THE SUMMER STANDING CROP OF PLANTS AND ANIMALS IN FOUR WISCONSIN LAKES*

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INTRODUCTION

Quantitative studies of the biota of several Wisconsin lakes have been in progress for a considerable number of years and the data obtained in four of these investigations are now complete enough to give an approximate idea of the ratio of the aquatic plants to the aquatic animals in summer. Generally speaking aquatic animals are dependent, either directly or indirectly, on aquatic plants for their sustenance; a certain amount of organic matter that may serve as food may be blown into the water by the wind, while another portion may be washed in from the drainage basin or brought in by streams. By far the greater part of the material that is utilized by the aquatic animals, however, is manufactured autotrophically by the aquatic plants of the lake. The relative abundance of the aquatic plants, therefore, becomes a problem of great importance to the animal population of the lake. The manufacturers of the organic matter, namely the plants, include both the phytoplankton and the large aquatic plants that grow in the shallow water, while the animals range from protozoa to fish; the former constitute the producers and the latter the consumers of organic matter. The ratio between the two groups shows the trophic conditions of the consumers. Data are most complete for two lakes in northern Wisconsin (Weber and Nebish) situated near the Trout Lake Limnological Laboratory; with the exception of their fish populations, similar data have been obtained on two lakes in the southern part of the state, namely Green and Mendota. The two northern lakes have soft waters and the southern fairly hard waters so that direct comparisons of the biological productivity of the two types of water can be made. Plankton observations have been made regularly during the months of July and August from 1931 to 1941, inclusive, on the two northern lakes; from time to time during this 11-year period assessments of the large aquatic plants, the bottom fauna and the fish have also been taken,

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so the results give a fairly complete knowledge of the quantitative relationships between the constituents of the biota of these two lakes in summer. Since 1938 the plankton observations have been continued during the other 10 months of the year, but they are not included in the present report; they are reserved for a later paper.

The quantitative investigations on Green and Mendota have included the plankton, the bottom fauna and the large aquatic plants, but no estimates of their fish populations have yet been made; most of the quantitative studies on these two lakes were made between 1912 and 1924, with a few additional observations in more recent years. Data regarding the dissolved organic matter were obtained on the two southern lakes between 1922 and 1924 and on the two northern lakes between 1925 and 1936.

Acknowledgments

Several research assistants have taken part in these investigations, but the list is too long to mention each of them by name. Data regarding the large aquatic plants of Weber Lake have been obtained from Dr. L. R. Wilson, Dr. John E. Potzger and from Mr. L. A. Fraser on those of Nebish Lake. Rickett's reports have been used for the large aquatics of Green and Mendota. Dr. B. P. Domogalla contributed some chemical data on Green and Mendota in addition to those given in his two published papers. Dr. G. Eisenhart has supervised the computations and assisted in making plans for the fish population studies. The Works Projects Administration has given assistance in some phases of the investigations. Financial aid has been received from the Division of Fishery Biology, United States Fish and Wildlife Service, the Wisconsin Conservation Department, the Brittingham Trust Fund, the University Research Committee and the Wisconsin Alumni Research Foundation.

Methods

Plankton. On Weber and Nebish lakes the plankton was taken with a high speed Foerst centrifuge; this instrument has a bowl 75 mm. in inside diameter and a speed of about 18,000 r.p.m. so that it develops a centrifugal force of approximately 12,500 times gravity. This is sufficient to remove the plankton organisms, including about three-quarters of the bacteria, as well as a considerable portion of the organic detritus in a particulate form, and inorganic material in the form of silt; thus the term *seston*

is more appropriate for these catches than plankton. These centrifuge catches were dried, weighed and ashed for the purpose of determining the approximate amount of organic matter in them. Chemical analyses of some of the material have also been made in order to get some idea of its food value. The centrifuge used on Green Lake did not have such a high speed but corrections were made for this difference. A large clarifier type of centrifuge was used on Lake Mendota. It had substantially the same efficiency as the high speed instrument. Plankton observations covering the entire depths of the four lakes were made once a week during the summer, and sometimes twice a week on Lake Mendota. The quantitative data given in the tables thus represent averages of seven to ten sets of samples taken principally in July and August each year; a few sets taken in late June and early September have also been used.

Quantitative determinations of the zooplankton were made simultaneously with a plankton trap. They showed that the rotifers and microcrustacea constituted about 6.5 per cent of the organic content of the centrifuge catches in the two northern lakes and 6.0 per cent in the two southern lakes; these two percentages have been used, therefore, in computing the standing crop of zooplankton. Both the phytoplankton and the organic detritus recovered by the centrifuge are utilized for food by such forms as protozoa, rotifers, microcrustacea, insect larvae and bivalve mollusks; from the food standpoint, then, it is not necessary to distinguish between the living and dead phytoplankton organisms and the organic detritus that may be present.

Bottom flora and fauna. Petersen and Ekman dredges were used for the quantitative studies of the large aquatic plants and the bottom-dwelling animals. In certain localities a square made of strap iron 25 mm. wide and measuring 50 cm. on a side was used for samples of the large aquatics. This square, covering one-fourth square meter, was thrown overboard at random in shallow water and all of the plants inside it were collected by hand. This method was employed chiefly by Rickett in his studies on Green and Mendota. All of the samples of large aquatics in Weber and most of those in Nebish were taken with the regular Petersen dredge which sank into the bottom far enough to bring up the roots as well as the stems of the plants, hence both are included in the weights given for the large aquatics. For the bottom fauna, the Petersen dredge was employed in the shallow

water where the bottom consisted of sand and gravel, and the Ekman dredge in the deeper water where the bottom deposit consisted chiefly of mud. A large percentage of the catches came from the shallow water where a greater variation in numbers and in forms was noted; the average number of samples was 11 per hectare of lake surface.

Fish. Fish population studies have been confined to the two smaller northern lakes; the southern lakes are so large that no attempt has yet been made to estimate their fish populations. In the northern lakes the general method of Dr. David H. Thompson of Illinois has been employed. The fish were caught in modified fyke nets, marked either by placing a numbered metal tag on the gill cover or by clipping a certain fin, and then liberated at a central station. When about 1000 specimens had been marked in Weber Lake and about twice that number in Nebish Lake, fishing operations were discontinued for a week to allow the marked fish to redistribute themselves; this was followed by a second period of fishing which lasted about two weeks. The ratio of marked to unmarked fish caught in the second period of fishing made it possible to compute the total fish population by means of Schnabel's formulae (1938). Experiments have shown that this method is accurate enough for all practical purposes, since the error is less than 10 per cent.

Dissolved organic matter. This material includes the organic matter in true solution and that which is in such a finely divided state that it cannot be recovered with the high speed centrifuge; it also includes about a quarter of the bacteria, but they make only a small contribution because they are usually found in such small numbers in the open water, ranging from 100 to 500 per cubic centimeter as determined by the plate method. The quantity of this unrecoverable organic matter was ascertained by evaporating samples of water from different depths and then determining the amount of organic carbon, organic nitrogen and ether extract (fat) in these residues. The quantity of organic N $\times$ 6.25 gives the crude protein. In computing the organic matter from these determinations, the following percentages of carbon were assigned to the three primary constituents: crude protein, 53 per cent; ether extract, 75 per cent; carbohydrate, 50 per cent. Deducting the organic content of the plankton from the sum of these three items leaves what has been called the "dissolved organic matter" in these lake investigations; as already indicated it does contain a certain amount of particulate matter.

The weight data included in the tables for the various biotic constituents give the wet weight in kilograms per hectare on an ash-free basis. The wet weights best represent the natural status of the animals and plants in the water; such weights were obtained directly for the large aquatics, the bottom fauna and the fish. The wet weight of the plankton was obtained by multiplying the dry weight of the organic matter by the factor 10; this factor is based on results which show that the water content of a number of plankton organisms ranges from 90 to 95 per cent. In fact substantially the same percentages of water have been found in the large aquatics, the bottom fauna and the fish; thus the wet weights given in the tables can be converted to dry weights by dividing them by 10. The percentage of ash in the several biotic constituents varies widely, ranging from less than 5 per cent of the dry weight in some of the plankton organisms to more than 50 per cent in Chara; so it was deemed best to state the results on an ash-free basis which gives a better picture of the organic content of the lake as a whole and which is also advantageous in considering the producer-consumer relationships.

Character of Lakes

Table 1 gives some of the physical characteristics of the four lakes. It will be noted that Weber and Nebish are much smaller and shallower than Green and Mendota. Weber Lake is the smallest and shallowest of the four and it belongs to the seepage type; that is, it has neither an inlet nor an outlet. It loses water only by evaporation and by seepage through the ground. The drainage basin is very small so that most of its water supply comes from the rain and snow precipitated on its surface. This reduction of the land factors of its environment to a minimum

Table 1. Physical characteristics of the four lakes on which quantitative studies of the biota have been made. The color was determined by the platinum-cobalt standard; a 30 cm. white disc was used to determine the transparency and the depth at which the disc disappeared from view is indicated in meters.

Lake	Area in hectares	Depth in meters		Volume in cubic meters	Color	Transparency
		Maximum	Mean			
Weber	15.6	13.5	7.2	1,132,900	3	6.6
Nebish	38.5	15.8	5.2	2,015,300	8	5.6
Green	2972.4	68.0	33.1	974,325,000	4	3.7
Mendota	3940.0	25.6	12.1	478,370,000	8	2.2

gives Weber Lake unique characteristics and makes it as complete a self-contained aquatic habitat as nature can provide.

Nebish Lake is two and a half times as large as Weber and has a somewhat greater maximum depth, but a smaller mean depth. Its drainage basin is small also and it has no inlet. At unusually high stages of the water there is an overflow into a small detached basin which has no visible outlet but which has margins and bottom without a water tight seal. As a result the overflow water which it receives from Nebish escapes rapidly by seepage through the ground. Aside from this unique type of outlet discharge, Nebish Lake is equally as isolated from its land environment as Weber Lake.

Green and Mendota are much larger than the two northern lakes; they have inlets and outlets and relatively large drainage basins; thus they belong to the drainage type of lakes and are subject to a much greater influence of land factors in their environment than the two northern lakes. Green Lake has a maximum depth of 68 meters and it is the deepest lake within the borders of the state. Its large volume is shown by the fact that its mean depth is 33.1 meters.

Table 2 gives some of the chemical characteristics of the waters of the four lakes. Weber and Nebish have very soft waters, the former especially; they are situated in a region where the upper part of the glacial deposit contains relatively small amounts of carbonates. While the deeper deposits contain larger amounts of carbonates, the lake basin seal keeps the deeper ground waters from entering these two lakes and giving the water a larger mineral content. The bed rock in this region consists of

TABLE 2. Chemical characteristics of the waters of the four lakes on which biological studies were made. The conductivity or specific conductance is expressed in reciprocal megohms; the dissolved substances are indicated in milligrams per liter of water.

Lake	Conductivity	pH	Bound CO_2	SiO_2	Ca	Mg	Sol. P	NO_3
Weber	10	6.4	1.3	0.1	0.7	0.6	0.003	0.014
Nebish	19	7.0	4.0	0.2	2.3	1.7	0.002	0.014
Green	275	8.5	75.2	8.4	21.2	25.7	0.004	0.024
Mendota	270	8.6	69.0	0.5	22.4	24.2	0.005	0.025

granite which is covered by glacial deposits ranging from 42 to 70 meters in depth.

Green and Mendota are situated in limestone regions so that their waters have a much larger mineral content than those of the northern lakes. Carbonates are plentiful in their drainage basins so that the inflowing waters add a substantial amount of inorganic material to these two lakes. Because of their location in limestone areas, they both have fairly hard waters.

QUANTITATIVE DATA

Weber Lake

Some of the results obtained in the quantitative studies of the biota of Weber Lake are given in Table 3. These investigations covered the standing crop of the various forms during the months of July and August in the years indicated in the table. In one year an additional set of plankton samples was taken during the last week in June and in two other years sets were taken in the first week of September; these extra observations have been used in computing the summer means of these years since they correspond so closely in time with the other samples. The second column in the table gives results for 1936-38, inclusive, because complete assessments of the bottom flora and fauna were not made annually during this period; in fact the complete survey of these two groups of organisms extended from 1936 to 1939, thus these two items are given the same values in the 1936-38 column and in the 1939 column. Complete assessments

TABLE 3. Average amount of organic matter in standing crop of plants and animals in Weber Lake in summer; the quantity of dissolved organic matter is also given. The results are stated in kilograms per hectare of lake surface on a wet weight, ash-free basis.

	1933	1936-38	1939	1940
Total plankton	624	921	1026	1143
Phytoplankton	583	861	959	1069
Zooplankton	41	60	67	74
Bottom flora	366	447	447	553
Bottom fauna	73	123	123	147
Fish	38	29	17	23
Dissolved organic matter	2663	2264	.....	2866
Total weight of plants	949	1308	1406	1622
Total weight of animals	152	212	207	244
Ratio of plants to animals	6.2	6.1	6.8	6.6
Ratio of plants to animals, excluding fish	8.3	7.1	7.4	7.3
Ratio of other animals to fish	3.0	6.3	11.1	9.6

were made in 1933 and again in 1940, however, as indicated in the table.

The table shows that there was almost a twofold increase in the standing crop of plankton between 1933 and 1940. This increase was due in part, at least between 1936 and 1940, to the use of fertilizers; the lake is small enough to permit experiments of this character without excessive cost of materials. From 1932 to 1935 inclusive, mineral fertilizers were used, such as superphosphate, lime, nitrogen compounds and potash, but they seemed to have no effect upon the standing crop of plankton. The mean quantity of organic matter in the plankton during these four summers ranged from a maximum of 722 kg/ha, wet weight, in 1932 to a minimum of 604 kg/ha in 1935, with a mean of 651 kg/ha for the four-year period; the mean for the summer of 1931, the year before any fertilizers were added, was 675 kg/ha, or 24 kg/ha larger than the mean of the four following summers (1932-35) when mineral fertilizers were used.

In July and August, 1936, an organic fertilizer in the form of soybean meal was added to the lake and there was an appreciable increase in the standing crop of plankton; the mean was 952 kg/ha as compared with 651 kg/ha for the four previous summers in which mineral fertilizers were applied; this represented an increase of 45 per cent. The average standing crop was three per cent smaller in 1937 than in 1936 and only about 7 per cent smaller in 1938 than in 1936, but no fertilizers were added during these two summers; apparently the soybean meal was effective for three summers. In 1939 cottonseed meal was used and a further increase in the plankton crop was observed as shown in the table; the mean for that summer was 1026 kg/ha. There was a further increase to 1143 kg/ha in 1940 although no fertilizer was added in that summer. Likewise no fertilizer was added in 1941 and the mean crop of plankton declined to 824 kg/ha. From this result it appears that the cottonseed meal was effective for only two instead of three summers as noted for the soybean meal. However, this difference may be due in part to the fact that only one ton of cottonseed meal was added as compared with one and a half tons of soybean meal.

Corresponding to an increase in the standing crop of plankton from 1936 to 1940 was a similar increase in the weight of the bottom flora and fauna as indicated in the table. During this time the bottom flora increased from 366 kg/ha in 1933 to 553

kg/ha in 1940, while the bottom fauna rose from 73 kg/ha in 1933 to 147 kg/ha in 1940, a twofold increase. The fish, on the other hand, declined in weight from 38 kg/ha in 1933 to a minimum of 17 kg/ha in 1939, with a slight increase to 23 kg/ha in 1940. The total weight of plants (phytoplankton and large aquatics) increased from 949 kg/ha in 1933 to 1622 kg/ha in 1940, an increase of 71 per cent, while that of the animals rose from 152 kg/ha in 1933 to 244 kg/ha in 1940, an increase of a little more than 60 per cent. The somewhat lower percentage gain in the animals was due chiefly to the decrease in the weight of the fish.

The third line from the bottom of Table 3 shows the ratios of the wet weight of the plants to that of the animals on an ash-free basis. The plants include the combined weight of the phytoplankton and the large aquatics and the animals that of the zooplankton, the bottom fauna and the fish. It will be noted that these ratios are remarkably uniform for the eight-year period covered by these observations, ranging from a low of 6.1 in 1936-38 to a high of 6.8 in 1939. They mean that each kilogram of animals had a potential food resource of 6 to 7 kilograms of plants, and this ratio remained almost constant in spite of the annual changes found in the total weight of these two groups during the eight summers. That is, they reached a biological balance when the weight of the plants was between 6 and 7 times that of the animals. Apparently the biotic potential of the plants was such that they were able to take advantage of the more favorable trophic conditions produced by the addition of the organic fertilizers and the biotic potential of the animals, with the exception of the fish, enabled them to respond promptly to the improved food conditions resulting from the increase in the plants.

The second line from the bottom of Table 3 shows the relation of plants to animals when fish are excluded from consideration. Since fish are chiefly animal consumers, their exclusion gives a better idea of the more direct relations between plants and animals from a food and feeder standpoint; in addition also the fish populations of Green and Mendota are not known and these ratios with fish excluded can be compared directly with similar ratios for the two southern lakes. In Weber Lake the ratios with the fish excluded show a somewhat larger variation than with the fish included, yet they are reasonably close, ranging from 8.3

in 1933 to 7.1 in 1936-38. These ratios are really an index of the efficiency of the animals in utilizing the plant material for grazing purposes.

The last line in Table 3 shows the relation of the weight of the food directly available for fish (zooplankton and bottom fauna) to the weight of the fish. While the quantity of food gradually increased from 1933 to 1940, the weight of the fish declined during this time, reaching a minimum in 1939 with a moderate increase in 1940. The ratio of available food to fish rose from 3.0 in 1933 to 11.1 in 1939, which was more than a threefold increase. Thus the fish did not respond as promptly to the improved food conditions as the other animals which suggests that other factors than food were involved in the decrease of the fish population. Couey (1935) found that more than 80

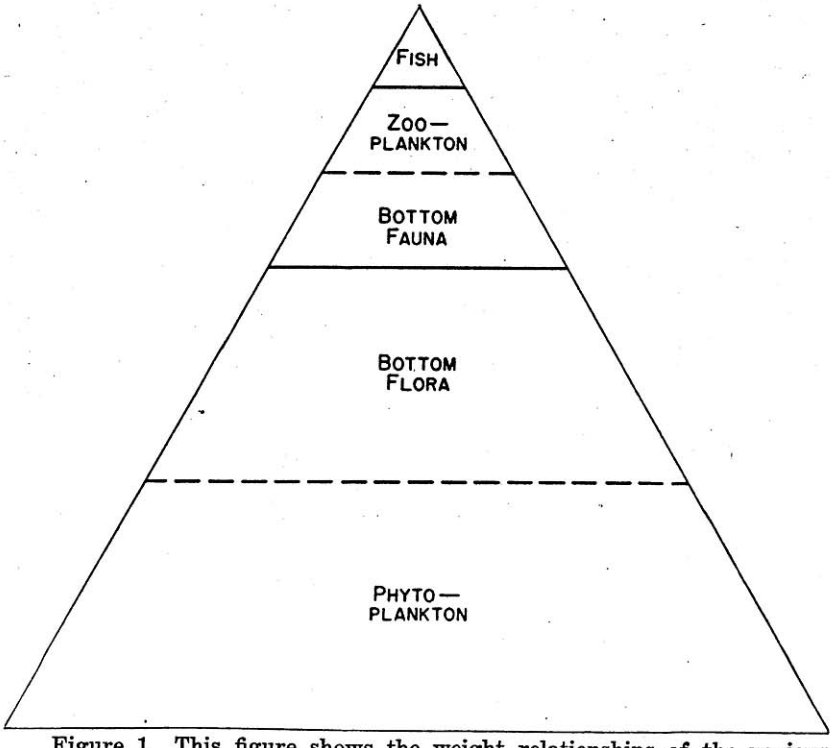

Figure 1. This figure shows the weight relationships of the various constituents of the biota of Weber Lake; it is based on the weights given in the 1940 column of Table 3. The weight of each constituent is proportional to the total area of the triangle; the original diagram was platted on a scale of 1 kg/ha = 12.4 sq. mm.

per cent of the food of the yellow perch of Weber Lake consisted of aquatic insect larvae and Cladocera; the same was true of the smallmouthed black bass, the only species of fish found in the lake at the time of his investigations (1931-32). Both of these food organisms showed an increase between 1933 and 1940, yet there was a decline in the weight of the fish.

Figure 1 shows graphically the weight relationships of the various constituents of the biota of Weber Lake during the months of July and August, 1940; it serves to illustrate what may be called the "pyramid of aquatic life" in the lake during those months. The entire area of the triangle represents the total weight of plants and animals, namely, 1872 kg/ha; the areas included in the various divisions of the triangle are proportional to the weight contributed to the total by each group. The original diagram was platted on a scale of 1 kg/ha = 12.4 sq. mm. The lower part of the diagram shows the broad foundation of aquatic plants on which the animal population rests; the two groups of plants (phytoplankton and large aquatics) are separated by a broken line in order to indicate the relative weight of each group. The upper part of the triangle represents the amount of organic matter contributed by the animals; the zooplankton and bottom fauna are separated by a broken line, while the fish are set off with a solid line since they may be regarded as the end product of all the biological processes that take place in the lake. The diagram shows clearly what a small proportion of the total weight of the biota is contributed by the animals, with the fish forming only a small cap for the pyramid. The percentage of organic matter contributed by the various groups of organisms is indicated in Table 5. The phytoplankton and the large aquatics together furnished substantially 87 per cent of the material and the animals 13 per cent, of which the fish constituted only 1.23 per cent.

This type of diagram does not show the food relationships between the plants and the animals nor those existing among the animals themselves. Most of the animals are vegetarians and feed directly on the plants, but some forms are carnivorous and prey upon other animals; the fishes particularly are chiefly carnivorous and only a few species of them are vegetarians.

In addition to the organic content of these groups of plants and animals the dissolved organic matter needs to be taken into consideration. The quantity of this material found in Weber Lake

is given in Table 3. The mean for 21 series of samples taken between 1925 and 1936, inclusive, is 2866 kg/ha as indicated in the 1940 column of the table. This quantity is 52 per cent larger than the organic content of the standing crop of plants and animals in that year. Somewhat smaller amounts were found in 1933 and in 1936, yet the dissolved organic matter was more than twice as large as the organic content of the plants and animals in 1933 and 49 per cent larger in 1936.

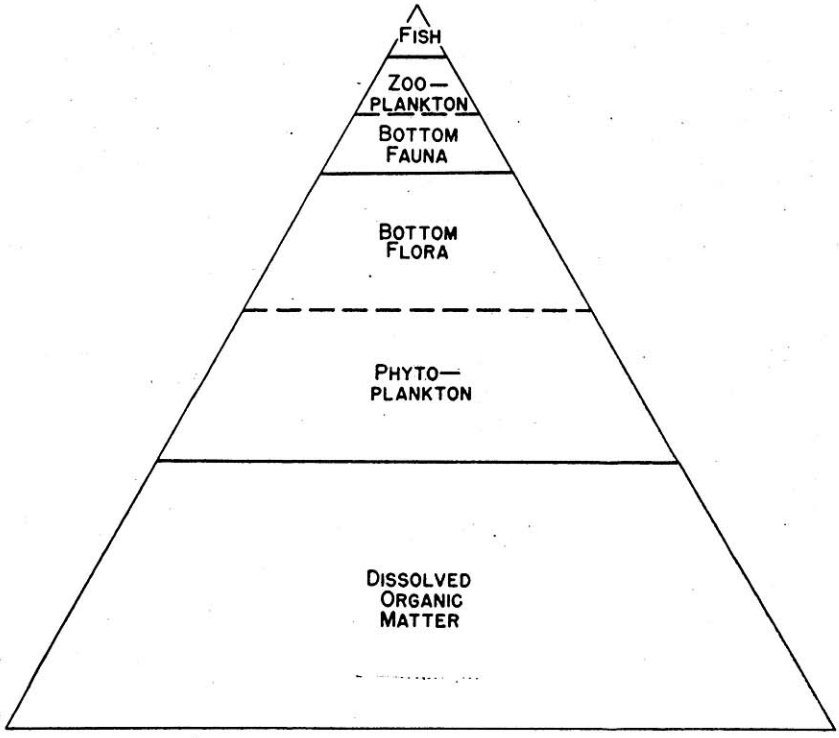

Figure 2. This figure shows the weight relationships of the biota and the dissolved organic content of Weber Lake. The weight of each constituent is proportional to the total area of the triangle. The original diagram was platted on a scale of 1 kg/ha = 4.9 sq. mm.

Figure 2 shows the quantitative relationships of the plants and animals to each other and also to the dissolved organic content of the water of Weber Lake. It gives a general picture of the organic content of the water together with those of the bottom flora and fauna. The diagram shows clearly what a large proportion of the pyramid is required to represent the quantity of dissolved organic matter and it also demonstrates what a small

role the animals play in that part of the organic content of the lake which is included in these studies. Percentages for the various items in this organic matter budget are given in Table 5. The dissolved organic matter makes up a little more than 60 per cent of the total included in the diagram, while the fish constitute only one-half of one per cent and the other animals a little less than 5 per cent.

With the exception of the comparatively small number of bacteria which it contains, the dissolved organic matter consists of material that is on its way back to the elemental status from which it came originally, namely, water, carbon dioxide and nitrogen compounds. The major part of it comes from the phytoplankton and thus represents the surplus of organic matter produced by these organisms which has not been used by the animal consumers up to this stage; that which is still in a particulate state is available for the food of some animals, especially some of the zooplankton forms.

Up to the present time, the survey of the bottom deposits in the deeper water has been limited to the upper 15 cm. so that nothing is known of the total depth of the deposits or their organic content at greater depths. In the upper 15 cm. chemical analyses show that 43.3 per cent of the dry weight of the mud consists of organic matter with the following composition: 12.1 per cent crude protein; 1.2 per cent ether extract; 30.0 per cent carbohydrate (Juday, et al., 1941). According to Steiner and Meloche (1935) about half of the organic matter is ligneous in character. Henrici and McCoy (1938) found that the average dry weight of one cubic centimeter of the upper 15 cm. of the Weber Lake deposits was 0.032 gram. The typical mud deposits are limited to the region below a depth of 8 m. which has an area of 79,200 sq. m. Computations based on the foregoing data indicate that the organic content of the upper 15 cm. of the deposits within the 8 m. contour line amounts to 1,644,952 kilograms, wet weight. Since some of this organic matter is derived from the 0-8 m. zone as well as from the deep water, the whole lake must be taken into account in computing the average amount per unit of area; that is, the organic matter deposited on the bottom in the shallow water is eventually carried out to the deeper water by the action of the waves and currents. Taking the area of the entire lake into consideration, the organic content of the

upper 15 cm. of the bottom deposits amounts to an average of 105,378 kg/ha, wet weight.

Just how long a period it has taken to form the upper 15 cm. of the deposit can only be conjectured. Conger (1939) estimated that the rate of deposition in Crystal, a nearby seepage lake, was only about 0.25 mm. per year on the basis of 10,000 years of elapsed time since the close of the glacial period or half that amount on a 20,000 year basis. At the rate of 0.25 mm. per year the upper 15 cm. in Weber Lake would represent an accumulation extending over a period of 600 years or twice that number of years on a 20,000 year scale. This upper layer is not as compact as the deeper layers of the deposits so that it probably represents a somewhat shorter period of time than the average for the total deposit; it is evident however, that the upper 15 cm. of the deposit in a lake having the characteristics of Weber would require a few hundred years, at least, for its deposition.

Twenhofel and Broughton (1939) found much smaller amounts of organic matter in the strata below a depth of 15 cm. in the deposits of Crystal Lake and it seems reasonable to suppose that the same is true of the deeper strata in the Weber Lake deposits. Henrici and McCoy (1938) found a considerably larger bacterial flora in the upper 9 cm. of the bottom deposits of Weber than between 9 and 21 cm. which may be regarded as an indication that organic substances are more plentiful in the upper 9 cm. of the deposits.

Nebish Lake

The results of the quantitative investigations made on Nebish Lake during July and August, 1941, are given in Table 4. Regular observations on the plankton of this lake were begun in 1931 and have been continued each summer up to and including 1941. The general purpose of these studies was to use the plankton results for comparison with those obtained on Weber Lake where fertilizers were being used; the waters of the two lakes are similar in their physical and chemical characteristics, but that of Nebish Lake has a somewhat larger mineral content than that of Weber (Table 2). Also they are only about 8 km. apart so that they are both subject to the same general climatic conditions; likewise both are surrounded by second growth timber.

TABLE 4. Average amount of organic matter in standing crop of plants and animals in Nebish Lake in July and August, 1941; the quantity of dissolved organic matter is also indicated. The results are stated in kilograms per hectare of lake surface, wet weight, on an ash-free basis.

Total plankton	650
Phytoplankton	608
Zooplankton	42
Bottom flora	590
Bottom fauna	122
Fish	35
Dissolved organic matter	3829
Total weight of plants	1198
Total weight of animals	199
Ratio of plants to animals	6.0
Ratio of plants to animals, excluding fish	7.3
Ratio of other animals to fish	4.7

While some quantitative studies of the bottom fauna were made in 1931 and 1935, the number of samples taken each year was not large enough for the estimation of the bottom population of the entire lake. A cursory survey of the large aquatic plants of Nebish Lake was made in 1935 also, but it was chiefly qualitative in character. Thus no complete quantitative survey of these two groups of organisms was made until the summer of 1941. The investigation also included estimates of the fish populations each summer from 1938 to 1941. The results of the 1941 survey are given in Table 4.

During the 11 years covered by the plankton studies of Nebish Lake, the quantity of organic matter in the standing crop varied from a minimum of 525 kg/ha, wet weight, in 1931 to a maximum of 1002 kg/ha in 1940, with a mean of 714 kg/ha for the entire period. The table shows that the average standing crop of 1941 was below the general mean, namely 650 kg/ha. The bottom flora of Nebish in 1941 yielded a somewhat larger crop than that of Weber Lake in 1940, or 590 as compared with 553 kg/ha. The weight of the bottom fauna, on the other hand, was appreciably smaller in Nebish in 1941 than in Weber in 1940; it amounted to 122 kg/ha in the former as compared with 147 kg/ha in the latter. The standing crop of fish was larger in Nebish than in Weber, namely 35 to 23 kg/ha.

The dissolved organic content of the water was about one-third larger in Nebish than in Weber, or 3829 kg/ha in the former as compared with 2866 kg/ha in the latter. The quantity in the

Nebish Lake water was nearly three times as large as the organic content of the plants and animals combined. The ratio of plants to animals in Nebish Lake was just a little below the minimum of Weber Lake, or 6.0 as compared with 6.1. Excluding the fish the 1941 ratio of plants to other animals is substantially the same for Nebish as for those of Weber Lake in 1939 and 1940, or 7.3 as compared with 7.4. The ratio of the weight of the zooplankton and bottom fauna to that of fish in Nebish Lake is 4.7, which is larger than that found in Weber Lake in 1933, but much smaller than those of Weber in 1939 and 1940. The ratio of plants, zooplankton and bottom fauna to fish in Nebish Lake was 37.1; in a general way this represents the potential food resource of each kilogram of fish. The weight of the fish in Nebish Lake constituted 2.5 per cent of the total weight of plants and animals; this is twice as large as the percentage found in Weber Lake, namely 1.2 per cent (Table 5).

TABLE 5. The percentages which the various forms contribute to the total weight of plants and animals per unit of area and to the total quantity of organic matter (plants, animals and dissolved organic matter) in Weber and Nebish lakes.

	Weber Lake, 1940 Per cent of plants and animals	Per cent of total organic matter
Plankton	61.26	24.15
Phytoplankton	57.29	22.59
Zooplankton	3.97	1.56
Bottom flora	29.63	11.69
Bottom fauna	7.88	3.11
Fish	1.23	0.49
Dissolved organic matter	....	60.56
	Nebish Lake, 1941	
Plankton	46.53	12.44
Phytoplankton	43.53	11.63
Zooplankton	3.00	0.81
Bottom flora	42.24	11.30
Bottom fauna	8.73	2.33
Fish	2.50	0.67
Dissolved organic matter	....	73.26

The weight relations between the various constituents of the biota of Nebish Lake are shown graphically in Figure 3; it corresponds to Figure 1 for Weber Lake. A comparison of these two figures shows that the phytoplankton constitutes a smaller

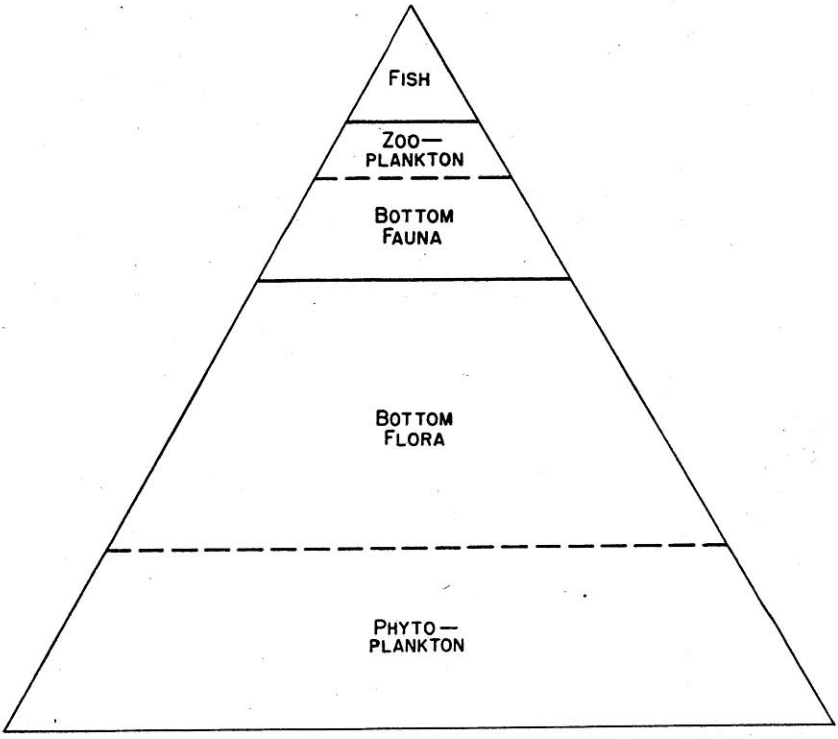

Figure 3. This figure shows the weight relationships of the various constituents of the biota of Nebish Lake; it is based on the weights given in Table 4. The weight of each constituent is proportional to the total area of the triangle. The original diagram was platted on a scale of 1 kg/ha = 16.6 sq. mm.

proportion of the plant base of the pyramid of Nebish than that of Weber Lake, but the reverse is true of the bottom flora of the two lakes; a small part of these differences is due to the slightly different scales on which the two diagrams are platted. In both lakes the animals constitute substantially the same proportion of the total biota; in Nebish Lake the animals represent 13.2 per cent of the total weight and in Weber Lake 13.0 per cent. The cap of the pyramid which represents the fish of each lake is somewhat larger in the Nebish than in the Weber Lake diagram.

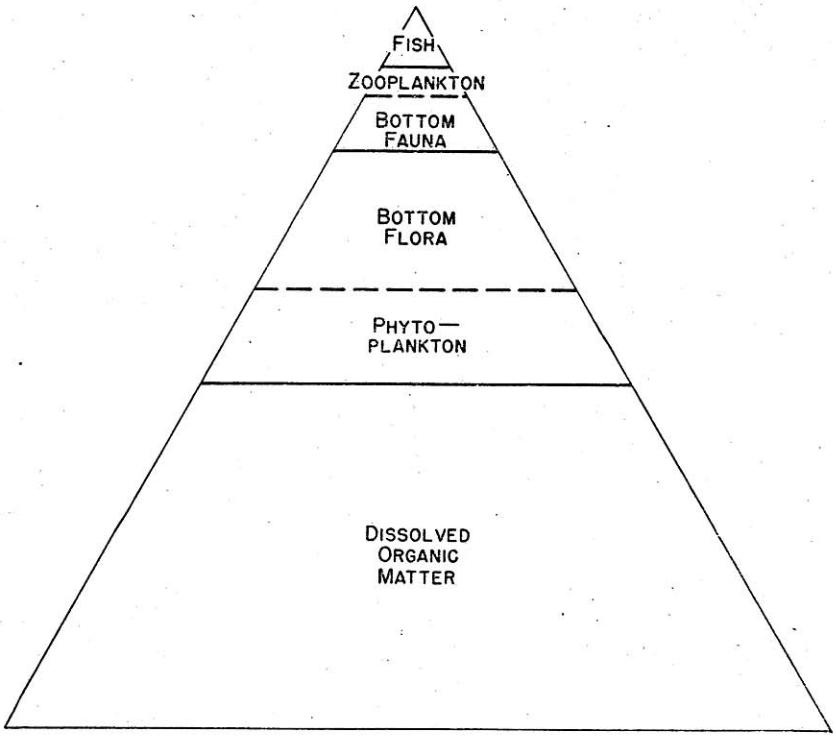

Figure 4. This figure shows the weight relationships of the biota and the dissolved organic matter of Nebish Lake. The weight of each constituent is proportional to the total area of the triangle. The original diagram was platted on a scale of 1 kg/ha = 4.4 sq. mm.

Figure 4 shows the relative proportions of the plants, the animals and the dissolved organic matter of Nebish Lake; it corresponds to Figure 2 of Weber Lake, thus including the total organic content of the water as well as the bottom flora and fauna. It will be noted that the dissolved organic matter base of the pyramid is appreciably larger than that of Weber Lake and that the plant and animal portions are correspondingly smaller. In Nebish Lake the dissolved organic matter makes up 73 per cent of the total organic content, while in Weber Lake it constitutes only 60 per cent (Table 5).

As a result of the larger percentage of dissolved organic matter in the water of Nebish Lake, no special comparisons between the plants and animals of the two lakes as shown by these two figures can be made; but they serve to show what a small propor-

tion of the organic content of the two lakes is contributed by the animals. In Nebish Lake the animals constitute 3.8 per cent of the total organic matter represented in the pyramid, of which 0.7 of one per cent consists of fish, while in Weber Lake the animals contribute 5.1 per cent, with a little less than 0.5 of one per cent consisting of the fish.

The weights of the fish populations of Weber and Nebish lakes seem unusually small, but they compare favorably with some of the results that have been reported by other investigators. Tarzwell (1940) reported the weights of the fish populations of several lakes and among them are seven, three situated in Nova Scotia and four in Michigan, which had standing crops ranging from 19 to 49 kg/ha; the records for these seven lakes are based on poisoning experiments and thus represent the actual weights of the fish populations.

Data are not available for the computation of the organic content of the bottom deposits of Nebish Lake. The organic content of the upper 15 cm. was 54.3 per cent of the dry weight as compared with 43.3 per cent in the deposits of Weber Lake. The organic matter of the bottom deposits of Nebish Lake consisted of 16.6 per cent crude protein, 2.2 per cent ether extract and 35.5 per cent carbohydrate.

Green Lake

Green Lake ranks second in area in this group of four lakes; it is first in maximum and mean depths as well as in volume (Table 1). The water has only a small amount of color as determined by the platinum-cobalt standard and it has a medium transparency as compared with the other three lakes. The mineral content of the water is much larger than in Weber and Nebish so that it ranks as a fairly hard water lake (Table 2).

The results of the biological survey of Green Lake are given in Table 6. The standing crop of plankton was larger than those of the other three lakes, amounting to 2944 kg/ha, wet weight. This is more than four times as large as the standing crop of Nebish Lake and two and a half times as large as that of Weber in 1940. It is also about one-third larger than that of Lake Mendota. The large crop of plankton in Green Lake when given on a unit area basis is due in part to the much greater depth of this body of water. Light conditions are such in Green Lake that the zone of photosynthesis or region of phytoplankton production extends to a depth of about 15 m. in summer, but the

TABLE 6. Average amount of organic matter in the standing crop of plants and animals and in the dissolved organic matter of Green Lake and of Lake Mendota. In Green Lake the plankton samples were taken in July and August, 1921-24 inclusive, and in Mendota in July and August, 1915-16. The amounts are given in kilograms per hectare of lake surface on a wet-weight, ash-free basis.

	Green	Mendota
Total plankton	2944	1995
Phytoplankton	2767	1875
Zooplankton	177	120
Bottom flora	4218	4600
Bottom fauna	138	414
Dissolved organic matter	27,901	15,201
Total weight of plants	6985	6475
Total weight of animals, excluding fish	315	534
Ratio of plants to animals, excluding fish	22.2	12.1

0-15 m. stratum includes only about one-third of the total volume of the lake. The large volume of water below this depth contains a certain amount of phytoplankton and a moderate population of zooplankton organisms so that the microscopic life of the lower water contributes a substantial amount of material to the plankton crop of the upper stratum when results are expressed in terms of a unit area of surface.

The table indicates that the standing crop of large aquatic plants was seven to ten times as large as those of Weber and Nebish lakes, but it was somewhat smaller than that of Lake Mendota. The main constituent of this crop in Green Lake was Chara which has a large percentage of ash, namely 41.0 per cent of the dry weight (Schuette and Alder 1929); this accounts in part for the smaller organic content of this crop of large aquatics as compared with that of Lake Mendota. In connection with the bottom flora, it may be noted that *Oscillatoria prolifica* was found growing saprophytically in a grayish mat 2 mm. thick on the bottom of Green Lake where the water was 65 to 68 meters in depth. (Juday 1934.)

The weight of the bottom fauna of Green Lake was smaller than that of Weber Lake in 1940, but larger than those of previous years; it was about 10 per cent larger than the weight of the bottom fauna of Nebish Lake in 1941 but only one-third as large as that of Lake Mendota. This comparatively small weight of the bottom fauna is due, in part at least, to the depth of the

water, the steep slope of the bottom and the low temperature of the bottom water which ranges from 2° in winter to about 6° C. in summer. Environmental conditions in Green Lake favor the Tanytarsus rather than the Chironomus type of bottom fauna and it is a well established fact that the former type of lake does not support as large a bottom population as the latter.

The dissolved organic content of the water of Green Lake is unusually large, amounting to 27,901 kg/ha on a wet weight basis; this is almost four times the total weight of the plants and animals, namely 7300 kg/ha. Again this large amount of dissolved organic matter per unit area is partly explained by the greater depth, hence greater volume, of the lake. While the quantity of dry organic matter in this dissolved material was only about two-thirds as large per unit volume in Green Lake as in Lake Mendota, yet the amount per unit of surface was much larger in the former than in the latter because of the larger volume of water in the former; on a dry weight basis the dissolved organic matter in Green Lake was 8.42 mg/1 as compared with 12.52 mg/1 in Lake Mendota.

Table 6 shows that the ratio of plants to animals in Green Lake, excluding fish, is 22.2, which is much larger than in the other three lakes; this means that there are 22.2 kilograms of organic matter in the phytoplankton and large aquatics to one kilogram of organic matter in the zooplankton and bottom fauna. Such a large ratio indicates that the animal population of Green Lake is much less efficient in converting the plants into animal material than those of the other three lakes. The relatively small weight of the bottom fauna was chiefly responsible for this situation.

Lake Mendota

Lake Mendota is the largest of these four lakes; it has a medium depth, with a maximum of 25.6 m. and a mean of 12.1 m. (Table 1). The color of the water is low, the same as that of Nebish Lake; the transparency is also low in the summer, with a mean of 2.2 m. for the disc readings. The mineral content of the water is substantially the same as that of Green Lake, so that it has a fairly hard water (Table 2).

The wet weight of the standing crop of plankton was three to five times as large as those of Weber and Nebish lakes, but it was more than 30 per cent smaller than that of Green Lake.

The standing crop of large aquatic plants was larger than those of the other three lakes; it exceeded that of Green Lake by about 8 per cent and it was eight to twelve times as large as those of Weber and Nebish lakes (Table 6). A much larger bottom fauna was found in Lake Mendota than in the other three lakes; its weight was 414 kg/ha as compared with 73 to 147 kg/ha in the others. While a large part of the hypolimnion of Mendota is devoid of dissolved oxygen for three months or more each summer, the lower layer of water does not become too foul for the bottom-dwelling organisms during this time; in fact large numbers of Limnodrilus, Tubifex, Pisidium, Chironomus and Chaoborus (Corethra) occupy the bottom zone at this time (Juday 1921); it is thus a Chironomus type of euthropic lake.

The quantity of dissolved organic matter in the water of Lake Mendota amounted to 15,201 kg/ha, which is only a little more than half as much as found in Green Lake, but it is two to seven times as large as noted in Weber and Nebish lakes. It is a little more than twice the organic content of the plants and animals, excluding the fish.

The ratio of plants to animals, excluding the fish, is 12.1, which is much smaller than that found in Green Lake, but it is almost twice as large as those of Weber and Nebish lakes. This indicates that the efficiency of Lake Mendota in converting aquatic plants into zooplankton and bottom fauna, the two main direct sources of food for fish, is much higher than that of Green Lake, but it is much lower than those of Weber and Nebish lakes.

Discussion of Results

Plants

By means of energy derived from subsurface solar radiation, most of the fundamental foodstuffs of a lake are manufactured autotrophically by aquatic plants from substances dissolved in the water or from materials present in the subaqueous soils. A certain amount of organic matter comes from outside sources, such as that blown into the lake by wind and that which is brought in by drainage waters from the shores and by inflowing streams in the form of particulate and dissolved organic matter. The aquatic chlorophyll-bearing organisms, however, constitute the chief producers of the primary organic content of the lake and this material, either directly or indirectly, is the main source of the food of the animals. In addition to that which is consumed

by animals, the plants themselves use a certain amount of the organic material which they manufacture in their own metabolic processes; experiments have shown that this is about one-third of the total quantity of organic matter manufactured by them, which leaves two-thirds available as food for the animals. These food relationships raise the question of the ratio of the weight of the standing crop of plants to that of animals; in other words, what is the ratio of producers to consumers?

Turning first to a consideration of the trophic conditions of the plants in the two types of lakes dealt with in this report, Table 2 shows the marked difference in the mineral content of their waters. The data listed in the other tables give direct evidence of the dynamic response of the aquatic vegetation to the differences in the chemical factors of their environment. That is, the standing crop of plants per unit of area was found to be much smaller in the soft than in the hard water lakes. There is some difference in the climatic conditions of the two regions in which the lakes are situated. The northern soft water lakes have a somewhat shorter growing season; their waters begin to cool earlier in the autumn and they become covered with ice some three weeks earlier than the southern lakes. In the spring also, they retain their ice cover about three weeks longer than the southern lakes; thus they are subject to low winter temperatures at least six weeks longer each year than the two southern lakes. On the whole however, the climatic factor can hardly be regarded as having much importance in determining the marked difference in the size of the standing crop of plants in the northern soft water lakes as compared with that of the southern hard water lakes.

The data indicate that the mineral content of the water is the chief factor in determining the plant production of these two groups of lakes. Just which minerals play the most important role in limiting the plant crop of the northern lakes has not been determined. Phosphorus and nitrogen compounds are generally considered as the chief limiting factors. Table 2 shows that the difference in the soluble or phosphate phosphorus content of the two types of water is about twofold. This is the form of phosphorus that can be used directly by the plants; the organic form can not be utilized until it is liberated from its organic combination or "regenerated." The nitrate content of the waters of the two southern lakes is about twice as large as that of the

northern lakes, so that both of these factors need to be taken into consideration with reference to the size of the plant crops in the four lakes. Fertilizing experiments on Weber Lake, however, show that both phosphorus and nitrogen compounds did not stimulate the growth of aquatic plants in that body of water; thus there is some doubt about their serving as limiting factors in the two soft water lakes.

In 1932 for example, enough superphosphate was added to Weber Lake to raise the phosphate content of the water to approximately ten times the amount found in 1931 when no fertilizers were used, but no response from the phytoplankton was observed. In the summer of 1933 both superphosphate and lime were added without any response; superphosphate, lime and nitrate were added in 1934 and no effect on the phytoplankton was noted. In 1935 similar negative results were obtained with nitrate and potash; in fact the phytoplankton crop of this year was smaller than in the three previous summers. Thus the small standing crop of phytoplankton of Weber Lake can hardly be attributed to any of these four mineral factors.

In the summer of 1936, 1360 kilos of soybean meal were used and a prompt response was obtained from the phytoplankton; the average standing crop was 50 per cent larger than in the three previous summers. The mean standing crop of phytoplankton for 1933-35, inclusive, was 586 kg/ha, while the 1936 crop was 890 kg/ha. Also the effect of the soybean meal seemed to last through the summers of 1937 and 1938 as well, since the phytoplankton showed only a three per cent decrease during the first and a seven per cent decrease during the latter summer. During the summer of 1939, 907 kilos of cottonseed meal were added to the water and a further favorable response was noted in the phytoplankton when the mean standing crop rose to 959 kg/ha, an increase of almost 8 per cent over the average of 1936. It rose to a maximum of 1069 kg/ha in 1940 without the addition of any more fertilizer, which was an increase of more than 11 per cent over the mean crop of 1936 and almost twice as large as the mean crop of 1933-35, namely, 586 kg/ha, when mineral fertilizers were being added. There was a sharp decline in the standing crop of phytoplankton in 1941, the amount falling to 770 kg/ha, a decrease of 28 per cent as compared with the 1940 crop; no fertilizer was added in 1941. These experiments seem to warrant the conclusion that an organic fertilizer, carrying

both mineral and organic constituents, is necessary to stimulate the growth of the phytoplankton in Weber Lake and presumably this would be true of similar soft water lakes in this region. An increase in the standing crop of large aquatic plants was also noted between 1936 and 1940 which indicates that they also were affected by the organic fertilizers (Table 3).

The larger quantities of calcium and magnesium present in the hard waters may play a rôle also since they exist chiefly as carbonates and bicarbonates and thus make a much larger stock of carbon dioxide available for the plants of hard water lakes than in the soft waters. They affect the hydrogen ion concentration of water, but pH is generally not regarded as an important factor in determining the productivity of lakes. Some of the trace elements, such as copper, boron, lithium, zinc and manganese, may have some effect in determining the productive capacity of the water, but this problem has not been fully investigated. Chemical analyses show that there is a concentration of boron, for example, in the phytoplankton and large aquatic plants, but the significance of the concentration has not been determined up to the present time. Much more extended studies will be necessary to determine what specific mineral factors are responsible for the differences in the productivity of the two types of water found in these four lakes.

While the mineral content of the water plays a major part in the total productivity of the two hard water lakes, there is a certain advantage in their greater depth and volume when the results are expressed in units of surface area; that is, the vigorously growing phytoplankton organisms are confined to the upper stratum of water where the solar radiation is great enough to enable them to carry on photosynthesis. Those that die or become senile settle into the lower water on their way to the bottom and thus contribute to the phytoplankton content of the lower strata of a deep lake. In a shallow lake they reach the bottom more promptly and become eliminated from the lower water. In Green Lake for example, the phytoplankton crop of the upper 10 m. of water amounted to 1086 kg/ha as compared with the 2767 kg/ha of the total quantity shown in Table 6. That is, about 38 per cent of the total crop of phytoplankton was found in the 0-10 m. stratum, with 62 per cent below this depth. This upper stratum represents the greater part of the zone of photosynthesis, so that it was occupied by the actively growing phytoplankton

organisms. The water of Green Lake absorbs solar radiation at such a rate that the amount is reduced to one per cent of the total delivered at the surface at a depth of about 11 m. and it seems probable that very little photosynthetic activity is found below this depth.

Because Lake Mendota is much shallower than Green Lake, the accumulation of phytoplankton in the lower water is not so marked. In Lake Mendota subsurface radiation is reduced to one per cent of the amount delivered to the surface at depths ranging from 4 m. to 8 m., depending upon the transparency of the water; it seems probable, therefore, that very little or no photosynthesis takes place below a depth of 10 m. Observations showed that the 0-13 m. stratum of Lake Mendota contained about 72 per cent of the standing crop of phytoplankton in early August, leaving only 28 per cent for the 14-25 m. region. The amount in the 0-13 stratum was 1673 kg/ha, or more than twice as large as the standing crops of phytoplankton in Weber and Nebish lakes, especially before organic fertilizers were added to Weber Lake. Thus, while there is some advantage in the yield of phytoplankton per unit of surface area due to the greater depth of water in Green Lake, this advantage is almost negligible in the case of Lake Mendota and the chemical content of the water must be regarded as the chief factor in the greater phytoplankton production in the latter lake.

The mineral content of the water plays an important part in determining not only the quantity but also the character of the lake flora. The summer standing crop of phytoplankton in the two soft water lakes consists chiefly of green algae (Chlorophyceae) and diatoms (Bacillarieae); the blue-greens (Myxophyceae) may be the dominant forms at certain times during the summer, but they are usually species of Chroococcus and they have not reached bloom proportions at any time during the period of these observations. The summer phytoplankton of the southern hard water lakes is dominated by Microcystis, Coelosphaerium, Lyngbya and Anabaena which are the blue-greens that usually produce the blooms on the lakes in the southern part of the state. In the northern soft water lakes, the large aquatic plants are usually limited to eight or ten species, while 30 or more species are found in the southern hard water lakes. Most of the soft water species are specific to that type of water.

From the food standpoint, the phytoplankton and the large aquatic plants present different problems to the animal population. The phytoplankton organisms, both living and dead, are distributed throughout the open water and are thus available in substantially all parts of the lake; they are the chief source of food for the microcrustacea and rotifers that occupy not only the upper but also the lower strata of water even in deep lakes and for the vegetarians that live on the bottom. A residue of unconsumed phytoplankton is deposited on the bottom and this is available for those organisms which ingest the bottom material and digest the organic content of this mud insofar as they are able to do so; much of this organic residue is ligneous in character, however, and not readily digested.

The large aquatic plants, on the other hand, occupy the shallower water where the subsurface illumination is great enough for them to carry on photosynthesis, so that they are available for food and for an attachment substratum only to the animals that are found in the shallow water zone; certain of these animals feed directly on the large aquatics, while others feed chiefly on the algae and bacteria attached to them. Thus the large aquatics furnish a more limited source of food than the phytoplankton. The quantities listed in the tables represent substantially the annual crop of large aquatics, while the data listed for the phytoplankton represent the average standing crop which is subject to a frequent turnover during the summer; under favorable conditions the algal cells may divide once, perhaps twice, each day during a vigorous period of growth. Taking into account the seasonal changes in light, temperature and other factors, it seems probable that the turnover in the standing crop of plankton averages once a week during July and August so that the summer yield would be about eight times the weight indicated for the standing crop in the tables; the turnover in the southern lakes would probably be more frequent than this.

The standing crop of large aquatics was determined chiefly in August when they had practically completed their annual growth; thus the weights given for them in the tables may be considered as the annual yield. They die off during the autumn and early winter and settle to the bottom where decomposition takes place. Through the action of waves and currents a large percentage of this material is transported from the shallower to the deeper water for final deposition. As they break up they

contribute organic detritus to the water and thus furnish a certain amount of food to the free swimming animals; that which remains on the bottom, both in the shallow and in the deep water, becomes a source of food for the bottom dwelling animals. Steiner and Meloche found that 10 to 20 per cent of some of the large aquatics consisted of ligneous material and this fraction is probably of little food value. Schuette also found 15 to 19 per cent of crude fiber in some of the large aquatics of Lake Mendota and this material is also regarded as having little food value.

Animals

Similar differences have been noted in the standing crop of animals in the two types of lakes. The weight of the zooplankton is appreciably smaller in the soft than in the hard water lakes, but the bottom fauna varies. In Green Lake for example, the bottom animals weigh substantially the same as those of the two soft water lakes; this indicates that depth and probably temperature are more important factors in determining the size of the standing crop of bottom animals than the hardness of the water. A somewhat smaller variety of animals is found in the soft than in the hard water lakes and a few show a specificity for the soft waters. The cladoceran Holopedium is confined chiefly, though not entirely, to soft waters; it has been found in considerable numbers in a typical marl lake in central Wisconsin. The most marked differences have been noted in the mollusk populations of the two types of lakes; no large bivalves, for example, have been found in the soft water lakes. Morrison (1932) reported that the characteristic mollusks of the soft water lakes were species of the small bivalve Pisidium and snails belonging to the genus Campeloma. He noted that Pisidium was very tolerant of acidity and lived in the softest water with a reaction of pH 5.7 and as little as 1.5 p.p.m. of bound carbon dioxide; their shells were very thin and fragile, however. Both Pisidium and Campeloma occur in Weber and Nebish lakes, the former in considerable numbers. The mollusk populations of the two hard water lakes are much larger and more varied than in the two northern lakes.

The ratios of plants to animals given in the tables show that an equilibrium is established between them in Weber and Nebish lakes when the weight of the former is about seven or eight times as large as that of the latter, excluding the weight of the fish

from the animal population. The food relations of the two groups of organisms are not as simple as these ratios might indicate, however, because some of the animals are predatory and do not feed directly on plants; this is especially true of the fishes where there may be two or three up to half a dozen links in the food chain connecting them with plants. Because most of the fishes are carnivorous, it is best to exclude them in order to get a better trophic index of the food-feeder relationship between plants and animals. In other words their exclusion gives a better idea of the direct utilization by the consumers of the material manufactured by the producers; such an index, therefore, shows more clearly the extent and effectiveness of the grazing activities of the vegetarian animals. Some of the zooplankton and bottom forms are predators also, but they constitute a rather small percentage of these forms and do not require any special consideration.

These ratios of plants to animals may also be regarded as indexes of the conversion of plant material into animals, which in a way represents the efficiency of a lake in the production of animals. As indicated in the tables the ratio of plants to animals, excluding fish, was found to be 12.1 in Lake Mendota and 22.2 in Green Lake, as compared with 7.3 in Nebish Lake and an average of 7.5 in Weber Lake. This means that the two hard water lakes have a much lower efficiency in the conversion of plants to animals than the two soft water lakes. According to these ratios Lake Mendota is only a little more than half as efficient in the use of its plant material and Green Lake only one-third as efficient as the two soft water lakes. The much greater depth and the low temperature of the bottom water of Green Lake seem to be factors in limiting the size of the standing crop of bottom fauna, thereby lowering the efficiency; with a bottom fauna as large as that of Lake Mendota, the ratio of plants to animals would be 11.7 instead of 22.2, which would bring Green Lake into line with the index of Lake Mendota, namely 12.1. Just why the two hard water lakes are so much less efficient than the two soft water ones is not evident from the data in hand.

Dissolved Organic Matter

The heterogeneous mixture of substances designated as dissolved organic matter represents chiefly the organic matter that is in various stages of decomposition and that which comes from the excretions of the aquatic organisms resulting from their

metabolic activities. Most of it may be considered as belonging to the final stages in the cycle of organic matter in lake waters. Aside from a relatively small number of bacteria, it consists of degradation products on their way to conversion into water, carbon dioxide and mineral salts, the original building blocks from which the organic matter was built up by the producers in the process of photosynthesis. Four different items are represented in this material: (1) a small percentage of the bacteria; (2) minute particles of decomposing organic material which cannot be recovered with a high speed centrifuge; (3) particles small enough to be regarded as colloids; and (4) organic matter in true solution. The first and second stages of this material are still available for the food of some of the aquatic animals, such as microcrustacea, rotifers, protozoa and some members of the bottom fauna; the third and fourth stages can be utilized only by bacteria, and when so utilized they again enter the food cycle because the bacteria may be consumed by certain animal forms.

The dissolved organic matter is in a constant state of flux; it is continually receiving both decomposing and excretory material from the biota on the one hand and losing organic substances that change over to inorganic compounds on the other. Since the amount of dissolved organic matter remains fairly constant in a lake during the summer as well as from year to year, the quantity being added is in substantial equilibrium with that which is removed at the end of the degradation process. There was an increase in the amount of this material in the water of Weber Lake when organic fertilizers were used to stimulate the growth of the phytoplankton; also unusually large increases in the standing crop of phytoplankton may add appreciable amounts to the dissolved organic matter, especially at the end of such a plankton pulse when these organisms have completed their life cycle and are declining in numbers.

The dissolved organic matter contains a large percentage of organic material that is not readily oxidized by bacteria. Steiner and Meloche (1935) found that the plankton, the chief source of this organic matter, contained 10 to 20 per cent of ligneous substances which are more resistant to decomposition than the other organic constituents and this ligneous portion thus tends to lag in the process of decomposition. ZoBell (1940) noted that the remains of plankton organisms were more readily oxidized by bacteria than the dissolved organic matter found

in the lake water. Also ZoBell and Stadler (1940) state that lignin is attacked less readily than the other major organic constituents found in lakes, but that it is slowly decomposed by certain bacteria present in lake water and in bottom deposits. Their experiments showed that these bacteria oxidized from 4.4 to 17.4 per cent of highly purified lignins in 30 days at 28° C. when the lignin concentrations were comparable to those found in lake waters.

The slowness of the decomposition of the dissolved organic matter may also be due in part to the low concentration of this material in the lake waters. In the four lakes included in this report, the range is from a minimum of 3.7 mg/1 in Weber Lake to a maximum of 12.5 mg/1, dry weight, in Lake Mendota; Nebish Lake yielded 7.3 mg/1 and Green Lake 8.4 mg/1. ZoBell (1940) states that many bacteria indigenous to natural waters can maintain themselves indefinitely when subcultured in lake water with less than 10 mg/1 of total organic matter, but this concentration seems to be in the neighborhood of their threshold of multiplication. He found also that the lower the concentration of the oxidizable material is, the more refractory it is to bacterial decomposition. It will be noted that three of the four lakes being considered in this report had less than 10 mg/1 of dissolved organic matter; only Lake Mendota exceeded that amount.

Summary

1. The size of the standing crop of plants and animals in two soft water lakes is compared with that in two hard water lakes.

2. The plant crop in the two hard waters weighed three to five times as much as that of the soft water lakes. The soft waters had only about one-fourth as many species of large aquatic plants as the hard waters.

3. On an average the animal population of the hard waters, excluding the fish, weighed two to three times as much as that of the soft waters.

4. The ratio of the weight of the plants to that of the animals, excluding the fish, was 7.3 in one soft water lake and 7.5 in the other, while it was 12.1 in one hard water lake and 22.2 in the other. Thus the soft water lakes were approximately two to three times as efficient in converting their plant material into animals as the hard water lakes.

5. The ratio of other animals (food) to fish was 4.7 in one soft water lake and ranged from 3.0 to 11.1 in the other; the fish populations of the hard water lakes were not determined. The fish constitute a very small cap for the pyramid of life in the two soft water lakes as shown in the figures, making up 1.2 per cent in one and 2.5 per cent of the total weight of plants and animals in the other.

6. The dissolved organic matter, which is chiefly a degradation product, is much larger in the hard than in the soft water lakes.

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