | 10.2 | 89.8 |
| Bass | Dec. 20, 1923 | 0 | .21 | .36 | .57 | 2.66 | 17.76 | 20.42 | 2.87 | 18.12 | 20.99 | 2.7 | 97.3 |
| Devils | July 11, 1923 | 0 | .24 | .18 | .42 | 1.37 | 5.08 | 6.45 | 1.61 | 5.26 | 6.87 | 6.1 | 93.9 |
| Do | Oct. 27, 1923 | 0 | .19 | .20 | .39 | 1.89 | 6.70 | 8.59 | 2.08 | 6.90 | 8.98 | 4.3 | 95.7 |
| Geneva | July 16, 1923 | 0 | .32 | .93 | 1.25 | 2.11 | 7.55 | 9.66 | 2.43 | 8.48 | 10.91 | 11.5 | 88.5 |
| Green | July 18, 1923 | 0 | .26 | .67 | .93 | 1.94 | 6.48 | 8.42 | 2.20 | 7.15 | 9.35 | 10.0 | 90.0 |
| Do | Oct. 16, 1923 | 0 | .30 | .59 | .89 | 1.85 | 12.28 | 14.13 | 2.15 | 12.87 | 15.02 | 5.9 | 94.1 |
| Kegonsa | July 20, 1923 | 0 | 8.62 | 10.66 | 19.28 | 4.56 | 10.90 | 15.46 | 13.18 | 21.56 | 34.74 | 55.5 | 44.5 |
| Madeline | Dec. 12, 1923 | 0 | .60 | 1.14 | 1.74 | 2.84 | 8.35 | 11.19 | 3.44 | 9.49 | 12.93 | 14.6 | 85.4 |
| Michigan | Feb. 28, 1924 | 0 | .14 | 1.48 | 1.62 | .89 | 6.15 | 7.04 | 1.03 | 7.63 | 8.66 | 18.7 | 81.3 |
| Monona | June 28, 1923 | 0 | 2.43 | 2.77 | 5.20 | 4.45 | 12.34 | 16.79 | 6.88 | 15.11 | 21.99 | 23.7 | 76.3 |
| Rock | July 6, 1923 | 0 | .46 | .56 | 1.02 | 3.44 | 14.14 | 17.58 | 3.90 | 14.70 | 18.60 | 5.5 | 94.5 |
| Turtle | Jan. 18, 1924 | 0 | .19 | .55 | .74 | 3.06 | 25.75 | 28.81 | 3.25 | 26.30 | 29.55 | 2.5 | 97.5 |
| Waubesa | July 20, 1923 | 0 | 3.74 | 4.41 | 8.15 | 4.65 | 10.32 | 14.97 | 8.39 | 14.73 | 23.12 | 35.2 | 64.8 |
| Wingra | June 26, 1923 | 0 | 5.51 | 11.70 | 17.21 | 4.51 | 15.83 | 20.34 | 10.02 | 27.53 | 37.55 | 45.8 | 54.2 |
| RIVERS | | | | | | | | | | | | | |
| Wisconsin | July 30, 1923 | 0 | 1.01 | 1.56 | 2.57 | 3.04 | 30.24 | 33.28 | 4.05 | 31.80 | 35.85 | 7.2 | 92.8 |
| Do | Nov. 21, 1923 | 0 | .34 | .67 | 1.01 | 2.46 | 18.98 | 21.44 | 2.80 | 19.65 | 22.45 | 4.5 | 95.5 |
| Yahara | July 6, 1922 | 0 | 1.19 | (1) | (1) | 2.32 | 18.54 | 20.86 | | | | | |

[1] Not determined.

So far as the dissolved organic matter is concerned, much the same comment may be made on Table 8 as on Table 2, from which it is derived. The total quantity of dissolved organic matter varies greatly in different lakes and in the same lake at different times. It may be less than 7 milligrams per liter (Devils Lake), or it may be more than 28 milligrams (Turtle Lake)—a fourfold range. The second observation on Green Lake was nearly 70 per cent larger than the first; and in the 14 observations on Lake Mendota the smallest quantity is less than one-half of the largest. These results are entirely in accord with those on the plankton, though the range of variation is much smaller.

There is much difference in the relation of nitrogenous to nonnitrogenous matter, just as there is in the nitrogen-carbon ratio of Table 2; and, as in that case, the average relation is much the same in the various groups. In the 14 cases from Lake Mendota the crude protein ranges from 12.6 to 36.9 per cent, a nearly threefold range; in the 14 cases from other lakes the minimum percentage is 10.6 per cent in Turtle Lake and the maximum is 29.5 per cent in Lake Kegonsa. The average per cent for Lake Mendota is 19.6; for the other lakes it is 20.1. This average is lower than it is in the plankton. Table 8 shows that in Lake Mendota the crude protein is 33.1 per cent of the total organic matter of the plankton; in the other lakes it is 31.1 per cent. The plankton report (p. 196) gives 44.5 per cent as the average for Lake Mendota during the years when that study was made.

The total organic matter of the water is obtained by adding the plankton and the dissolved matter, as is done in Table 8. In interpreting these figures the statement that was made earlier in this paper should be remembered. Not everything included under the first head is properly plankton, and the amount of nonplankton organic matter there included will increase with the efficiency of the centrifuging process. It is true, also, that not all of the "dissolved" matter really is dissolved. These divisions of the organic content of the lake water overlap to some extent, the degree of overlapping being dependent on the efficiency of the processes of separation. But, on the whole, the two categories fairly represent the facts.

The quantitative relation between plankton and dissolved organic matter is very variable. In the case of Lake Mendota the plankton may constitute nearly one-fifth of the total organic matter, or it may be less than one-sixteenth; in the other lakes the range is much greater. The plankton is more than one-half the total organic matter in Lake Kegonsa; nearly one-half in Wingra; and it is as little as one-fortieth of the total in Turtle Lake.

The mean of the 14 specimens from Lake Mendota shows that the crude protein of the plankton constitutes about one-sixth of the total protein, and the nonnitrogenous part of the plankton is little more than one-twelfth of the corresponding total. The range of variation in other lakes is so great in comparison to the number of observations that an average result has not much value.

## TOTAL ORGANIC MATTER, INCLUDING FATS

In this discussion the ether extract is regarded as fat. The quantities obtained were too small for further chemical treatment, but under the microscope they appeared as transparent droplets of fat.

Table 9 brings together the facts for those residues for which the fats have been determined as ether extract. The table relates chiefly to Lake Mendota, there being samples from only two other lakes for comparison.

The table gives the data and the results computed from them; the data include organic nitrogen, organic carbon, and ether extract; the computed results are crude protein, fats, and carbohydrates. To the fats is assigned a carbon content of 75 per cent; the other substances are computed as in Table 8. Thus, in Table 9 the organic carbon is distributed to three classes of compounds.

TABLE 9.—*Total organic matter, ether extract included, milligrams per liter*

| Lake | Depth | Date | Total dry | N | C | Ether extract | Crude protein | Fats | Carbohydrates | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Mendota | 0 | June 7, 1922 | 167.8 | 0.567 | [1] | 0.323 | 3.54 | 0.32 | [1] | |
| Do | 0 | June 18, 1924 | 169.0 | .307 | 5.58 | .380 | 1.92 | .38 | 9.44 | 11.74 |
| Do | 20 | Sept. 26, 1922 | 162.8 | .304 | 4.69 | .488 | 1.90 | .49 | 7.38 | 9.77 |
| Do | 20 | June 25, 1924 | 172.1 | .357 | 6.88 | .688 | 2.23 | .69 | 11.51 | 14.43 |
| Do | 0 | 10 samples | 164.3 | .457 | 5.98 | .482 | 2.86 | .48 | 9.09 | 12.43 |
| Do | 20 | 6 samples | 149.7 | .452 | 6.35 | .765 | 2.83 | .76 | 9.50 | 13.09 |
| Mean of 20 | | | | .441 | 6.06 | .504 | 2.76 | .56 | 9.27 | 12.59 |
| Geneva | 0 | July 16, 1923 | 114.0 | .337 | 4.52 | .217 | 2.11 | .34 | 7.00 | 9.45 |
| Green | 0 | July 18, 1923 | 143.7 | .310 | 3.95 | .352 | 1.94 | .31 | 5.98 | 8.23 |

[1] Not determined.

TABLE 10.—*Percentile distribution of dissolved organic matter*

| Lake | Protein | Fat | Carbohydrates |
|---|---|---|---|
| Mendota: | | | |
| Surface (10 samples) | 23.0 | 3.9 | 73.1 |
| Bottom (6 samples) | 21.7 | 5.8 | 72.5 |
| Mean (20 samples) | 21.9 | 4.4 | 73.7 |
| Green (1 sample) | 22.3 | 3.6 | 74.1 |
| Geneva (1 sample) | 23.6 | 3.8 | 72.6 |

The data from Lake Mendota comprise 20 samples and are numerous enough to warrant computing an average result. The results from Green Lake and Geneva show that the variation in the fats of different lakes is entirely similar to that in proteins and carbohydrates. The data from Lake Mendota, both in the single and the composite samples, show that there is a larger amount of fat in the water at the bottom than at the surface. It should be noticed that all of the single observations were made under summer conditions. The specimens that made up the composite surface sample were fairly distributed through the year; but all except one of the specimens from the bottom were taken during the period of the summer stratification of the water, when there would naturally be a maximum difference between surface and bottom.

There is a very close correspondence between the average results of the 20 specimens from Lake Mendota reported in Table 9 and the mean of the 14 specimens reported in Table 8. If the organic matter for Table 9 is computed on the same basis as in Table 8, the result will be as follows: Nitrogenous, 2.76 milligrams per liter; nonnitrogenous, 10.21 milligrams; total, 12.97 milligrams. The total exceeds that of Table 9 by 0.38 milligram. The per cent of protein, when computed from these data on the basis of Table 8, is 21.3, which is to be compared with 19.6 per cent in Table 8, derived from other data, and with 21.9 per cent in Table 10, resulting from a computation that includes the fats. The differences are plainly very small.

Table 10 shows the percentile composition of the organic matter in the more important items of Table 9. The figures for Lake Mendota may be compared with those for the plankton of that lake, as reported in the plankton report on page 196. There the average of 87 specimens gave protein, 44.5 per cent; fat, 7.5 per cent; carbohydrate, 48 per cent. These figures show clearly the relative decrease in the proteins and fats of the dissolved matter as compared with those of the plankton, and the corresponding relative increase of the carbohydrates.

If the total organic matter is computed from the data in Table 9 on the basis employed in Table 8, the excess due to computing all nonnitrogenous matter as carbohydrate ranges from 0.19 milligram in the case of Green Lake to 0.55 milligram in the bottom water of Mendota on June 25, 1924. The per cent of excess ranges from 2.2 to 3.9; the average excess in the 8 cases is 0.35 milligram per liter, and the average per cent is 3.0. This correction might be applied to the figures of Table 8, if desired, but the error due to method of computation doubtless is much smaller than those inherent in the variations due to sampling.

Table 11 exhibits the general results for Lake Mendota. The data for the plankton are the mean of 87 analyses of plankton taken from April 1, 1915, to June, 1917; the data for dissolved matter are from 20 residues, taken from 1922 to 1924. So far as the total amounts are concerned, the result would have been virtually the same if the figures from Table 8 had been used instead of those from Table 9. Further study certainly will make changes in the figures here reported but is not likely to alter the general situation shown by them.

TABLE 11.—*Lake Mendota. General result*

| | Plankton | | Dissolved | | Total | |
|---|---|---|---|---|---|---|
| | Milligrams per liter | Per cent | Milligrams per liter | Per cent | Milligrams per liter | Per cent |
| Crude protein | 0.88 | 44.5 | 2.76 | 21.9 | 3.64 | 25.0 |
| Fat | .15 | 7.5 | .56 | 4.4 | .71 | 4.8 |
| Carbohydrate | .95 | 48.0 | 9.27 | 73.7 | 10.22 | 70.2 |
| Total | 1.98 | 100.0 | 12.59 | 100.0 | 14.57 | 100.0 |

Thus, the water of Lake Mendota contains an average of nearly 15 milligrams of organic matter per liter; less than one-seventh of this is contained in the plankton that may be collected with the net or extracted with the centrifuge. The maximum amount of organic matter yielded by the plankton when it was a special study was 3.33 milligrams per liter on April 15, 1916; this is less than 40 per cent of the minimum amount of dissolved matter reported in Table 8. The minimum amount of plankton was taken on March 9, 1917, and yielded 0.91 milligram per liter. This is larger than several of the plankton catches reported in Table 8, but these were taken at one level only while the plankton catches for the plankton report represent all depths of the lake taken meter by meter. The water from which the dry residues came also was taken at one level; but while the amount of dissolved matter varies, it shows no such differences with depth as does the plankton.

## NATURE OF THE DISSOLVED ORGANIC MATTER

No special study has been made of the ether extract from the residues, but its appearance under the microscope shows that probably it is composed of normal fats. The exact nature and the nutritive value of the carbohydrate material have not been studied, either in the plankton or the dissolved matter. Something more definite may be said regarding the crude proteins.

The nitrogenous compounds of the plankton of Lake Mendota have been compared with those from the dissolved matter. Two composite samples of plankton were made up, one from the net plankton and the other from the nannoplankton. Each was made up from 10 catches, representing all seasons from April, 1915, to June, 1917. The organic nitrogen was determined by the methods used in the study of the residues, and it was separated into the three forms that were standard for the residues—free-amino nitrogen, peptide nitrogen, and nonamino nitrogen. The result is given in Table 12, where the analyses of the plankton are compared with the average results from the residues, as given by Domogalla, Juday, and Peterson (1925, pp. 273, 274). The residues include 29 samples of water from the surface and 21 from the bottom.

TABLE 12.—*Percentile distribution of organic nitrogen from Lake Mendota*

| Nitrogen | Plankton | | | Residues | | |
|---|---|---|---|---|---|---|
| | Net | Nanno | Total | Surface | Bottom | Total |
| | *Per cent* | *Per cent* | *Per cent* | *Per cent* | *Per cent* | *Per cent* |
| Free amino | 20.5 | 16.3 | 17.0 | 20.0 | 20.4 | 20.3 |
| Peptide | 50.5 | 39.5 | 41.4 | 39.8 | 38.9 | 39.3 |
| Nonamino | 29.0 | 44.2 | 41.6 | 40.2 | 40.7 | 40.4 |
| Total | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |

The net plankton contains nearly all of the animal matter that comes from Crustacea and rotifers; in computing the total results it has been given a weight of 17.4 per cent, corresponding to the average relation existing between net plankton and nannoplankton.

It appears, therefore, that the main classes of nitrogenous compounds exist in the residues in almost exactly the same proportions as in the plankton; there is much less difference between the means, as given in the table, than exists between the observations that go to make up the several means. In 15 samples from other lakes (nitrogen report, p. 282) the forms of soluble nitrogen showed much the same kind of variation as in Lake Mendota; the average of the 15 cases was as follows: Free-amino nitrogen, 17.2 per cent; peptide nitrogen, 38.7 per cent; nonamino nitrogen, 44.1 per cent.

The forms of nitrogen in the residues have been analyzed still further by Peterson, Fred, and Domogalla (1925, p. 293). It appears that such indispensable amino acids as tryptophane, cystine, tyrosine, histidine, and arginine are present in the residues from Lake Mendota and other lakes. Therefore, there is every reason to believe that the nitrogen compounds of the residues from evaporated lake water are suited for animal nutrition.

Lake water contains organic matter in quantities very large in comparison to those found in the water of the open sea. The question of the possible use of this material as food, therefore, presents a different aspect.

Only a small fraction of this organic matter can be removed by net, by centrifuge, or by Berkefeld filter, and the relatively large amounts left behind by the centrifuge may be called "dissolved," as contrasted with the particles that make up the plankton. They certainly contain crude proteins of the same kinds and in much the same proportions as are found in the plankton; the small amount of fat apparently is of the same kind, and there is no reason to believe that there is any essential difference between plankton and residues in the miscellaneous assortment of substances grouped under the name of "nitrogen-free extract."

In the study of the plankton of Lake Mendota an attempt was made to estimate the proportion of eaters and food (plankton report, p. 155). Numerous counts were made, which gave the number of Crustacea and rotifers, and the average dry weight of their organic matter also was determined. The result showed that the dry organic matter of the two main groups of eaters constitutes about one-third of the organic matter of the net plankton, in which are found virtually all rotifers and Crustacea, including Nauplii. The average net plankton is a little more than one-sixth (17.4 per cent) of the total plankton; in the particulate matter removable by the centrifuge, therefore, there is from 15 to 20 times as much organic matter as exists in Crustacea and rotifers. This would seem to be in itself a sufficient quantity of food, but not all of it is practically available for all of the eaters. Many of the plankton algæ are too large to serve as food for most rotifers, and some algæ, like the larger forms of Lyngbya, probably are too large to be eaten by any of the plankton animals. Gloiotrichia is perhaps in the same situation, and though Cyclops sometimes browses on the ends of its filaments it probably contributes much more to the weight of organic matter than to available food.

By far the larger part of the organic matter of the plankton is found in Naumann's groups (1918, p. 44) of the smaller organisms and the "larger particles of peritripton." This material should be available as food for all of the larger eaters in the plankton, and its weight is so many times that of Crustacea and rotifers that there would seem to be in the lake a sufficient supply of particulate food, so far as organic substance is concerned.

How far these algæ, even though of moderate size, can be utilized as food by plankton animals is another question. Naumann (1921) has shown that food remains in the intestine of most of the limnetic Cladocera only for a very short time (15 to 30 minutes), and that almost all of the algæ pass through the intestine without being affected by the digestive process. These Crustacea seem to get their nourishment from the minuter organisms and from similar particles of débris. Copepods and rotifers (Naumann, 1923) seem able to make a more complete use of the food material ingested.

The facts presented in the present paper offer a new basis for the investigation of the nutrition of plankton animals. Looking at the proteins alone, there is dissolved in the water three times as much as exists in the plankton, perhaps four times as much as the plankton offers as available food for Crustacea and rotifers. These soluble proteins are as nutritious, so far as their chemistry gives evidence, as are those of the plankton. The question of their use, therefore, is a question of fact to be settled by study, just as the question of the utilization of algæ as food by Daphnia must be settled.

The same statements may be made regarding the nonnitrogenous dissolved matters, with a confidence proportional to our knowledge or ignorance of the relation of these substances to the corresponding elements of the plankton. Outside of the centrifugible plankton there is four times as much ether extract as within it; the organic carbon assignable to carbohydrates is ten times as great outside of the plankton as within it.

It is evident that many questions are raised here, both of fact and theory, to which there are no answers at present. The story of the organisms and the organic substances of the lake water is comparable in its difficulties and complexities to the story of the cells and the organic matters in the human blood. It will take time to work out the story of the lake, and it may be long before we know the nature, the origin, the renewal, and the fate of the substances that we have here called dissolved.

It may be even harder to read the story of the possible or actual utilization of these substances as food. We may fairly assume that they have the potentialities of food; but dissolved matter in proportions of 6 to 30 in a million parts of water makes a very dilute nutriment, unless for creatures that have some special apparatus for selecting just these materials out of the water.

The carbon dioxide of the atmosphere, from which the land plants derive their carbon, constitutes 1 part in 2,500 by volume and more than this by weight; and of this, the carbon is more than one-fourth. In the water of Lake Mendota the organic matter of the dissolved protein constitutes only 1 part by weight in about 400,000 of water; the average total organic carbon, instead of being more than 1 part in 10,000, is less than 1 part in 150,000; and this great dilution is in a fluid far less mobile than air and one in which there is only a small relative movement between organisms and surrounding medium.

## SUMMARY

1. The water of Lake Mendota contains in its plankton an average of about 0.140 milligram per liter of nitrogen and about 0.990 milligram of organic carbon.[1]

[1] A very large series of determinations of the amount of organic carbon and nitrogen in fresh water is to be found in the sixth report of the English commission on pollution of rivers, presented to Parliament in 1874 (House of Commons Documents, 1874, vol. 33). This report contains many hundreds of determinations of organic carbon and nitrogen from potable waters, made by Frankland and Armstrong. Twenty-three lake waters were examined, chiefly from soft-water lakes. The mean amount of organic carbon found in these waters is 2.30 milligrams per liter; the organic nitrogen is 0.314 milligram per liter; the nitrogen-carbon ratio is N : C :: 1 : 7.2. If the organic matter is computed on the same basis as in the present paper the result is nitrogenous, 1.06 milligrams per liter; nonnitrogenous, 2.80 milligrams per liter; total organic matter, 4.76 milligrams per liter.

This report has received little notice from limnologists. The methods of analysis were slow and complicated and did not come into general use. In some cases they might lead to inaccurate results. Our attention was called to the report by a reference in a paper by W. H. Pearsall, entitled "Phytoplankton and environment in the English lake district" (Revue Algologique, March, 1924). He evidently accepts the data of the report for the lakes to which he refers; and, in general, the report shows conditions quite similar to those found by us in soft-water lakes of northeastern Wisconsin during the field seasons of 1925 and 1926. Pearsall's paper was received after the present paper had gone to press

The residues from large samples of evaporated water, from which the plankton has been extracted, yield an average of about 0.393 milligram per liter of organic nitrogen and about 5.80 milligrams of organic carbon. The nitrogen and carbon from the residues are called "dissolved." (See Table 2.)

2. The residues from the water of Lake Mendota yield ether extract to an average amount of more than one-half milligram per liter of water (0.564 milligram, Table 5). Green Lake and Lake Geneva yield comparable though smaller quantities.

3. Part of the organic matter in the residues is, no doubt, particulate, but most of it seems to be dissolved. The quantitative relation of these two classes needs further investigation.

4. The crude protein of the residues may be computed from the nitrogen (factor 6.25), and the organic carbon may be distributed to proteins (assigning them 53 per cent C) and to nonnitrogenous matter (computed as 45 per cent C); if the ether extract has been determined the nonnitrogenous matter may be divided into fats (75 per cent C) and carbohydrates (45 per cent C). The average difference between these two methods of computation is about 3 per cent of the total organic matter. (See Tables 8 and 9.)

5. On the first basis of computation the water of Lake Mendota contains an average of nearly 14 milligrams per liter of organic matter, of which about one-tenth is in the plankton. On the second basis, and employing for the plankton the larger average results of the plankton report, the total is nearly 15 milligrams per liter of water, of which less than 2 milligrams are in the plankton. (Tables 8 and 11.)

6. The average nitrogen-carbon ratio in the plankton is about 1 to 6; in the dissolved matter it is about 1 to 14 or 15. In both cases the figures are subject to much variation.

7. The average dissolved protein is from three to six times as great as that of the plankton; the dissolved nonnitrogenous material is about 10 times as great. (See Tables 8 and 11.)

8. Studies of residues from 12 other lakes and 2 rivers show conditions essentially similar to those of Mendota, both in regard to plankton and dissolved organic matter. (See the several tables.)

9. The question of the fundamental food supply of the lake must be reexamined in view of the presence of these relatively large amounts of dissolved organic matter.

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