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THE LIFE OF DEVILS LAKE NORTH DAKOTA

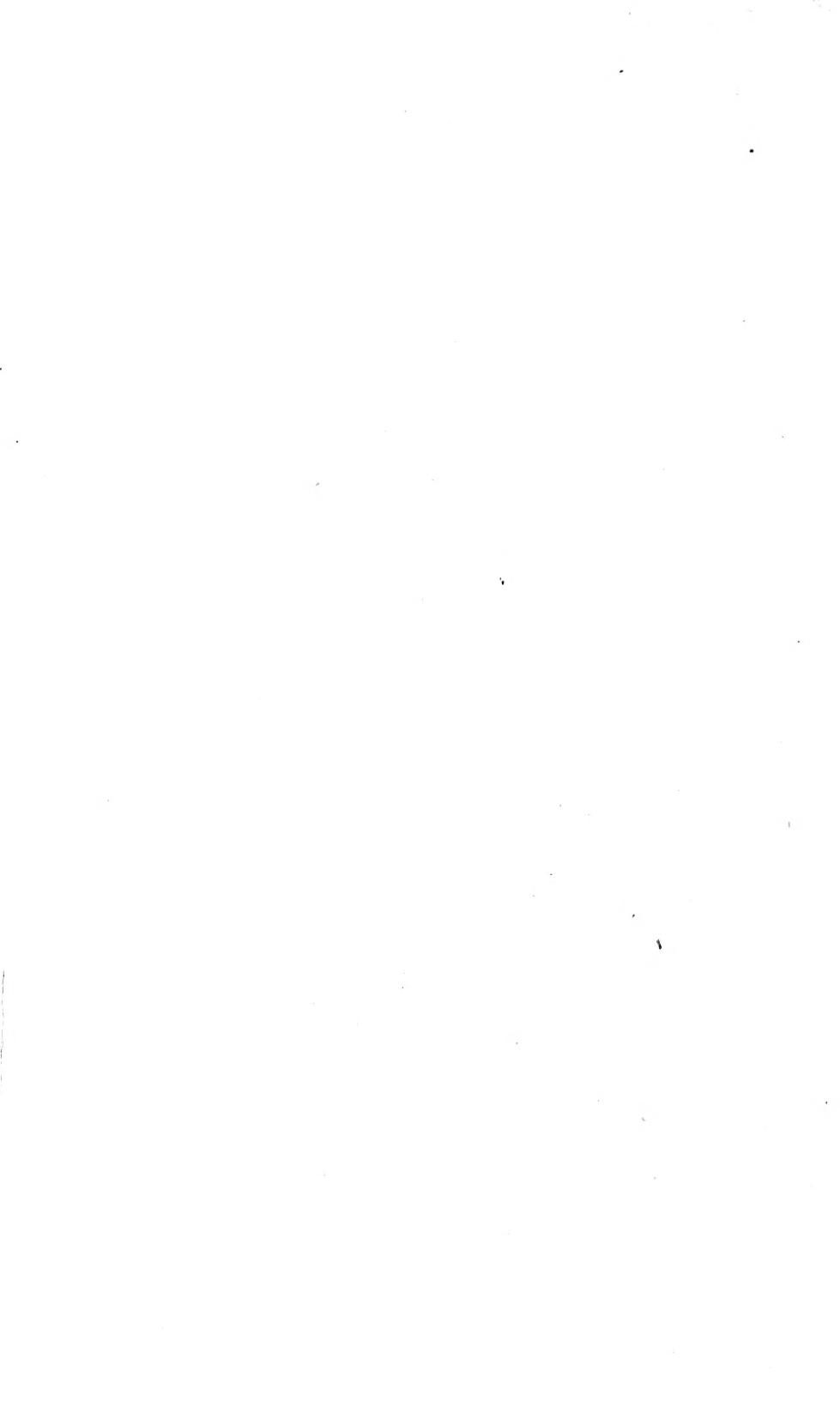
BY

R. T. YOUNG



PUBLICATION OF THE NORTH DAKOTA
BIOLOGICAL STATION
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INTRODUCTION

In 1909 a biological laboratory was established by the State of North Dakota, under the auspices of the State University, on the shore of Devils Lake. Since that time the writer, acting at first as assistant and later as director, has been engaged in studying the life of the lake, and this report is the result of such studies. His thanks are due principally to the former director, Dr. M. A. Brannon, now Chancellor of the University of Montana, to whose initiative the laboratory owed its establishment, for his encouragement and friendly assistance during the first five years of this work. He has also received much valuable assistance from his present colleagues, Professors H. E. Simpson, G. A. Abbott and Karl Fussler and E. D. Coon, and from Drs. F. H. Heath, C. E. King and Messrs. Robert Hulberd, Eric G. Moberg and R. H. Johnstone, formerly of the University of North Dakota. Professor Simpson's valuable work on the Physiography of Devils Lake (1912) is the basis of that part of the present report descriptive of the history of Devils Lake. Drs. Heath and King have furnished the major part of the chemical data. Mr. Moberg, as my former assistant, has aided in the collection of material and has made most of the planeton counts, while the other gentlemen have kindly assisted me in various ways.

Several specialists have aided in the identification of organisms, without which assistance the work could not have been carried on. Messrs. C. F. Rousselet and David Bryce have identified the rotifers, Professors C. J. Needham and R. Mattheson and Messrs. C. R. Plunkett and C. K. Sibley the insects, President E. A. Birge and Professors Chancey Juday, A. Willey and C. Dwight Marsh the Crustacea, Dr. N. A. Cobb, the nematodes, Dr. Karl Viets and Professors R. H. Woleott and Ruth Marshall, the mites, and Drs. Geo. T. Moore and Nellie Carter, the algae. Professor C. H. Edmondson has spent several weeks at the station in 1914 and 1917, working on the Protozoa, and has worked over several collections sent him at other times. Professor C. J. Elmore has identified the diatoms, in part from collections sent to him, and in part from material collected by himself during a visit to the lake in 1915. To all of these gentlemen the writer's thanks are due for their invaluable aid. Professor Jacob Reighard and President E. A. Birge have given very helpful advice regarding methods and apparatus, the former loaning the proof of a chapter in Ward and Whipple's "Fresh Water Biology" which deals with these subjects.

The charts accompanying the paper are the work of Mr. Wilfred F. Lowe.

The first two years were spent chiefly in collection of apparatus, development of methods and in a general preliminary survey of the lake. Since that time collections, both qualitative and quantitative,

of the organisms inhabiting the lake, together with physical and chemical studies of its water, have been made at frequent intervals from 1911 to 1914 with the exception of certain periods in 1912 and 1913, during which time the absence of the writer interfered with the conduct of the work, and during the winter when few collections were made. A few collections were made in 1909 and 1910, but these were preliminary to the main series. An additional series was also made between December, 1922, and July, 1923. The collections and determinations, aside from the purely preliminary work, have thus covered a period of twelve years (1911-1923).

The major part of the work has been devoted to a study of the plankton of the lake in its ecological relations, this forming the most important part of the life of the lake. Several general chemical analyses (both organic and inorganic) have been made during the study, and analyses of certain constituents, especially the ammonias, nitrates, nitrites, carbon dioxide and oxygen, have been made during part of the time at much more frequent intervals. This will be explained in detail in the proper place. In connection with the collections and analyses temperature records have been kept, and a study of the distribution of light at various depths has been made. The data of the U. S. Weather Bureau Station in the city of Devils Lake, eight km. distant, have been drawn upon extensively, and these have been amplified to a certain extent by our own more or less fragmentary records of air temperatures and precipitation taken at the station.

There are several reports on various phases of the biology of the Devils Lake region beginning with that of Pope (1908), but nothing as yet of a comprehensive nature. There are brief notes on the physiography of the region in Upham (1896) and Willard (1921), while Simpson (1912) gives a thorough treatment of this subject.

HISTORY AND LOCATION

The northern United States and Canada are dotted with numerous picturesque lakes bounded by rolling hills—legacies of the great ice sheet, which thousands of years ago held this region in its frigid grasp. During its retreat from the upper Mississippi Valley its waters were in part collected in a great lake (Lake Souris) in northern central North Dakota and southwestern Manitoba, occupying the watershed of the present Mouse River, and in part that of the Assiniboine, while further to the north in the valley of the Saskatchewan, was glacial Lake Saskatchewan.

Before the ice had retreated sufficiently to uncover the northern outlets of these lakes, both of the latter at first drained southward into the Missouri River. Later new outlets were opened, at first thru the James River and later the Sheyenne into Lake Agassiz. With the retreat of the ice north of the Sheyenne River its drainage was collected in a broad, shallow valley running from northwest to southeast between longitude 98 and 99 and latitude 47 and 48, while south of this depression a tumbled mass of moraines served as a dam to the glacial waters, thru which different channels at various times conducted them southward into the Sheyenne. Thus was formed the glacial lake Minnewaukan* the forerunner of the present Devils-Stump Lake complex in North Dakota.

“We can little comprehend the vast flood of water which passed this way from the southern and western front of the great ice sheet. From the far northwest, including even the basin of the great Assiniboine River and glacial Lake Saskatchewan, 300 miles to the northward, came the flood of glacial waters through this great chain of lakes and their connecting rivers, which must have somewhat resembled straits, to the Mississippi River and Gulf of Mexico. This was flood time in the Devils-Stump Lake region, when Lakes Minnewaukan and Wamduka stood at their highest level.”* The chief of these outlets led from the western side of the present Stump Lake into the Sheyenne.

With the development of this outlet the waters of Lake Souris and the extensive drainage area to the north found an easier path of discharge thru Lake Minnewaukan, which at its prime must have carried a very large volume of water from the melting ice. Another

*Minnewaukan or Spirit Water was the Indian name translated by the white man into Devils Lake. This translation is probably traceable to an Indian legend associating the spirit of the lake with the wild winds which so often transform it into a foaming mass of fury, and which, according to the legend, at one time overwhelmed a party of Sioux warriors returning from a successful foray against their Chippewa neighbors to the north. Wamduka is the Sioux name of Stump Lake from its fancied resemblance to a serpent, and applied by Simpson (1912) to that lake at the time of its earlier connection with Devils Lake. Because of the fact that both lakes were at first one body a single name is preferable; hence I have chosen the name of the larger, Minnewaukan, to apply to both.

*Simpson, l. c. p. 142.

change in drainage channels gave Lake Souris an eastern outlet into Lake Agassiz through the Pembina River, and Lake Minnewaukan, its chief source of supply cut off, began to drop and soon was divided into two parts—Stump Lake and Devils Lake, the later history of both of which has been one of steady recession.

The Devils Lake region is in the midst of what Simpson (l. c.) has termed the "Drift Prairie Plain". It forms an intermediate area between the old Lake Agassiz floor, which forms what is now known as the Red River Valley, on the east, and the Great Plains Plateau, which sweeps westward thru Montana to the Rocky Mountains.

"The Drift Prairie Plain varies in width from about 200 miles at the north to 100 miles at the south and has a general elevation of from 1,500 to 1,800 feet above sea level. This plain has a gradual but gentle slope eastward from the Coteau du Missouri to the Pembina escarpment and Coteau des Prairies and southward from the international boundary line to the South Dakota line. This double slope determines the direction of the drainage, causing the several main streams to take a general southeasterly course. The topography of this plain is that of the young drift type characteristic of all that portion of the prairie plains which lies within the limits of the latest ice invasion, and varies from gently undulating through rolling to hilly, the form being due almost entirely to the original disposition of the unmodified glacial drift upon a nearly level plain. The soft, shaly character of the underlying rocks is such that they do not influence the surface topography to any marked extent, except where occasional groups of low well-rounded hills or full bodied ridges rise above the plain, and these are so well veneered with drift that only their form reveals their origin.

More important because more numerous, though less conspicuous, are the groups of hills and knobby, irregular ridges which stretch across the prairie in a northwest to southeast direction. At times the ridge effect is pronounced and they lengthen out into long looped curves, and again there seems to be simply a confusion of low rounded hills, both types being so characteristic as to suggest at once to the student of physiography their origin in glacial moraines. This prairie is otherwise a gently rolling drift plain cut by a few abnormally deep and well defined valleys such as those of the James, the Sheyenne, and the Maple rivers, trending southward and eastward, marked by many shallow, irregularly winding coulées and dotted by thousands of small lakes and marshy areas, occupying numerous sags and swales, which testify to the undrained condition of the land."

*Simpson, l. c. pp. 107 8.

Map Showing Topographic Features of North Dakota

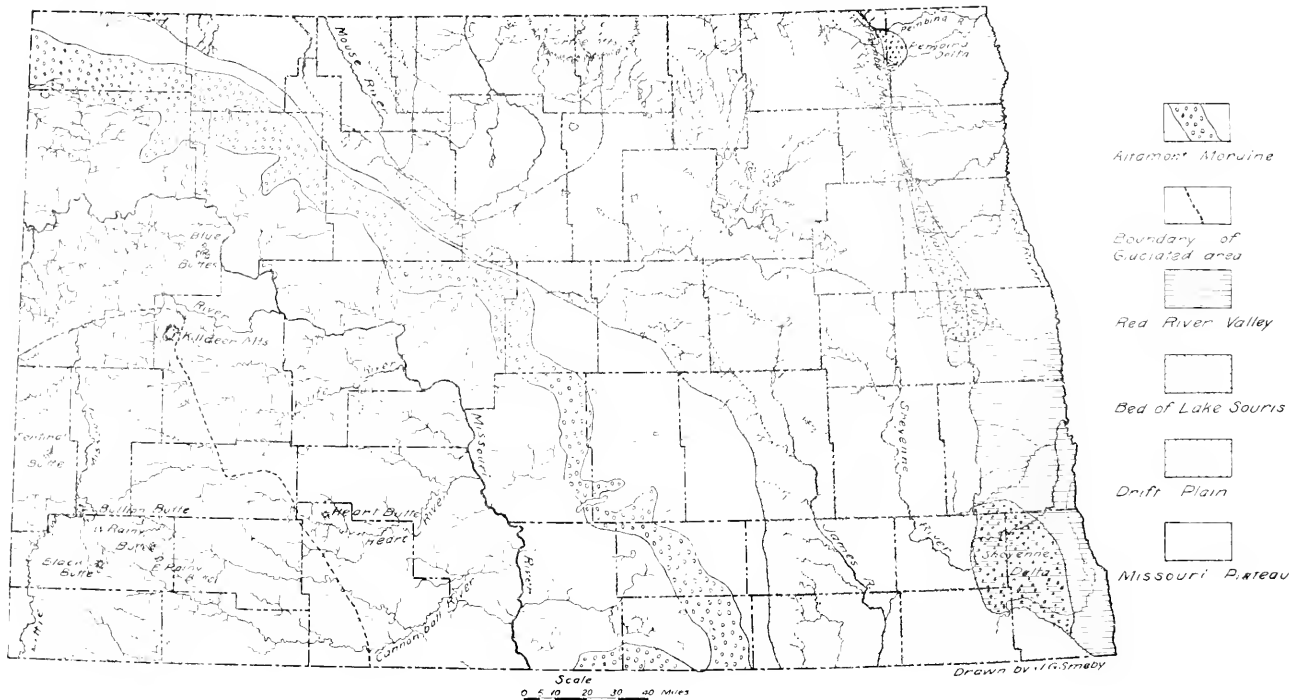


Plate 1. From Leonard (1919).

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Plate 2. Above, Devils Lake from North Shore, with Sully's Hill in background.
Below, East Lake, summit of "A" cliff in middle foreground.



Plate 3. Upper, shore of Main Lake, showing C. D and E benches.
Lower, A and B cliffs of Lake Minnewaukan, with the large tree midway between them.
From Simpson (1912).

The Devils-Stump Lake complex occupies the southern part of a drainage basin extending from the Turtle Mountains on the north to the morainal mass of hills just south of Devils Lake, and with poorly defined eastern and western boundaries. Its estimated area is 9000 sq. km.*

“There is a gradual slope throughout the basin southward to these two lakes; the fall is so slight, however, and the surface so irregular that the drainage is but very imperfectly developed. Small lakes and ponds abound, especially in the southern portion. Coulées are few and very shallow, rarely containing running water except in wet seasons. Formerly these coulées and the chains of lakes connected by them emptied considerable water into Devils Lake through Mauvaise Coulée and by several converging coulées into both the eastern and western arms of Stump Lake. Mauvaise Coulée was the most important drainage line of the entire basin. Its headwaters were gathered beyond the international boundary line and in its course southward it drained the Sweetwater chain of lakes by Lake Irvine through which it passed, and entered Mauvaise (or Minnewaukan) Bay of Devils Lake as a large and permanent stream. Today no surface streams flow into either Devils Lake or Stump Lake except very minor flows during spring thaws and after excessive falls of rain. Both lakes, however, undoubtedly receive the extensive underground seepage from the drift cover of the large drainage basin, the waters of which move slowly down the slope from the north over the impervious floor of Pierre shale and through the lower sandy portions of the drift. Little of the surface drainage of this inland basin ever reaches either of these lakes. In fact, but a very small fraction, almost negligible, of the rain falling in the basin reaches the lakes by running off over the surface. The amount that reaches the lakes and the Shyenne River by underground seepage is no doubt greater, but this amount cannot satisfactorily be estimated.”*

The history of Devils and Stump Lakes may be read in a series of more or less well marked beaches paralleling their present shores. There are two of these old shore lines that are well marked, indicating the earlier levels, and several later ones which are only occasionally distinct. The two former have been designated by Simpson (l. c.) the A and B and the latter the C, D, and E, beaches respectively. There is some evidence that after the ice had left the basins of what are now Devils and Stump Lakes it extended an arm between them forming a dam to the waters of the former. In this event the outlet must have been thru one of the channels leading directly south from Devils Lake to the Shyenne,

*Chandler (1911)

†Simpson, l. c., pp. 109-10.

two of which have been described by Simpson, one from what is now Ft. Totten Bay and the other from Minnewaukan Bay. Indications of such a barrier are a small moraine extending north and south across the divide between Devils and Stump Lakes and the existence of "small cliffs and wave-cut terraces at elevations of 7 to 20 feet above the level of the A beach The evidence of earlier stages . . . are, however, fragmentary and inconclusive The life history of such must necessarily have been brief and unimportant."

The first definite shore line, or A beach, marks the lake level when the outlet from what is now Stump Lake to the Sheyenne River existed, and marks a level of 445 m. above the sea, and 12 m. above the present surface. During the existence of this outlet the water surface was evidently held approximately level for many years, as is attested by the distinct bluff which was formed by wave action at various points, (plates 3 and 4). At other points well marked beaches were formed by the deposition of sand and gravel by waves, with the occasional addition of boulders, due undoubtedly to ice shove. That this latter has played an important part in developing the shores of the lake is evidenced further by the boulder piles in the main section of Devils Lake known as Bird Island and the Rock Pile, (plate 5) and similar islands in Stump Lake, which show evidence of ice work, and by the frequent destruction or displacement of piers and boat houses in spring. At this time the melting ice, driven before the fierce winds which characteristically sweep these prairies, is frequently piled to heights of 2 to 3 m., and must exert a tremendous pressure against the shores (plate 4).

With the loss of the supply from Lakes Saskatchewan and Souris, the outlet of Lake Minnewaukan into the Sheyenne River was cut off and the lake dropped from the level of the A beach to that of the B, 2 m. lower, marking the period previous to its separation into Stump and Devils Lakes. That the level of the lake remained approximately constant for many years at this period is shown by the well marked cliffs and beaches developed at this time. In some places indeed the B cliff was so far developed as to undermine and destroy the preceding A cliff (plate 4). Temporary periods of rise and fall between the A and B stages are indicated by minor bluffs and beaches between these.

According to Upham (1895) the elevation of Devils Lake was 441 m. about 1830, while traditions telling of the existence of certain islands as late as 1867 indicate that this level was maintained up to about the latter date. The later levels (C, D, & E) are poorly marked, only rarely developing small bluffs, the most recent temporary levels being indicated chiefly by zones of plants along the

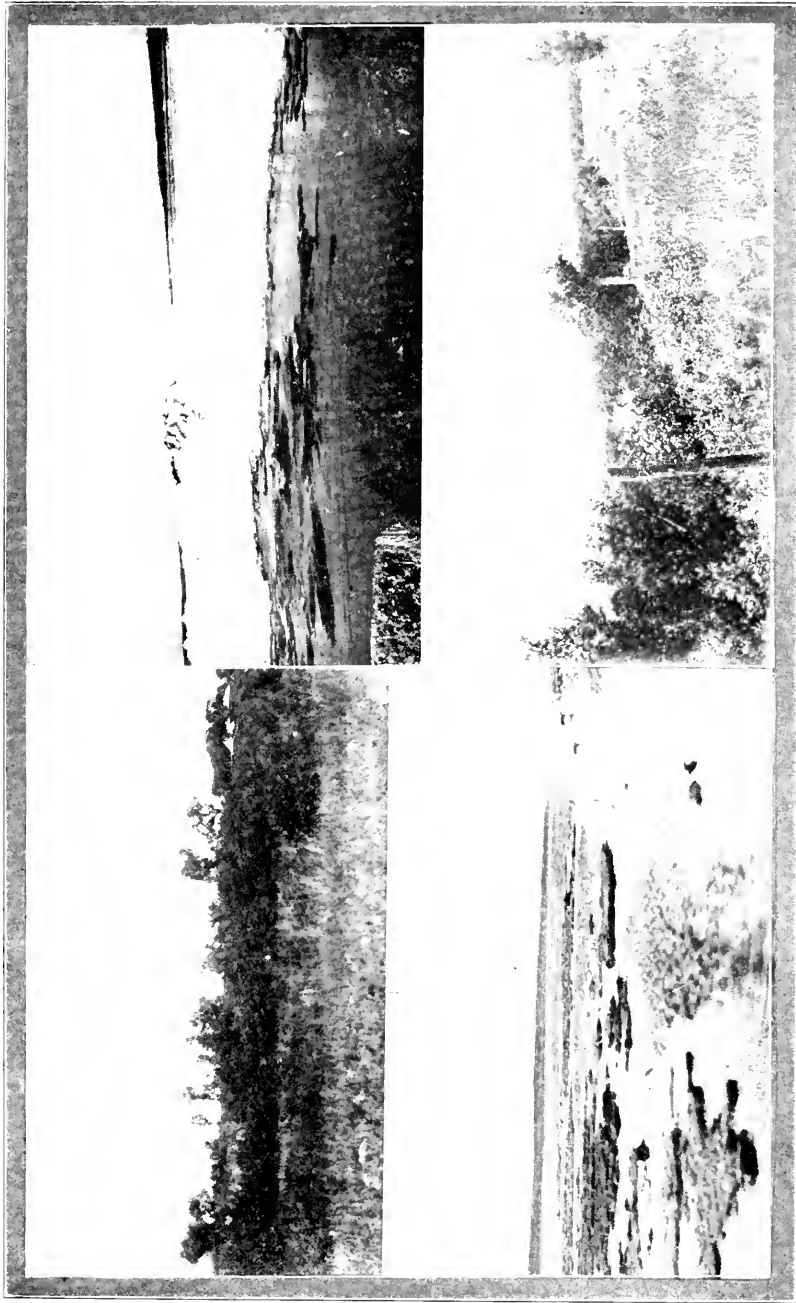


Plate 4. Upper left, "A" and "B" cliffs, from old lake bed.

Upper right, Ice on shore of Devils Lake in spring.

Lower left, Ice breaking up in Devils Lake in spring.

Lower right, View looking west from top of "A" cliff, Main Lake in left background.

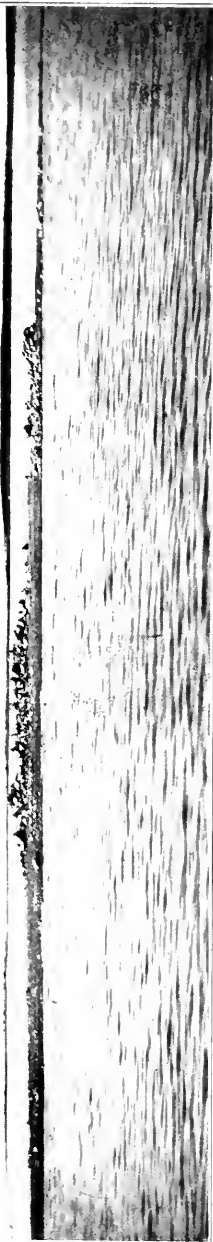


Plate 5. Above, Bird Island in Main Lake.
Below, shore of Stump Lake (Simpson, 1912).

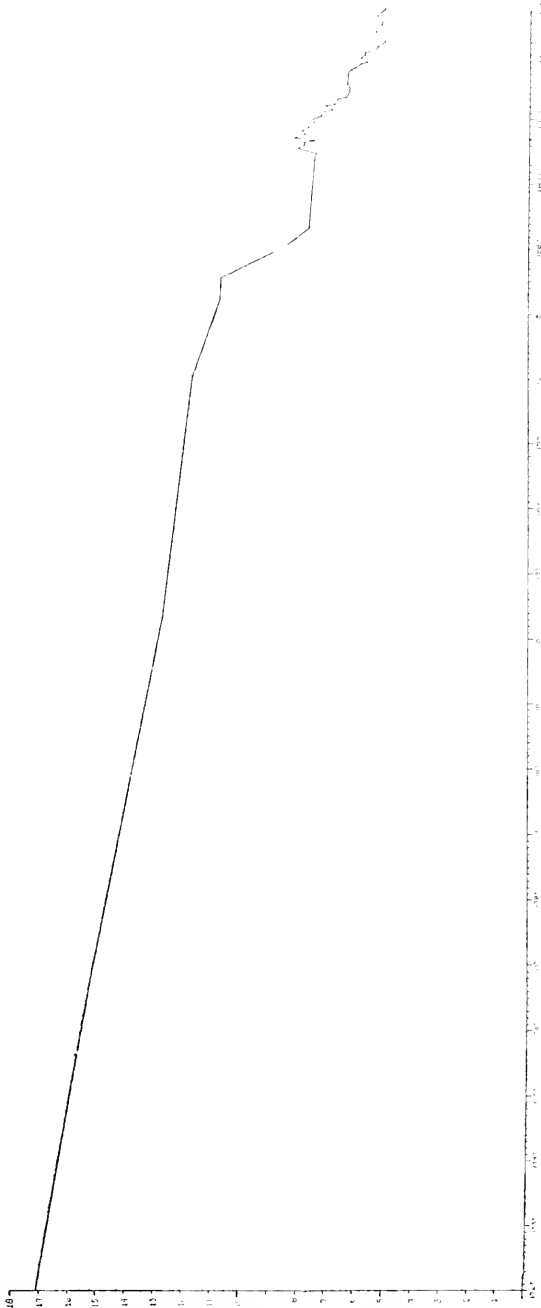


Figure 1. Showing levels of Devils Lake, depths in meters as ordinates, dates as abscissas. Prior to 1867 the latter are approximate only. The "A" stage is indicated at 1877 on the chart.

shore which have found foothold in small depressions formed above the small sand beaches thrown up by the waves, where a little moisture gathers (plate 3).

Between 1867 and 1901 more or less well authenticated data are available on the levels of Devils Lake, while since the latter date a gauge has been maintained and numerous yearly readings are on record. Figure 1 shows graphically the lake levels from the date of the A stage to the present, the former being unknown, and the rest of the earlier ones being only approximate.

In spite of our record of the steady fall of the Devils-Stump Lake complex, there is considerable evidence of an earlier, still lower, stage than the present. Stump Lake derives its name from the remains of an old forest which once occupied its floor. Many of these stumps are still standing, while many others exist as fallen logs (plate 5). A few of these logs occur in Devils Lake, but they are most numerous in Stump Lake. This forest must necessarily postdate the glacial epoch, the termination of which in this region is marked by the A beach. The period of lower level, perhaps of absolute dryness of the lake must then have succeeded that of the A stage. On the other hand, history and tradition testify to the existence of a stage at least approximating that of the B stage within recorded time. How high the lakes rose, and at what time, after their lowest period; whether the beaches from the B downward were developed before or after such periods, or partly both, we have no certain knowledge. It seems most likely however that the prominent B beach was developed before such a low period ensued, rather than later, as the supply of the lake was more likely to have been held constant for a longer period at that time, while recent changes have been relatively rapid.

Other evidence of the existence of a former lower lake level are the rocky islands in both Devils and Stump Lakes. The fact that these islands until recently were below the lake surface and yet are largely the work of ice shows that they must have been formed during a period of lower level.

This evidence corresponds moreover with that from other sources regarding climatic changes in the past.

Thus Huntington (1914) and others by means of measurements of the annual rings of growth of the Sequoias, have already demonstrated alternate periods of moisture and aridity in California during three thousand years. Similar evidence has been adduced from the former shore lines of lakes in different parts of the world (Huntington 1915 et. al.) and from the rise and fall of ancient civilizations, as indicated by both historic and archaeological evidence (Huntington, l. c.).

CLIMATE

The cause of the decline of the Devils-Stump Lake complex is excess of evaporation over intake. The sources of such intake are two, with a possible third, rainfall, run-off and possibly underground seepage.

The weather bureau record of rainfall at the city of Devils Lake for the twenty-four year period from 1897 to 1920 inclusive shows that the mean annual rainfall is 44.6 cm., the greatest fall occurring in spring and early summer, during the growing season, while late summer and autumn, the harvest time, are apt to be dry.

Records taken at the Biological Station on the north shore of Devils Lake about five miles distant from the town, from June 29 to August 27, 1914, show a precipitation of 10.1 cm. with occasional additional traces, making a total of about 10.2 cm. compared with a total of 10.5 cm. for the weather bureau station in Devils Lake. During summer the rainfall is apt to be local and inconstant, so that while one area may receive a good supply, another, a short distance removed, may receive but little.

The snowfall is usually light, averaging 82.8 cm. for twenty years. Under the high wind the lake surface is usually swept bare, and the snow piled in heavy drifts about its shores.

The amount of run-off reaching the lake cannot be estimated. With the loss of the supply from the Mauvaise Coulée about 1885*, probably due to the extensive settlement and consequent cultivation of the territory contiguous thereto in the early eighties, coupled with the drouth in the latter half of this decade, the drainage basin was reduced to the area immediately bordering the lake, in which there are no streams and only a few feeble springs. Most of this land moreover is either cultivated or wooded, so that there is very little run-off.

The extensive cultivation of the soil is a well known cause of lowering the water table in the ground thru increased evaporation from the surface and especially thru the transpiration of plants, but it has an even more important effect in preventing run-off.

The major part of the run-off occurs during the spring thaw, when the ground is frozen to a depth of several feet. The amount of this run-off depends not alone on amount of snowfall, but even more on the character of the thaw. When the latter is sudden, practically all of the melting snow reaches the lake, causing a marked rise; when gradual, most of the water percolates into the ground and the lake level is but little changed. The average amount of this rise for ten years has been about 0.15 m.

*As a result of exceptionally heavy snowfall in the winter of 1915-16 this coulée was flowing approximately 13249 cu. m. per day on Aug. 15, 1916.

The amount of seepage water reaching the lake is likewise an unknown factor. The porous mantle of glacial till overlying the impervious Pierre clay undoubtedly furnishes a certain supply in this way; especially in spring when the melting snow surcharges the ground with moisture, as may be seen in the little pockets in the fields which are too wet for plowing. The slight slope of most of the drainage basin, however, coupled with the fact that during the summer the rainfall is seldom more than enough for the growing crops, must keep this supply at a minimum. Conversely the loss thru seepage must be a negligible factor owing to the impervious clay underlying the lake.

The daily amount of evaporation at the lake shore determined by readings on a Livingstone porous eup atmometer from Aug. 4 to Sept. 5, 1914, shows, as would be expected, a great range of variation. These readings, however, have a comparative value only, and are of no significance in themselves.

Factors determining evaporation are three—temperature, wind and humidity. Like other interior regions at this latitude and altitude the climate of the Devils Lake region is marked by great extremes of temperature, maxima and minima for 24 years from 1897 to 1920 at Devils Lake being 41.1°C on July 28, 1917 and 42.2° on January 12, 1916.

Daily extremes are considerable. The average daily range of temperature at Devils Lake city compiled monthly for 19 years is 11.98°C . The greatest average variation occurs in August, but the maximum was in January (30.84°).

Maximum and minimum temperatures at the lake shore were taken from June 13 to Sept. 5, 1914, with a few omissions. These showed a maximum daily range of 23.3° as compared with one of 22.8° at Devils Lake city. The former, however, occurred in June, and the latter in August, so there is evidently no very close correspondence in the temperature range of the two localities.

The annual and monthly mean maxima and minima from 1900 to 1920 are shown in table 1. The annual average number of sunny days* is 125 while at the summer solstice the number of hours of sunshine is sixteen.

Twilight lasts till about 11:00 p. m. and the first flush of day appears about 3:00 a. m. This great amount of sunshine ensures rapid growth and early maturity to the crops of grain for which the northwest is famous, and doubtless determines in large measure the development of organisms in Devils Lake in early summer. Midday in summer is rarely oppressive and the nights are almost invariably delightful, days of excessive heat being rare, and usually enduring for but brief intervals. Devils Lake usually freezes be-

*Over 70% sunshine.

tween the 15th and 25th of November, while it is usually free from ice between April 20 and 25. The ice commonly reaches a thickness of one metre, a few centimetres of which are frozen snow.

The comparatively low relative humidity (table 2) and the characteristically high winds of the region, are mainly responsible for the rapid evaporation, rather than the occasional brief extremes of temperature.

TABLE 1

Showing mean maximum (A) and minimum (B) monthly and annual temperatures (C°) at Devils Lake City from 1900 to 1920.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
A	-10.2	-9.6	-0.8	10.9	18.1	22.8	26.3	25.2	20.3	12.5	2.8	-7.2	9.3
B	-22.1	-21.3	-12.7	-1.9	4.1	12.4	12.7	11.1	6.3	-0.2	-8.5	-16.7	-3.3

TABLE 2

Showing monthly and annual mean relative humidities at Devils Lake city for a period of 13 years.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
7 a. m.	88	88	85	80	77	79	83	85	85	84	86	88	84
7 p. m.	84	83	75	57	51	57	57	55	59	65	78	84	67

Wind is one of the most important factors, not only in lowering the level of Devils Lake; but in moulding its shores, thru ice and wave action, and in determining its currents, the distribution of its inhabitants, its dissolved gases, and other chemical constituents, its temperatures and turbidity.

The average total annual wind movement at Devils Lake for 13 years was 163531 km., maximum velocities of 97 km. per hour being occasionally reached. The prevailing directions are N W. and S. E.

The average annual precipitation at Devils Lake is 44.6 cm., while during a period of 14 years (1907-1920) the level of the main part of Devils Lake fell from 435.1 to 433.1 m, or 2.0 m, an average annual fall of 0.15 m.

The amount of water represented by this drop can only be estimated since no accurate survey of the lake has been made since 1883, and the shore lines are constantly changing. According to the report of the state engineer (Atkinson, 1912) on the survey for a proposed diversion of the Mouse River into Devils Lake, the amount of water needed to make good the annual excess of evaporation is 24,635, 790 cu. m. Basing an estimate on the above data and allowing for the total rainfall reaching the lake, plus 50% additional in run-off and seepage, the average amount of evaporation for the past 15 years may be estimated at 0.8 m. or 131,390,880 cu. m. This figure is of course the merest estimate, based on the average rise from melted snow in spring, when most of the run-off occurs and amounting to about 35% of the annual rainfall, with an additional 15% for run-off during the rest of the year and for

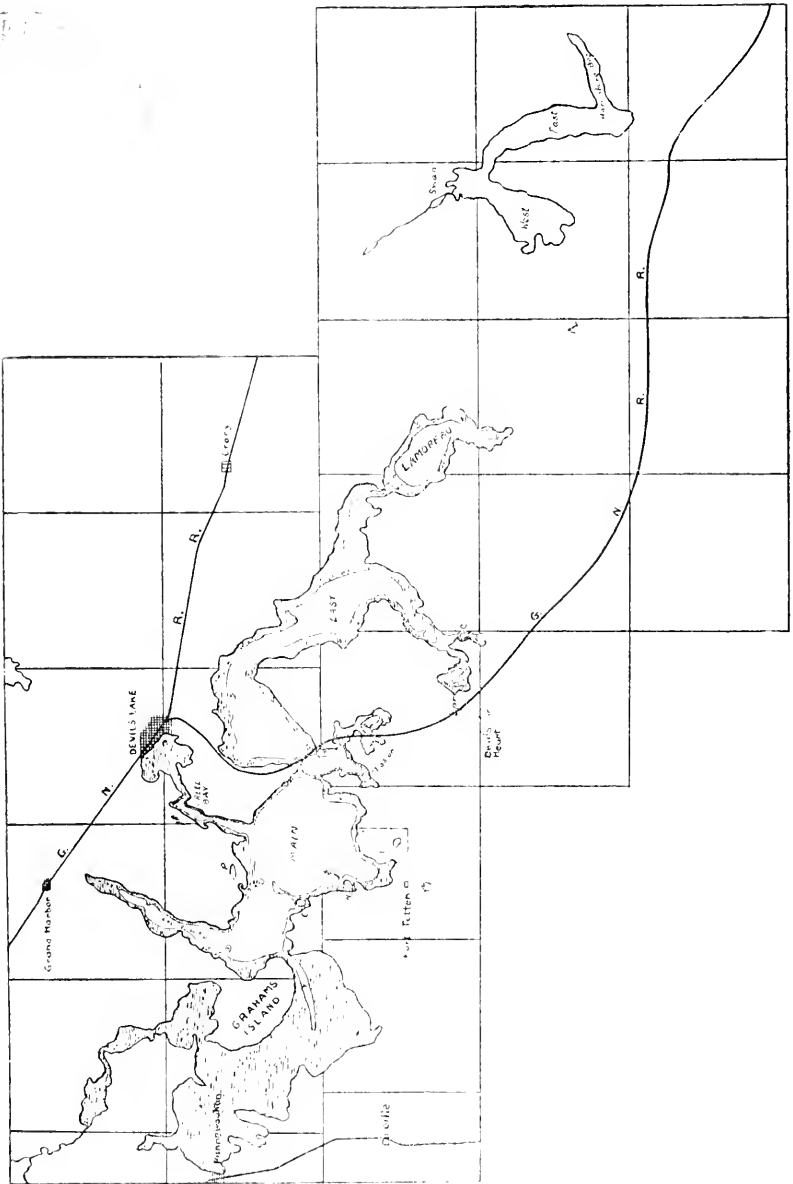


Figure 2. Map of Devils Lake Complex, the shaded areas indicating dry lake bottom.

seepage. During the summer of 1916 in spite of an estimated daily flow of 13,249 cu. m.² from the Mauvaise Coulée, the lake fell about 0.24 m. from May 1 to November 5.

The future of Devils Lake can only be read in the record of the past. With present climatic conditions continuing it will probably disappear during the next forty or fifty years. The annual drop is apt to increase with decrease in depth. "From him that hath not shall be taken away even that which he hath" is applicable to lakes as well as to men. The eastern section of Devils Lake, which was separated from the main body in 1903 by a highway at the Narrows, and which in 1913 had an average depth of 1.8 to 2.4 m. was more than 0.9 m. lower than the latter in 1922, and is now (1923) little more than a mud flat, covered in places with a few centimetres of water, while Minnewaukan Bay, which in 1916 contained 0.9 to 1.2 m. of water (plate 10) virtually disappeared in 1917, while the main body fell only 0.4 m.

Whether climatic cycles may ensue to raise the lake to its former high estate must be left to the future to decide. Such changes, however, are reckoned in centuries, not years. The immediate prospect is one of continued and increasing fall and ultimate dryness, the fate of so many other glacial lakes in North America. The youth and maturity of Devils Lake are past, the period of old age has arrived.

MAIN LAKE, PHYSIOGRAPHY

As may be seen from the map (fig. 2) Devils Lake has the form of a long, narrow body with several arms at right angles to the latter. These arms or bays probably mark the course of tributaries of the old pre-glacial river in whose valley the lake now lies. The area of Devils Lake in 1883 was approximately 401.5 square km. with a shore line over 290 km. long. Today the area probably does not exceed 180-200 km. and the shore line has also been considerably reduced, tho not to the same extent as the former.

The recession of Devils Lake, together with the construction of highway embankments at various points across the lake, has resulted in the development of several smaller lakes, besides the separation of the glacial lake Minnewaukan into the present Devils and Stump Lakes. Some of these smaller parts, which are spring fed, have retained their freshness; while others have a high concentration of salts, the proportions of which vary of course in each individual case. At present Devils Lake proper is divided into four chief parts—Minnewaukan Bay*, Main, East and Lamoreau Lakes; the principal of which, and that on which most of the data in this treatise are based, is Main Lake. This is an irregular sheet of

*Aug. 15.

*Virtually dry—1924.

water approximately 130 sq. km. in extent and at present** of about 5 m. maximum depth. It has two main arms extending north—Creel Bay, about 5 km., and Six Mile Bay about 6 km. long, each averaging from 0.8 to 1.2 km. in width. At the eastern end Main Lake is cut off from East Lake by a highway across the Narrows, while to the southeast Mission Lake was cut off by a dam in 1908. The floor of Main Lake is mostly covered with a very fine, impalpable, black, foul smelling ooze, but in places sandy or gravelly bottom is found, with occasional glacial boulders scattered over the lake floor. The greater part of the lake bottom is nearly level, with a gradual rise about the shores, which in places are covered with glacial boulders, and in others are low, muddy flats.

PHYSICS

The physics and chemistry of the water naturally varies with the changing level of the lake, and with the seasons of the year.

The specific gravity in 1907, as given by Pope (1908) was 1.006, while in 1912 this had increased to 1.0099.

The color of the water, determined by the platinum-cobalt standard of the U. S. Geological Survey, usually ranges from 15 to 70, the lower figure representing conditions in winter, when chemical and physical changes are at a minimum, while the higher represents the condition in spring, accompanying the run-off from the melting snow, with its large amount of dissolved material from the humus in the soil. There is no appreciable difference in color between the surface and the bottom of the lake.

On March 11, 1923, the water from a hole cut in the ice near the shore was a deep wine color, which faded very markedly after standing a few days. Not having any color standard solutions available at the time a color reading was impossible. The color moreover was not comparable with the platinum-cobalt standard, being distinctly pinkish, so much so, in fact that an alkalinity reading with phenolphthalein was impossible. The ice in the neighborhood of the hole was thickly filled with *Ruppia*, and the color was apparently due to an extract of the latter. That this should have occurred to such an extent at a temperature of about 0° C. seems remarkable.

Comparative analysis of the water from the shore hole and from one some distance out in the lake, made on March 22, when the color had nearly disappeared, showed, as was to be expected, a much higher amount of both free and albuminoid ammonia in the shore sample.*

* 1924

*Mid lake—free NH_3 0.52, albuminoid NH_3 2.71 ppm.

Shore—free NH_3 3.56, albuminoid NH_3 7.24 ppm.

Turbidity has been determined by means of the Jackson turbidimeter described by Whipple and Jackson (1900). This ranges from 70 to below 25 p p m.** of SiO_2 and averages slightly higher at the surface than the bottom, the reason for which is not clear, but is probably a slight excess of phytoplankton at the former level. The difference, however, is slight and inconstant. The turbidity is largely due to bacteria and algae (chiefly blue-greens), but considerable quantities of amorphous matter were present in all the plancton collections except in winter when only traces of it occurred. This amorphous matter is probably in part the result of deterioration of the plancton in samples which have stood for several years, and in part composed of air borne dust and more largely of the flocculent ooze from the lake bottom. While I have no positive evidence on this point, there is little doubt that the lake is frequently stirred to the bottom by high winds and that the ooze thus disturbed takes a long time to settle.

To the action of the wind is also probably due the rather uniform distribution of the plancton between surface and bottom, at least at the depth of 3-4 m., where most of my collections have been made, and the occasional massing of the algae along the shore at certain planes, especially in the case of *Nodularia*, the principal filamentous form in the lake.

Horizontal currents are due to the wind, and hence are variable in strength and direction. No exact measurement of these currents are available but approximate determinations have been made by timing the drift of submerged bottles over measured courses.

Exact measurement of these currents would have little significance unless made over a period of years to include the maximum, minimum and average effects of wind. To show in detail wind influence it would also be necessary to make current determinations both as to velocity and direction for all parts of the lake, illustrated with charts. Time and equipment have rendered such detailed study impracticable, and it is further doubtful if the results of such a study would justify the necessary time and effort. The approximate results obtained are sufficient to illustrate the important role which wind may play in the horizontal distribution of the organisms (especially filamentous plants) in the lake. The determinations were made on August 27, 1917, during a high wind, and showed a current of about 13 cm. per second, or approximately 1.4 km. in three hours, at which rate a mass of plancton might readily drift from one side of the lake to the other in a day.

The determination of the penetration of light in water is a matter of some difficulty. The problem has been attacked by many investigators, employing several types of apparatus. The simplest

**In winter less than 10 ppm., compared with a silica standard.

of these consists of a white disk, which is lowered in the water and the depths of disappearance and of reappearance upon raising noted, the mean of which gives a reading which may be compared with similar readings on other waters, or on the same water at other times, or under different conditions. A modification of this type of apparatus is the turbidity rod of the U. S. Geological Survey, in which a platinum wire is substituted for the disk of the Secchi apparatus. In another modification an electric light replaces the disk. Another type depends on the exposure of a sensitive plate or film at various depths for various intervals, the relative degrees of penetration varying inversely as the times of exposure. This method has been employed by several investigators in both marine and fresh water work, using many different kinds of apparatus for this purpose. A third plan is that of Regnard who used the resistance of a selenium cell as registered by a galvanometer to determine the strength of light at different depths in the harbor of Monaco.* Birge and Juday, in their work on Wisconsin lakes and elsewhere, have employed an instrument, the pyrlinometer, which measures the radiation effect of the sun at various depths, by means of electrical thermo-couples and a galvanometer. Finally Shelford and Gail (1922) have employed a photo-electric cell consisting of potassium mounted in an atmosphere of hydrogen contained in a glass cell, which is connected in circuit with a battery of 80 to 160 volts, and a galvanometer, by means of insulated wire. The amount of current passed thru the cell is proportional to the intensity of the light striking it, and the cell is most sensitive to the blue rays.

A detailed discussion of the relative merits of these various devices need not be given here. Suffice it to say briefly that all give values which are relative only.

The first, since it involves a personal factor, is valuable only when used by the same observer at all times. It furthermore tells nothing as to amount or quality of light penetrating to various depths.

The second method involves the elimination of certain rays by absorption in passing thru the glass window covering the sensitive film. The amount and quality of the rays absorbed by the glass can be tested spectroscopically, however, and in any event is probably small.

A more serious objection to this method is the difference in *relative* density with different times of exposure, and development.*

Another serious objection is that, in comparing the density of plates or films of different exposures with any standard, or with each other, the personal error enters and it is difficult, or impossible,

*Fide' Shelford and Gail (1922). I have not had access to Regnard's original work.

*See Nutting (1912)

to obtain closely accurate results. An essential condition of this method is, of course, uniformity in the plate or film employed. By using the same kind in all experiments, practical uniformity of results is probably assured.

The objections to the third method have been detailed by Shelford and Gail (l. c.) and may be summarized by the statement that the sensitivity varies in different cells and under different conditions (temperature, time of illumination and quality of light).

The pyrlimmometer of Birge and Juday measures the radiator (heat) energy of light, rather than its chemical effect, which latter is the more important factor to be determined,—since the heat effect can be found by thermometric methods.

The objections to the use of a photo-electric cell would appear to be its expense, difficulty of construction and operation, especially on rough waters and the absorption of some rays by the glass cell.

In all of these methods probably the greatest difficulty involved is in the variable condition of the water surface and of the air at different times. When the surface is rippled there is obviously much greater reflection than when it is smooth. The difference in penetration of the light thru the surface layer may vary momentarily more than 100%. Thus Shelford and Gail (l. c. pp. 160-1) have shown that on Puget Sound the light penetrating the surface varied in three minutes from 67.3% of the total (in the air) to 26.0% with changes in the surface, due to tide ripples. Even marked changes in intensity of light, as recorded by photo-electric cells, may occur within brief intervals in bright sunlight. "Marked difference in apparent brightness of the sunlight and in the reading may take place in five or ten minutes when no clouds are visible." (Shelford and Gail, l. c. p. 155).

The results obtained by these various investigators naturally vary widely according to the various methods and conditions of the experiments. No two waters are exactly alike in character, nor does any one body remain constant at all times. In general, the penetration is greater in winter than in summer, partly because of the direct influence of temperature on the absorptive power of water, partly because of the amount of plancton and amorphous matter present at these seasons; the individual waters will vary greatly at different times and under different conditions.

Helland-Hansen*, using photographic plates, found in the Atlantic Ocean a penetration of from 900 to 1500 m., while Grein (1913)**, employing a similar method, found a penetration of about 1500 m. Andersen and Walker (1920), in their work on the Sandhill lakes of Nebraska, found an elimination of light at 4 dm. vary-

*See Murray & Hjort (1912, p. 257).

**Fide Shelford & Gail (l. c.).

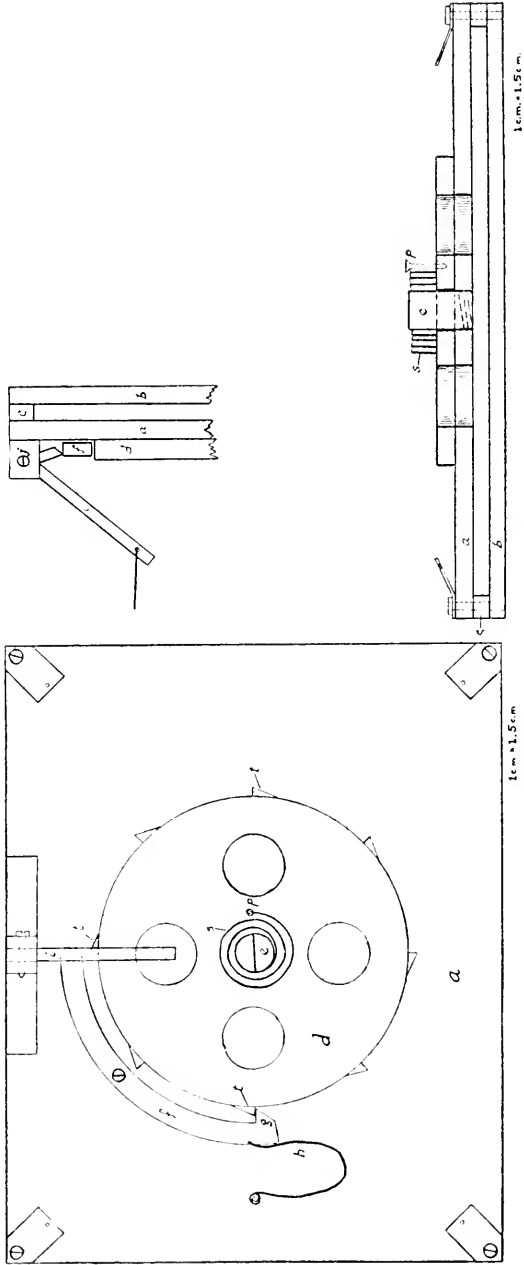


Figure 3. Diagram of light apparatus. See text (p. 23) for description. Right, plan; left, sectional views.

ing from 89 to 95%, while at 8 dm. it ranged from 96 to 99% depending on the time of exposure.

In the (Traunsee) Linsbauer (1905)*** found a reduction in light between the air and a 10 m. depth of 98.6%; while Whipple (1914) found that the Secchi disk disappeared at a depth of 1.8 m. in the highly colored (92 on the Pt.-Co. U. S. G. S. scale) water of the Chestnut Hill Reservoir near Boston, as compared with a depth of 30 m. in the comparatively clear waters of Lake Tahoe in California.

In my own work on Devils Lake I have employed the apparatus, which is illustrated in (fig. 3). It consists of two brass plates a and b, separated by a metal strip c, around three sides, so spaced as to admit a photographic plate and cover between them. The opening on the fourth side is closed by a plate carrying a tongue, which closely fits the opening in the box so as to render it light tight. Two springs bring the plate into position against a. In a are four holes placed 90 degrees apart. Upon a is a circular disk d, with a tongue on its lower surface fitting into a groove in a. d also has four holes so placed as to exactly match those in a, when d is in the proper position. d is revolved by means of a spring coil, s, attached to a pin, p, on d and a plug, e, which passes thru d and is screwed into a. Around the edge of d are eight equally spaced teeth, t,t'. Attached to a point on a is a bar, f, with a tooth at g. When s is wound up, f is pressed against d by a spring, h, in such a manner that g engages one of t and d is held in position covering the holes in a. By means of a vertical arm, i, which swings on a pivot, j, and carrying a cog which engages one end of f, g may be released and d revolved thru 45 degrees by the action of the spring coil, s, thereby exposing one of the holes in a. i is controlled by a cord in the hand of the operator. Releasing i allows g to engage the next tooth, t. d is automatically prevented from revolving too far, and thereby closing the hole in a too soon, by the end of the bar f opposite g which engages the tooth t' when t is released. The closure of the hole is affected in the same manner as its exposure by simply pulling the string attached to i. The apparatus is supported by four cords attached at one end to each corner and at the other end to a small plate, which is lowered to any desired depth by means of a marked line. The film is protected from water by a glass cover sealed to the plate by eelloidin. The plates employed were Cramer's "isochromatic."

For making the experiments clear, still days were chosen so far as possible, a combination which is very unusual at Devils Lake, occurring perhaps half a dozen days all told in any year. Some of the experiments, however, were made thru the ice, when the wind factor was, of course, eliminated.

***Fide' Steuer (1910).

In each experiment the time and weather conditions were noted and one exposure made in air for comparison with those under water.

The results obtained with this apparatus, some of which are illustrated in plate 6, show marked differences on different dates dependent on the altitude of the sun and the turbidity of the water. Many other factors enter in, such as condition of the air and of the surface, but the first two are most important.

Regarding the influence of the condition of the surface on the readings, both Shelford and Gail (l. c.) and Anderson and Walker (l. c.) agree that a large proportion of the light is cut off by a rough surface and that this proportion may change very greatly from time to time. I have not made a careful study of this point, as most of my readings have been made in comparatively quiet water. Two series of exposures to test it were, however, made on October 10, 1923, between 2:13 and 2:24 p. m., one where the water was almost calm, the other where the surface was rippled. They show only a slight difference in surface penetration in nearly calm and rippled water.

The results show a much greater diminution of light in Devils Lake than in Puget Sound (fidé Shelford and Gail), about the same as that in Seneca, Cayuga, and Canandaigua Lakes, N. Y. (fidé Birge and Juday 1921), but considerably less than that found by Anderson and Walker in some of the Sandhill lakes in Nebraska. Neither the first nor the last of these, however, have recorded the turbidities at the time of observation, which makes impossible any direct comparison of our results. Birge and Juday have recorded the transparency in terms of the Secchi disk, their results showing very clearly the influence of turbidity on transmission of solar energy.

My own observation show further a marked difference in percent of transmission between July, August and November. This agrees with the results of Anderson and Walker and is to be expected from the difference in altitude of the sun on those dates.

A brief examination has also been made of the penetration of red and blue, as compared with white light; using for this purpose filters of red and blue glass, whose transmission has not been tested spectroscopically, together with Cramer's "spectrum process" and "iso" plates. The results indicate a lower penetration of blue, and red, than of white light.

Temperature records have been taken with all of the planeton collections. In some cases the Negretti-Zambra thermometer has been used, but generally they have been taken on a chemical thermometer. These have not been standardized and varied somewhat.

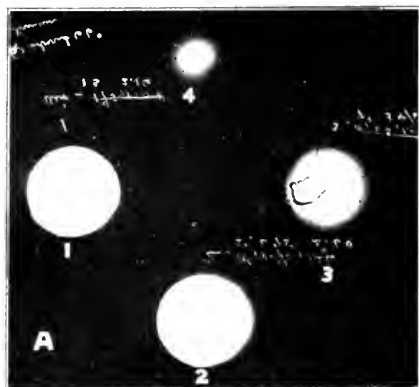
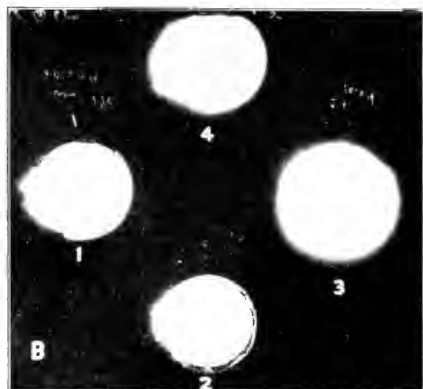


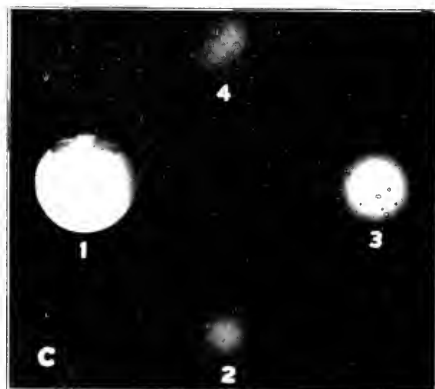
Plate 6. A. Comparative light intensities in air and at 0.6, 2.1 and 2.7 m. depths on October 6, 1923.

- 1—exposed 1 sec. in air.
- 2—exposed 2 1-5 sec. at 0.6 m. depth.
- 3—exposed 3 4-5 sec. at 2.1 m. depth.
- 4—exposed 5 sec. at 2.7 m. depth.



B. Comparative light intensities in air and just below the surface of the lake on October 7, 1923.

- 1—exposed 1 1-5 sec. in air.
- 2—exposed 1 1-5 sec. at surface.
- 3—exposed 2 1-10 sec. at surface.
- 4—exposed 2 9-10 sec. at surface.



C. Comparative light intensity in air and at $9\frac{1}{2}$ m. and $12\frac{1}{2}$ m. on November 4, 1923.

- 1—exposed 1-5 sec. in air.
- 2—exposed 29⁺ sec. at 2.9 m. depth.
- 3—exposed 60⁺ sec. at 2.9 m. depth.
- 4—exposed 120 sec. at 3.8 m. depth.

*Possible error of 1 sec.

the maximum difference in no case exceeding 1° C., and usually being less than that. Some additional readings have been made, especially along shore in summer time to determine temperature extremes in various parts of the lake.

Beside these readings a series of records were made with a thermograph during the summers of 1914-15, to obtain a comparative record of temperatures in air, at the surface and near the bottom for all hours of day and night, for a period of several weeks, one of which is shown in figure 4. These show, as might be expected, the greater changes occurring at the surface, as compared with lower levels of the lake.

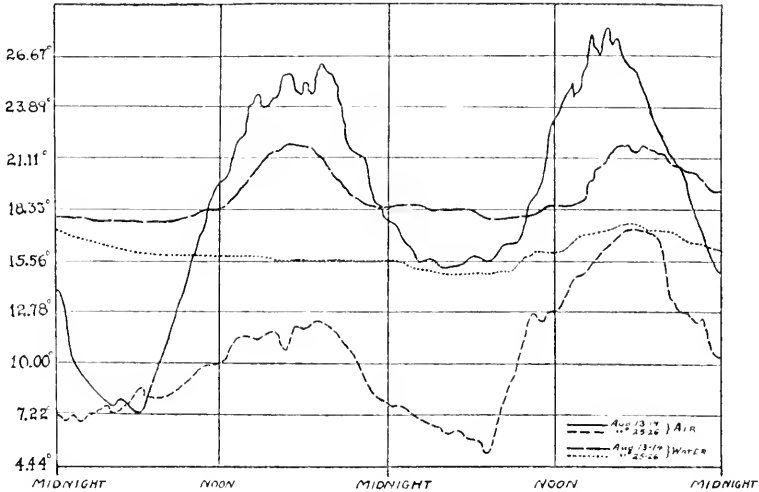


Figure 4. Thermograph records on Creel Bay for air and surface on August 13-14 and 25-26, 1914.

In a shallow lake such as Devils Lake no thermocline develops and there is usually but little temperature difference between top and bottom. In hot summer days the surface temperature rises a few degrees above the bottom, but there is no distinct break between the two. Similarly the shallow water near shore, especially on quiet sunny days, reaches a higher temperature than the surface water in mid lake. Vice versa the surface and shore water are cooled at night more than the bottom, so that more or less mixing of the water occurs daily.

As the lake warms in the spring the shore water naturally warms faster than the main body, a condition similar to that developing on warm summer days, while reverse conditions occur as the lake cools in autumn. Figure 5 well illustrates these differences.

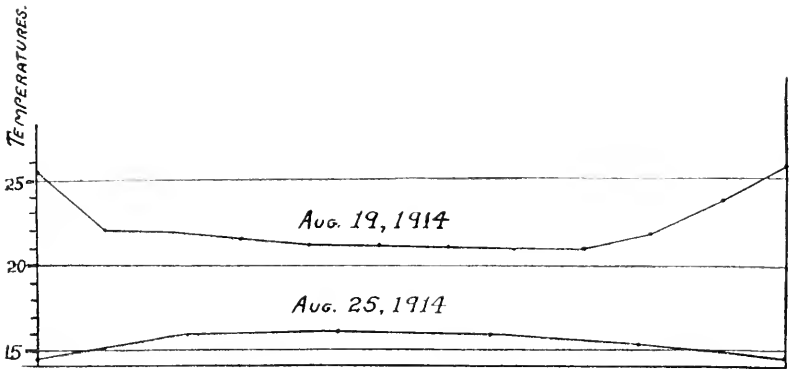


Figure 5. Graphs illustrating surface temperatures across Creel Bay on August 19 and 25, 1914.

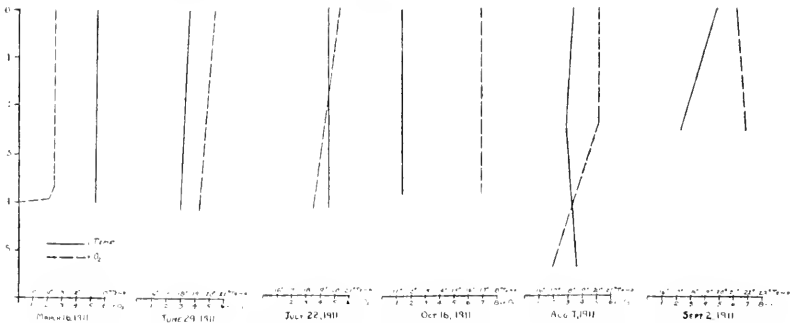


Figure 6. Temperature and oxygen curves for Main Lake. Ordinates represent depths in metres, abscissas, temperatures in degrees centigrade and cc. of O_2 pr. l.

In fall, as the lake freezes, the water at the surface, next to the ice, is cooled slightly faster than that at the bottom, and its expansion near the freezing point causes the cooler water to remain at the surface for a time. Gradually, however, conduction equalizes the temperature of the two regions, which thereafter remains constant until spring, when, the warming of the surface layer, and its consequent condensation, again produces thoro mixing of the entire body of water, the surface and bottom temperatures thereafter remaining nearly constant until summer conditions ensue. Temporary and slight variations occur, dependent on the changing conditions produced by melting ice and snow, alternate freezing and thawing during the early spring and the varying temperature of the air.

Some typical temperature and oxygen curves for different seasons are shown in figures 6, 7 and plate 7.

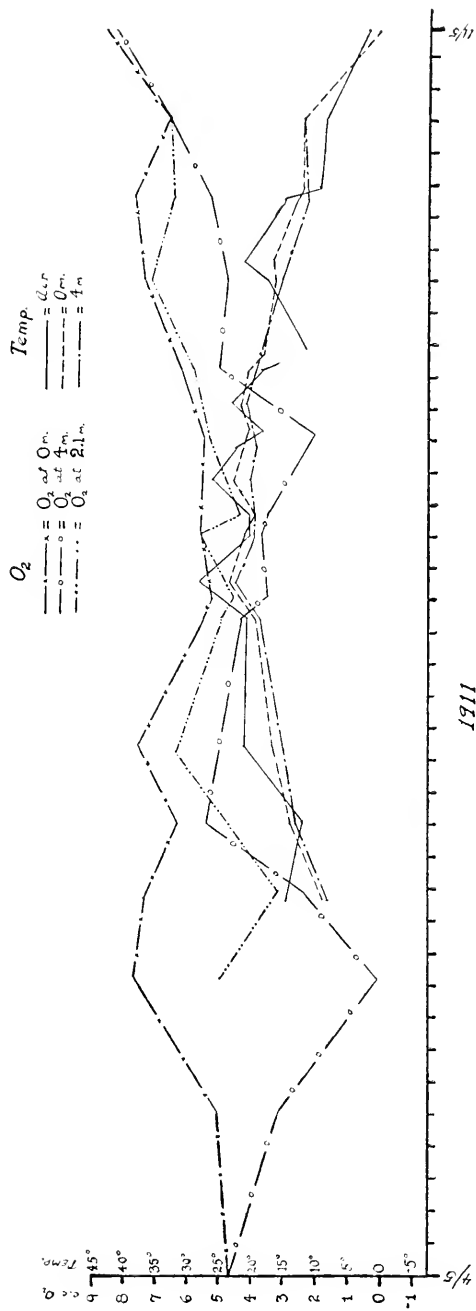


Figure 7. Seasonal curves of temperature and oxygen in Main Lake, 1911. Ordinates represent temperatures in degrees centigrade and cc. of O₂ pr. l.

CHEMISTRY

The chemistry of Devils Lake water naturally varies with the variation in the lake level. A large number of analyses have been made in different years by different chemists. Many of them are partial, but there is a good series, which is complete for all the most important constituents of the water. The methods employed have been, in general, those recommended by the American Public Health Association. The results show an increase in salt concentration, accompanying the decrease in lake level, from 8471 ppm. in 1899 to 15210 in 1923. This chemical change is, as will be seen later, probably the most important factor in determining the changes in the inhabitants of the lake. The analysis (table 3) shows the character of Devils Lake water to be typical of other brackish water lakes of the interior.

Table 3, showing chemical analyses of lakes in Devils Lake complex, all in 1919, except as noted.

Locality	Main	East	Mission	Lamoureux	Stump (1912)	A	C	Spring	P
Normal carbonates as CaCO_3	365	571	320	290		350	290	374	84
Bicarbonates as $\text{Ca}(\text{HCO}_3)_2$	458	902	525	480		525	564	448	56
Total solids	13462	11755 (1907) 62929 (1920)	218 (1907) 48179 (1920)	14932	19000 25450 (1923)	19603	9113	15755	16165
Calcium	70	203	82	107	239		25	91	317
Magnesium	844 (1913)	931	1532	727	876	883	445	691	735
Sodium	2548	8232	4012	4012	3302	3946	2146	4201	3660
Potassium	204			133	764				273
Al_2O_3 and Fe_2O_3	95	88	134	63		42	24	45	32
Chlorine	1310	3250	2750	1442	1803	1950	995	1610	1283
Sulphates (SO_4)	7187	19960	16129	8070	10084	10488	4589	8320	8988
Iron					4.0				
SiO_2		168			29.4				
Osmotic pressure in atmospheres	6.3 (1920)	12.8 (1920)	9.7 (1920)	6.75 (1920)		8.9 (1920)			

The salt content of surface and bottom layers is alike, but some differences exist between different parts of the lake, dependent on the scanty supply of fresh water drainage at one or two points, influx of sewage, and probably to some extent also on other less obvious factors, such as temperature, depth, kind and amount of organic matter in the ooze and kind and number of organisms present in the water.

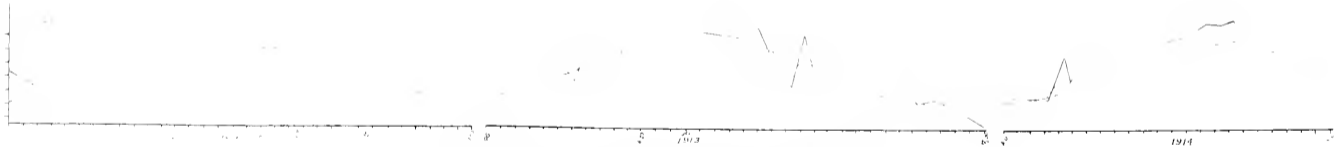


Plate 7. Temperature curves for Maui, Lihle, 1912-14. Ordinates represent temperature in degrees Celsius.

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The organic material, represented by free and combined ammonia, naturally varies markedly, not only with season, but also with locality and depth (fig. 8).

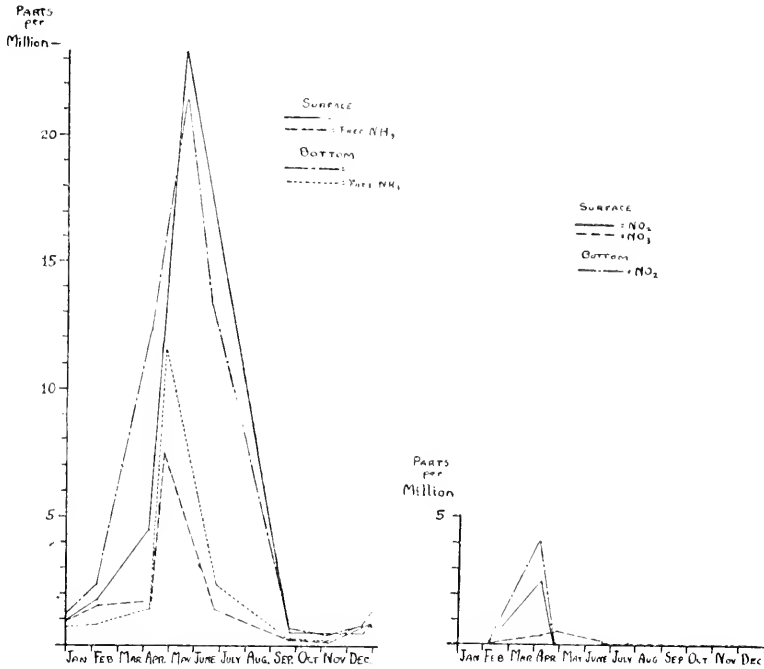


Figure 8. Seasonal occurrence of organic material in Main Lake, Jan.-Mar., 1914, Apr.-Dec., 1913.

Dissolved gases also show marked variations with time and place, which, to a certain extent, when plotted, take the form of cyclical curves dependent on the seasons.

Especially is this true of dissolved oxygen. The amount of this present in the lake depends on temperature, which in part determines the absorptive capacity of the water for gases and the photosynthetic activity of plants; on amount and velocity of the wind, determining amount of aeration; on the number and activity of the organisms present, and on the extent of decomposition taking place in the water.

The apparatus used for collecting oxygen samples is that recommended in "Standard Methods" of the American Public Health Association.

Exact determination of oxygen in the lower layers is a matter of considerable difficulty, due to currents generated by the raising and lowering of the apparatus. When an oxygen free stratum

several inches thick occurs at the bottom, it is usually possible to definitely establish this fact, but if this stratum is very thin, or if oxygen is present at the bottom, but in quantities much smaller than at higher levels, it is practically impossible to obtain duplicate readings checking each other within less than 25 or 30%. Especially is this true in windy weather, when the motion of the boat increases the currents generated in raising and lowering the apparatus.

There is some question regarding the accuracy of the Winkler method, which was employed in this study, for the determination of dissolved oxygen. Birge and Juday (1911) found a fairly close agreement in the results of the Winkler and boiling out methods. They were working, however, on waters, none of which approached Devils Lake in salt concentration. In waters of such high concentration as the latter, the iodimetric method employed by Winkler is liable to be affected by the various salts present. Relative thereto, Dr. Heath, chemist at the station in 1914-15, says in ms. notes on his results:

“For a variety of reasons this method appears to be inaccurate when applied to such a salt solution as Devils Lake water . . . The presence of nitrates in the water causes the Winkler method to give too high results for oxygen, and nitrates may interfere by a variety of chemical changes. When the amount of nitrate is known a correction may be applied, but even then there are so many complicating factors that the method is unsatisfactory. It is probable that the other substances present in the water also interfere with this determination to a certain extent.”

The results obtained by the Winkler method, however, agree well with those obtained by other workers elsewhere and with what might be expected in Devils Lake. The boiling method, moreover, is tedious, and difficult to use in the field, for which reasons the Winkler method has been used and probably gives results which are sufficiently accurate for comparative purposes.

During the winter, when the ice sheet reaches an average thickness of one metre, there is little opportunity for aeration, and by spring the oxygen in the lower levels is greatly diminished if not entirely absent. With the melting of the ice and influx of a considerable body of fresh water from air and melting snow, the oxygen content rises sharply, gradually diminishing again during the warm days of summer. After a few hot still days, which but rarely occur, the bottom water may be almost or entirely free from oxygen, but a fresh breeze quickly changes this condition and restores oxygen to the lower layers. With the advent of cool fall weather the oxygen content again rises, remaining at a maximum until the lake is once more sealed by ice.

The lowering of the oxygen in the lower levels is due, not to the absence or scarcity of chlorophyll-bearing organisms at these depths, where they are about as numerous as they are near the surface, but rather to the decomposition of the organic matter contained in the ooze covering the lake floor. This decomposition evidently occurs even at zero temperature, judging by the diminution of oxygen in the bottom level during the winter.

Similar, though much less marked differences, occur between the shore water and that further out in the lake, while local differences may occur, due to aggregations of plants at different points.

No free carbon dioxide appears in any of the analyses and is probably never present at any point in the lake, though it is possible that at times of high water it might temporarily appear at the mouth of the sewer from Devils Lake city, which discharges into the lake. In the form of bound (mono-) and half bound (bi-) carbonates it usually shows but little difference between surface and bottom, and the shore and middle parts of the lake. At the bottom and near shore the bicarbonates are higher than elsewhere. When the ice is melting the surface water is temporarily much lower in carbonate alkalinity than the lower water. With the disappearance of the ice and stirring of the lake by the wind, this difference promptly disappears. (Figure 9.)

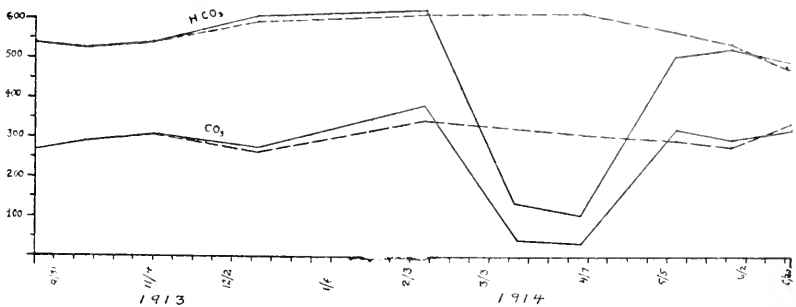


Figure 9. Distribution of CO₂ in Main Lake at 4.0 m, from 9 24 13 to 6 20/14. Ordinates represent parts pr. million.

Numerous tests have been made for hydrogen sulphide, but the results are not very conclusive.

Birge and Juday (l.c.) have suggested the inexactness of the standard methods for the determination of H₂S and recently Heath and Lee (1923), as the result of studies based primarily on Devils Lake water, have pointed out the difficulties in its determination, due to the presence of various salts and their reaction with iodine. These authors suggest the substitution of a colorimetric method for the iodimetric one.

Dr. Heath in ms. notes thus summarizes the results of his work on Devils Lake:

"The waters of the Lake seem to carry no dissolved hydrogen sulphide except in a few places where contaminated by sewage. The mud on the bottom and the water in immediate contact with it carry the gas in small amounts."

Comparatively little is known regarding the relation between dissolved nitrogen and aquatic life. It probably is always present in water, forming a large percentage of the dissolved gas. Judging by its inert character, it seems improbable that it plays any important part in the life of aquatic animals, although there is some evidence to show that in excess it may be injurious to fishes (Marsh and Gorham, 1905). It may possibly be an important part of the food of aquatic plants, though this is not definitely known.

But two tests have been made for nitrogen in Devils Lake, both in the summer of 1914. Two 1200 cc samples gave by the boiling method 84.9% and 89.8% respectively of nitrogen in the dissolved gases, the remainder being oxygen. In these two tests no methane, carbon monoxide or free hydrogen were detected. These are the only tests which have been made for these gases.

BIOLOGY

The biological investigation of any area comprises an enumeration of its inhabitants, and a determination of their distribution and abundance in time and space, in reference to their physical environment and their reactions upon one another. Without the cooperation of many specialists the first phase of the problem is impossible, while the second phase is of course dependent on the first. Due acknowledgment of the aid received in the prosecution of this work has already been made and need not be repeated here. The list of species is admittedly incomplete since some of the identifications have not been finished, and part of the work was preliminary in character. This is notably true of the nematodes, insects, and bacteria.

In spite of these deficiencies, however, it has not seemed advisable to delay publication further, since to obtain complete lists of species would probably require several years delay, and by that time the fauna and flora of the lake would probably differ markedly from their composition when the work was begun. In fact at the present time distinct changes have taken place, and in the case of some parts of the lake (East and Mission Lakes) the present fauna and flora have little resemblance to those of a few years previous. Furthermore, the data at present available are sufficient to give a fairly adequate idea of the life of the lake and its responses to its changing environment.

The biological problems may be grouped under three main heads; first, the life zones of the lake and their characteristic inhabitants; second, the seasonal distribution of the plancton, and third, an annotated list of species.

LIFE ZONES

The life zones of the lake are not well defined regions because of its shallowness, the gradual slope of the bottom, and especially because of the influence of the wind in mixing its waters. They may in general, however, be defined as four, namely (1) littoral, the shore zone to a depth of 0.6 m., (2) *Ruppia*, the region between 0.6 and 2.0 m. in depth, where *Ruppia* grows abundantly, (3) pelagic, the area over 2.0 m. deep, and (4) bottom, the ooze covering the floor of the lake. Zone 1 is characterized in places by *Enteromorpha* which grows abundantly on the rocks at some points along shore. It is not common, however, occurring only where the shores are covered with rocks, chiefly on the islands or "rock piles" in the lake. Its presence indeed is so exceptional that it should perhaps not be considered a "characteristic" of this zone.

Apart from *Enteromorpha*, zone 1 has no specific characteristics. *Cladophora* also occurs here to a considerable extent, attached to the rocks or to submerged logs, but this is more characteristic of the following zone. It is a region where, at times, certain species occur in large numbers, only to disappear again as quickly. This erratic occurrence of organisms in zone 1 is due chiefly to two factors: first, temperature, and second, wind. The former is one of the most important factors controlling the multiplication, movement and consequent distribution of organisms in the lake. Consequently it is not surprising that wide variations in the abundance of organisms in the littoral zone should accompany the temperature differences in this zone, to which reference has already been made.

Wind is also an important factor in determining the distribution of organisms in this zone, especially the massing of filamentous algae which occasionally occurs here, as already noted.

Further reference to these features will be made in the discussion of plancton distribution. In general it may be said that zone 1 is marked rather by the absence than the presence of characteristic forms.

The *Ruppia* zone is the most interesting, as well as important one in the lake. It is interesting because of the variety of its inhabitants, and important because of the influence of the great mass of *Ruppia*, which develops here in summer, upon the chemistry of the water, as an important source of the organic matter in the ooze accumulating on the lake bed and as a breeding place for numerous organisms, both animal and plant.

This zone is characterized primarily, as its name implies, by the *Ruppia*, which grows here abundantly, and secondarily by the organisms which live attached to the *Ruppia* or to other organisms which grow upon it. Chief of these is *Cladophora*, which forms extensive masses and which, perhaps no less than *Ruppia*, is responsible for the evolution of large quantities of oxygen in sunny weather, and contributes an important amount of the bottom ooze thru the decay of its filaments. The exact quantitative role which any one of several organisms plays in a situation of this sort is a difficult one to determine and no attempt has been made to do so in this case. It is, moreover, of minor importance since both organisms exert a similar influence, the effect produced being a collective one.

Growing on the *Ruppia* and *Cladophora* are numerous microscopic forms, chief of which are sessile diatoms, peritrichous Protozoa and attached rotifers. There are many free-living forms also which are numerous here and rare, or absent, elsewhere in the lake. Chief among these are the Protozoa, rotifers, nematodes, and mites, while a few others occur.

The extent of zones 1 and 2 is naturally a variable one, dependent on the slope of the lake bottom at different points.

The pelagic zone, which comprises the major part of the lake, has no forms peculiar to it, since all of its organisms occur in the other two zones as well. It is characterized by the greater uniformity in the distribution of its inhabitants, tho great differences occur here also, as will be seen later, and by the absence or rarity of those forms which characterize zones 1 and 2.

The bottom zone, which comprises the ooze on the lake floor, is characterized positively by the presence of the larvae of *Chironomus*, by nematodes and the rhizopod *Arcella*, and negatively by the absence of pelagic species, tho some of the algae, especially *Coelosphaerium* may occur there. This zone is frequently lacking in oxygen, as has been mentioned previously, and will be discussed later in connection with its inhabitants.

PLANKTON METHODS AND RESULTS

The determination of the distribution in time and space of its inhabitants is the central problem in the investigation of any area, for this problem involves the reaction between organisms and environment, and the adaptation of the former to the latter, which are the essential questions of ecology. This determination is a matter of considerable difficulty, for both land and water animals. Many attempts have been made to devise satisfactory apparatus for plankton collection, but thus far none has been invented which is uniformly satisfactory for all kinds of organisms. Full discussions of the advantages and disadvantages of various types of

apparatus are found in the works of many authors,* and need not be repeated here, where it may suffice to summarize the difficulties involved in their use.

1. Nets, even of the finest bolting cloth available, allow the escape of a large part of the nanno-plancton.

2. The amount of water filtered by the net is a function of its form, the rate at which it is handled, the age of the silk and the consequent extent of clogging, and probably also of the temperature and the amount of plancton present.

3. Plancton traps and pumps which depend upon the use of nets for the concentration of the catch are subject to the first difficulty above mentioned.

4. Pumps are open to the further objection that their current may serve to drive away some of the more active negatively rheotropic organisms from the intake.

5. Water bottles collect only small amounts of water, and further cannot be filled without the creation of some current, subjecting them to the same criticism as applies to pumps.

6. The centrifuge in general handles only small amounts of water, and if constructed of larger capacity is bulky, and consequently impractical for general field work. Further, unless run at a high rate of speed, some of the organisms, such as filamentous algae, especially diatoms with flotation spines, may not be fully thrown down. The large centrifuges require electricity, while the small hand instruments require considerable strength and endurance on the part of the operator to run at a speed of 3,000 revolutions per minute, for periods of one minute, which is hardly adequate for the precipitation of the lighter forms.

7. The Sedgwick-Rafter method, involving the use of a funnel tube closed by a piece of bolting cloth and a column of sand, is open to objection 1 above, since the sand in combination with the bolting cloth does not retain all of the finer organisms. When there is sufficient amorphous material and zooglea in the water to retain the nanno-plancton it retards filtration, and the apparatus works very slowly, if at all, six hours or more being required with some collections, even tho the scum on the surface of the sand be broken occasionally with a glass rod. Many of the organisms are retained by the sand when filtration is ended and some may be retained by the walls of the tube itself. A careful discussion of its accuracy has been given by Whipple (1914) who considers it accurate to 10%. In obtaining samples for filtration, moreover, the difficulties mentioned above under 4 and 5 apply.

*See especially Steuer (1910), Whipple (1914), Reighard in Ward and Whipple (1918, Chapter III), and Juday (1916).

8. Concentration of the plancton by filtration thru paper, in addition to the errors involved in collection of the samples and enumerated above, involves also one due to the adherence of a considerable amount to the paper and its consequent loss in the counting cell.

Were the errors involved in any method constant, they would not cause any serious difficulty in plancton investigations, but in every case they are the function of several variables and hence are themselves variable. Thus in the use of a pump the current at the intake depends on the rate of pumping, which is necessarily inconstant for hand driven pumps, while machinery for the purpose is expensive, bulky and generally impractical for field work.

This variation in current rate at the intake may influence the number of organisms which escape due to their rheotropism. Furthermore the movement of the end of the hose due to the rocking of the boat, which is obviously a very variable quantity, may influence their reaction, and the same objections apply in the case of the water bottle, where the rate of flow is a function of the pressure and this in turn of the depth.

Furthermore the rheotropic reaction on the part of plancton organisms is very probably a function of temperature and other less obvious factors in the life of the organism.

Satisfactory preservation of material is one of the most serious difficulties in any plancton investigation. If the material is to be counted fresh, it must be done promptly, especially in warm weather, or it will deteriorate, and this is impractical in the case of collections made in the field at some distance from a laboratory. If the material be living when counted the movement of larger forms such as crustaceans and rotifers disturb the contents of the counting cell so that accurate counting is impossible. Furthermore at the time collections are made, press of more immediate duties may render counting impractical. On the other hand preserved material, especially those forms such as the alga *Dictyosphaerium* and bacterial zoöglea, which are held together by delicate gelatinous sheaths, is almost certain to deteriorate in course of time, so that if counting be delayed for months or years a very serious error is introduced.

The enumeration of the plancton has to be made with low powers (about 100 diameters) which renders the specific determination of some of the smaller forms difficult or impossible.

Still another difficulty in obtaining accurate plancton records, and one to which sufficient consideration has not been generally given, is the irregularity in the distribution of the plancton organisms themselves. This irregularity has been noted by occasional investigators in the past, but it has nevertheless been generally assumed that one sample taken at any point in a given body of

water is representative of any other sample collected at a different point, provided environmental conditions at the two points are identical. This question has recently been carefully investigated at Devils Lake by Moberg (1918), who found an average variation ranging from 70% for some of the algae (*Coelosphaerium*, *Chroococcus*, etc.) to 185% for the crustacean *Moina*.*

Maximum variations for the entire series are of course much larger. Thus in one series *Diaptomus* showed a range of 400% of variation from the mean and *Monia* 297%, and in another series *Braehionus satanicus* showed one of 376%.

While Birge (1897) maintains the general uniformity in horizontal distribution of plancton, he finds nevertheless in a series of collections made at different points on the same day* a range of variation from the mean from 49% for *Cyclops*** to 180% for *Daphnia pulicaria* and *Ergasilus*. These variations, while not necessarily proving the existence of swarms, as Birge points out, do nevertheless show an irregularity of horizontal distribution so great as to invalidate any general conclusions regarding plankton distribution unless based on a large number of counts.

"My observations show so much variation in catches made at the same place and in succession that I have little confidence in the differential method of determining vertical distribution; unless a very large number of observations is made and averaged, so as to eliminate the chance of variation in the single observation." (Birge 1897, p. 376.)

Marsh (1898) in a series of collections made at the same place on Green Lake, Wisconsin on two successive days, found that *Diaptomus* ranged from 291 to 2966, and similarly large variations were found by him in other genera.

Birge himself (l.c.) and other writers have described the occurrence of swarms, chiefly among the Cladocera and I have observed them in both *Moina* and *Diaptomus*.***

Similar results have been obtained by other investigators (Reighard, 1894, Apstein, 1896, Gandolfi-Hornoyold and Almeroth, 1915, et al.), altho, in general, with smaller variations. Moberg's work was done, chiefly on 500 cc samples, but in two series 19 litre collections were taken. His results warranted the following conclusions. "1) The zoöplankton in Devils Lake shows a great irregularity in horizontal distribution, and this irregularity cannot be correlated with any variations in amount of phytoplankton or in the chemical and physical environment. It is more likely due

**Asplanchna* showed a range of 219%. The number here is too small, however, to have much significance.

*Time required for the series not stated. Presumably they were made under as nearly as possible similar conditions.

**Including two species.

***See Moberg (1918, p. 266, f. n. 8).

to the habit of swarming among plankton animals, due perhaps to a social instinct, similar to that found in many other groups of the animal kingdom. Plankton swarms are at times visible, even at considerable distances, to the naked eye. 2) With larger samples (19 litres) the variations tend to be reduced, but even here they are at times greater than in the smaller ones ($\frac{1}{2}$ litre). 3) These variations invalidate the usual assumption that a given sample of water is representative of a large area, at least in respect to its animal inhabitants, and necessitate the collection of large numbers of samples before definite conclusions regarding their distribution or movement can be drawn."

These difficulties, however, while serious in themselves, are usually insufficient to obscure the *comparative* results of an ample series of collections, and it is these comparative results in which the ecologist is chiefly interested. It may, of course, be desirable to know the *actual* amount of plancton per hectare which a given body of water will produce, in order to know the number of fish which that body will support. But who knows the number of cubic centimetres of plancton per cubic metre of water which will furnish adequate sustenance for a fish of a given weight and given species? And in general the suitability of any water for the cultivation of fish, or other economic animals, depends more on temperature, chemical character of water, breeding grounds, and oxygen supply, than on the available amount of food; for in any water where the physico-chemical environment is suitable for fish life there is pretty sure to be adequate plancton for the support of as many fish as the water is suited to contain.

On the other hand the *comparative* variation in amount of plancton in both time and space, correlated with changes in the environment, answers the ecologist's questions regarding the reaction between organism and environment and adaptation of the former to the latter.

While no one method is adequate for the purpose, it has not seemed practical for various reasons to employ more than one, and I have accordingly employed that one which seemed best adapted to the general purpose from every standpoint. This method has been checked and supplemented from time to time by others, but the results which follow are based almost entirely upon it.

In collecting samples I have used a water bottle closed with a two hole rubber stopper, thru one hole of which extended a glass tube with a rubber hose connection reaching to the surface, the other hole being closed with a wooden plug attached to a string. The bottle was contained in a metal box, weighted and open on the sides, so as to insure easy sinking, attached to a marked chain. When the box was lowered to the desired depth, as indicated on

the chain, the plug was jerked from the cork and the water allowed to enter in a steady stream as the air escaped thru the rubber hose. When oxygen samples were taken at the same time as the plancton, the sample of the latter was taken from the larger bottle of the Winkler apparatus used in collecting the former.

Prior to September 4, 1913, surface and shore collections were taken by immersing a bottle below the surface. Thereafter they were made by scooping it up and transferring to a jar. Comparative tests of the methods of sampling by means of the scoop, the bottle, the Winkler apparatus and the pump have been made for the surface, and in the case of the two latter methods, for the bottom as well. In these tests from 48 to 100 cc. of the samples collected by each method was carefully measured and the animals contained in it counted by eye in a white porcelain dish. The method is not a very accurate one, but is sufficiently so to demonstrate any considerable or constant variation in the different methods. With the scoop water was taken both from the surface and from seven to ten centimetres below. With the Winkler apparatus and pump the intake was necessarily held a few centimetres below the surface, and as nearly as possible at the same level in all collections. The samples were taken as nearly as possible in the same spot and with brief intervals between each collection. The results of these tests show no constant difference between the various methods, and such differences as occur are smaller in general than those found by Moberg (l.c.) in the horizontal distribution of the plancton. In the shore samples, however, where the number of Crustacea was large, there is a distinct advantage for the scoop method.

A comparison of the results obtained by the plancton trap, described by Juday (1916), the pump, Sedgwick-Rafter, centrifuge and filter paper methods indicates no constant difference for the Crustacea and rotifers in favor of either the Sedgwick-Rafter, pump or trap methods, such differences as exist being inconstant and doubtless due to variable distribution already referred to.*

With the bacteria and algae the results vary. For the filamentous forms (*Nodularia* and *Lyngbya*) the Sedgwick-Rafter method gives distinctly larger results. For *Coelosphaerium*, *Oöcystis*, *Merismopedium* and *Micrococcus* there is a distinct advantage in favor of the centrifuge; while in the case of *Dictyosphaerium*, *Chroöcoccus* and *Chaetoceros*, there is but little difference one way or the other.

In these experiments a small hand centrifuge, holding 15 cc. of water in each tube and run for one minute at approximately 3,000 revolutions was employed and it was very difficult to throw down all of the *Nodularia*. With a larger machine, operated at

*See pp. 36 S.

a higher speed and for longer periods the results would doubtless have been different.

Examinations have been made of the filtrate from the Sedgwick-Rafter tubes which show a considerable loss of such forms as *Coelosphaerium*, while, vice versa, filter paper, even if carefully washed, retains a considerable quantity of material, so that in either case the results are too low.

The usual plancton series includes readings at the shore, the surface, some distance from shore, and at depths of 0.6, 2.1 and 3.0 to 4.3 m., the latter reading depending on the depth of the lake at the point and time of collection. There was some variation from this general plan, especially in the earlier years of the work, when the collections were preliminary to the main series. Some of the collections were lost so that the series is not quite complete. It is sufficiently so, however, to give a good idea of the plancton abundance and distribution thruout the periods of observation.

The counts have been made mostly by my former assistant, Mr. E. G. Moberg. Some of them are my own, however, but these have been checked with his by comparative counts on the same material. Whenever possible it is desirable that readings should be made by the same observer, in order to remove the personal equation, which cannot otherwise be eliminated entirely from work of this character.

The series prior to August, 1913, are more or less fragmentary. Beginning at this time, however, readings were taken at intervals of usually a week to ten days until September, 1914. In some cases readings were taken at intervals of one to two days, while there are one or two intervals of two weeks duration. During winter and early spring the interval was lengthened to from three to six weeks. An additional series of readings with two to three week intervals* was taken from Dec. 3, 1922, to July 23, 1923.

Readings were made at several levels instead of a single one to ascertain the distribution of organisms at various depths. In several instances these readings were taken in parallel series for different hours of the day and night in an effort to determine the vertical migration of the zoöplancton. The results of these readings, which were very indefinite, will be discussed later. The series of readings from top to bottom gives a much better record of the plancton abundance than would readings at only one level.

The accompanying charts give a graphic representation of the occurrence of the various selected species and groups, during the periods of observation from 1911 to 1923.** The chart of one year is not strictly comparable with that of another, in respect to total numbers, at least for some of the algae and bacteria; since the period

*In one case six weeks.

**Based on one litre samples.

elapsing between the time of collection and that of counting was different for different years, with the result that some of the collections deteriorated more than others. Especially is this true of the 1914 series, which for the most part was not counted until 1919 and in which considerable disintegration of some of the algae and bacteria occurred. No record has been made of *Dietyosphaerium* for this year, since it appears in the counts only sporadically and has evidently deteriorated. Deterioration of the closer colonies, such as *Coelosphaerium*, occurred to a much less degree and probably did not materially affect the records, while the diatoms were unaffected. In general the counts of any one season are closely comparable with one another since they were made for the most part at nearly the same time.

A study of the charts in general reveals several interesting facts.

1. There is, in general, no evident relation between depth and plancton abundance, conditions at the surface and at lower levels not usually differing greatly, except in respect to light, which factor is considered at greater length later.* The absence of a thermocline in Devils Lake renders conditions here very different from those in deeper lakes elsewhere. Oxygen may occasionally be greatly reduced or absent at the bottom, but the layer of water in which this occurs is thin, and it is quite possible that oxygen, in the dissolved condition at least, is of less importance than has generally been believed. This question is discussed at greater length elsewhere, in connection with the organisms inhabiting the ooze.**

2. There are great variations in the collections at all points, the most conspicuous in the case of those taken near shore. They may be due in part, in the case of some of the colonial algae, to imperfect preservation of material, altho this is unlikely, since the various samples must in most cases at least, have been influenced equally by this factor. In the case of the animals, swarms no doubt are very important, tho the extent of their influence is still a problem.*** Even among the algae, Moberg, in his study of horizontal distribution, found great variations, too great to be attributed to errors in collecting or in counting the samples, and apparently due to chance. In any event the plancton, both plants and animals are *not* distributed uniformly, as is generally assumed. In the shore collections these variations are probably due largely to temperature. Wind may also play an important part, especially with the filamentous algae, but other, less evident factors, appear to enter.

*See p. 46.

**See p. 106.

***In this connection, see Moberg (1918).

3. There is no close correspondence between temperature and plancton abundance. It is true that in winter most species are either absent from, or very rare in the collections; but from spring to autumn there may occur several maxima and minima of plancton numbers, which are apparently wholly unrelated to temperature. These naturally differ for different species and different years, but in general, occur, one in early summer, and the other in early autumn. The causes are obscure and are probably manifold. In spring there is usually a considerable influx of drainage water, carrying with it dissolved materials, including much organic matter, from the soil. Following this influx, and with increasing light and rising temperature, there is a great development of both algae and bacteria, especially the latter, accompanied in turn by a great increase in animals, especially the rotifers. The maximum of early summer is succeeded by a more or less well marked period of depression during July, which may be succeeded by other periods of maxima and minima in August. In the fall there generally occurs a high point in the distribution curves accompanying a falling temperature and decrease of light. These waves of production are irregular and inconstant and their explanation is obscure. It is not impossible that in midsummer the temperature is too high for the successful development of many of the organisms in the lake; or that, with their development in early summer the dissolved materials in the lake necessary for plant growth are largely consumed, with consequent inhibition of development; it is further possible that the great growth of bacteria may be responsible for the production of some toxins inimical to the growth of other forms. The first of these hypotheses seems the more likely, but none of them are entirely satisfactory and the reason remains obscure. Similar periods of maxima and minima in plancton production have been described by other writers, but it is difficult to compare the seasonal distribution of plancton in different lakes because of 1) differences in its environment and 2) differences in its component species. A detailed comparison of my own work with that of others would require far too long a discussion. It must suffice to indicate some of the more important results.

1.) In studying the distribution curves for any lake, one is at once struck with the numerous minor irregularities which they display. Take for example, the curves illustrating the vertical distribution of the Crustacea and nauplii in Lake Mendota on September 8, 1896 (pl. XLII, Birge, 1897). According to these there were more adult Crustacea by about 35% at the 6 than at the 4 m. level, and slightly more at 3 than at 2 m.; in spite of the fact that they were decreasing rapidly from above downward, except in the first half metre. The nauplii vice versa, while

increasing from above downward, were nearly 50% fewer at the 4 than at the 3 m. level.

Again, consider the Diaptomus charts of Marsh (1898, pl VII). In August, 1896, there occurred, according to the chart, two well marked maxima and minima, with numbers ranging from 1563 to 3803*, a difference of nearly 150%. Similar, tho less marked irregularities are shown in the curves of Birge (l.c.).

Irregularities in vertical distribution, similar to those just mentioned, have been discussed by Birge and Juday (1911, p. 116) who consider them evidence of stratification of the organisms concerned. They deny the likelihood of their causation thru errors in collection or counting, but apparently overlook the possibility of irregularity in *horizontal* distribution being responsible for an *apparent* irregularity in *vertical* distribution, nor do these authors attempt an explanation, merely contenting themselves with the statement that "such results . . . should be expected . . ."

These differences may, of course, be accentuated, or the reverse, by the scale and time interval chosen, and the number of collections averaged. Taken in the aggregate they are of little significance and do not obscure the main features of the curves. Considered separately, however, they do have significance, in all probability indicating the irregularity of horizontal distribution already referred to.**

2. There appears to be no constant relation between the environment and the periods of maximum and minimum production. Reproduction is, in most cases at least, greater in summer than winter, so that, obviously the factors of light and temperature play the all important roles in determining abundance. But even this rule has exceptions. Diatoms frequently develop in enormous numbers in winter, as noted by Marsh (1900, p. 176) in Green Lake, Wisconsin, and others. The above statement obviously does not mean that plankton production is independent of environment. It is *closely dependent* thereon. But the factors are so many, and so closely interwoven with one another, that it is difficult, if not impossible, to determine any general laws governing their interdependence.

There is often a plancton maximum in spring associated with increase of temperature and light, with overturn and consequent mixing of the water and influx of food materials in the run-off from rain and melting snow. In addition to this maximum there may occur other less constant maxima in mid-summer and autumn. This is the general type of plancton production presented by Devils Lake, Lake Mendota*** and the lake of Zurich,**** etc.

*Total catch.

**See pp. 36-8.

***Ibid' Birge (l. c.)

****Ibid' Lozeron (1902).

In no two lakes, however, are the environmental conditions, or the fauna and flora exactly identical; it would therefore be too much to expect that the behavior of the plancton should be the same in both. The behavior of any organism at any time, and in any situation, constitutes a problem in itself, and a very complex problem at that.

3. While, in a general way, the forms of the curves of any species are similar in two successive years, nevertheless their size (i. e. the number of individuals present) varies greatly. This is at once obvious on inspection of the plancton curves for two or more successive years for any lake. Compare, for example, those given by Birge (l. c. pl. XXV) for *Diatomus* in Lake Mendota in 1894-95 and '96.

“The feature of the annual distribution of the crustacea which surprised me most in the progress of my work is the great difference between the numbers of the same species of crustacea present in successive years. I do not refer so much to the larger or smaller numbers of forms like *Cyclops*, for whose variations causes can be assigned, at least in part, but rather to such facts as those shown by *Daphnia retrocurva* and by *Diaphanosoma*, which are either absent, or present in very small numbers in one season and appear in great numbers in another year. For such variations it is very difficult to assign even conjectural causes.

“A similar fact has appeared in the succession of the algae. It is not true for lake Mendota that the forms of algae succeed one another in a definite order in successive seasons, so that one can be sure of finding certain forms at certain times of year, as would be the case with plants of woodland or prairie.” (Birge, l. c., p. 317.)

Robert (1919-20), after reviewing the work of several authors, together with his own, reaches the conclusion (p. 41) that “Nous ne pensons pas qu'un seul des facteurs généralement invoqués: température, circulation ou stratifications des eaux, puisse à lui seul expliquer la date d'apparition des maxima et minima du plancton. Ceux-ci dépendent sans doute de facteurs fort complexes et difficiles à isoler, parmi lesquels ceux que nous avons étudiés jouent probablement un certain rôle.”

Only the principal plancton species are represented in the charts. Many others are of sporadic occurrence, probably being carried from the *Ruppia* into the pelagic zone by the action of the wind. A few forms, such as *Characium*, which grows epiphytically on the Crustacea and elsewhere, are of frequent but inconstant occurrence in the collections; while others, such as *Cothurnia* and *Pediastrum* occur in too small numbers to have much signi-

fiance in the study of the plancton distribution. They will be considered individually in the annotated list.

Only two phyla of animals have any considerable representation in the plancton. These are the Crustacea and the rotifers. Of the former there are three important genera of one species each, and of the latter two genera and three species.

Of the Crustacea *Diatomus sicilis* is of most importance, both because of its numbers and its presence at all seasons of the year. At times it is out-numbered by *Cyclops* and *Moina*, but these occur in considerable numbers for comparatively brief periods, while *Diatomus* is always more or less common.

The nauplii are mainly those of *Diatomus*, but no attempt has been made to differentiate between them and those of *Cyclops*. The latter are probably too few in general to affect the distribution curve to any extent. In general the maxima of the nauplius curve alternate with the minima of that of *Diatomus* as might be expected. The number of nauplii is, in general, much greater than those of *Diatomus* and *Cyclops* combined, which undoubtedly indicates a high mortality in the larval stage. In Lake Mendota also Birge (1897) reaches a similar conclusion regarding their mortality.

Contrary to his experience, on the other hand, I find the nauplii apparently absent in Devils Lake in winter, tho gravid females and eggs of *Diatomus* occasionally occur at this time.

Birge (l. c.) finds the nauplii more abundant in summer near the thermocline, while, with the disappearance of this layer, their distribution becomes more uniform. In Devils Lake nauplii are somewhat more numerous near the bottom than the surface in summer, the difference not being evident in spring and fall. The reasons for this difference in distribution is not clear. Nor does Birge offer any satisfactory explanation.

The curves for the various species will be considered in connection with each individually. In the case of the zoöplancton, especially the rotifers, the numbers and abruptness of the waves indicate a brief life cycle and rapid development, but we have as yet few data regarding the life span of any planctont. Needham and Lloyd (1916) state that "the rotifer, *Hydatina* is said to have a length of life of some thirteen days," but give no authority for their statement. Steuer (1910, p. 269) gives the ages of a few copepods based on the investigations of Burckhardt (1900) and Ekman (1904), the average being 13 months.

This figure appears high for the average life span of fresh water copepods. Judging from the curves for Devils Lake and for Lake Mendota and Green Lake, Wis., as given by Birge (1897) and Marsh (1898), the average life span is very much less than

this. But the facts, so far as known at present, do not warrant any final conclusion.

Of the three species of rotifers which appear in the plankton in any considerable numbers, two (*Pedalion* and *Brachionus satanicus*) far outnumber the third (*Brachionus plicatilis*). The two former, in respect to numbers, and probably also in respect to mass, are the most important constituents of the zoöplankton.

The greater part of the phytoplankton is composed of the blue-green algae and bacteria, altho diatoms and a few other green algae are present in considerable numbers. It is difficult to draw any general conclusions from the distribution curves, as they vary greatly, not only for different species, but for different seasons in the same species. These variations may be due in part, especially in the case of the shore collections, to the effect of wind in driving the filamentous forms especially onto a lee shore; in part to the influence of temperature, rainfall and other factors. In general there is a maximum both for algae and bacteria in the spring or early summer and in fall, with occasional smaller maxima between. Some possible causes of these fluctuations have already been briefly outlined, but no final explanation can yet be given.

The light reaction of zoöplankton is generally believed to be a very definite one, the animals retiring from the surface by day and distributing themselves more evenly at night. That the zoöplankton of Devils Lake is positively phototropic can be clearly shown by keeping them in a blackened jar, with a small opening for admission of light. After a few hours they will be found swarming about the window. Vice versa toward sunset and after the sun has been clouded for sometime they become nearly equally distributed. Further, the effect is less striking in *indirect* than in *direct* sunlight. If there are two openings in the jar, one (A) in the direct rays of the sun and another (B) at 90 degrees thereto, the majority of the Crustacea and rotifers gather at A, while a secondary gathering occurs at the edge of B nearest to A.

In the lake, however, they are under the influence of a complex of variable factors, such as temperature, currents, dissolved salts and gases, food, etc., and their resulting behavior cannot be so easily analyzed. Ritter (1912) and others have well emphasized the need for correlation between laboratory and field studies of animal behavior. In the study of a simple response the laboratory method is undoubtedly better, because of the ease of controlling the conditions of experiment, but in order to know how the animal will respond to its natural environment, it is necessary to go to nature to find out.

In Devils Lake, the light influence is obscured by so many others that it is impossible to determine its effect, a careful series of observations, extending over a period of years, having failed to

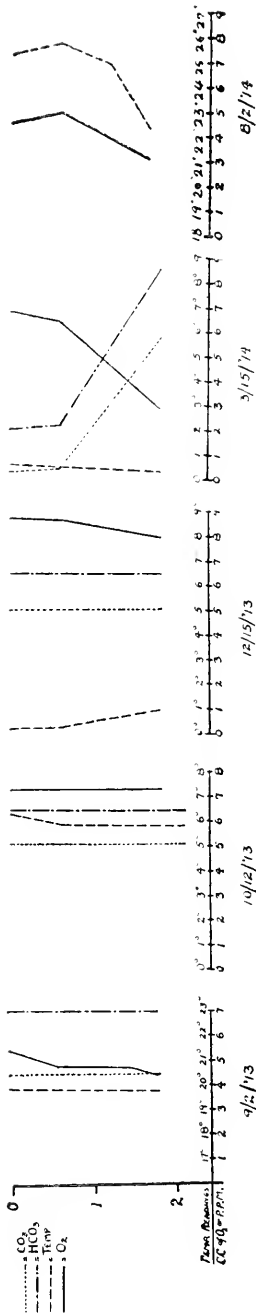


Figure 10. Charts of O₂, CO₂, and temperature in East Lake. Dates of collection accompany each chart. Ordinates show depths in metres; abscissas, degrees of temperature, cc. pr. l. of O₂ and 100 ppm. of carbonates.

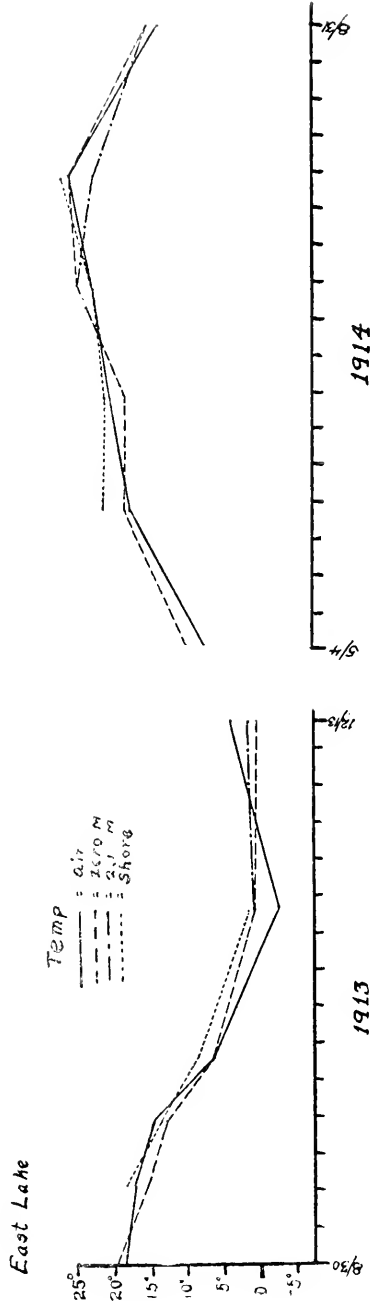


Figure 11. Seasonal curves for temperature in East Lake, 1913-14. Abscissas represent dates; ordinates, degrees of temperature (centigrade).

show any influence of light on the distribution of the planeton animals. In most of this work 500 c. e. samples were used, but in two series 19 litres were pumped thru a Kofoid net, the amount being measured with a water meter. The tests usually covered a period of twenty-four hours in quiet weather, and were taken on a line across Creel Bay, at both shores, and at the 0, 0.6, 0.9 and 3.0 m. depth near the middle of the bay.

The collections were made at approximately the following hours: 12 N. 5, and 9 p. m., 12 M., and 9 a. m.

One reason for the failure of the tests to give definite results is possibly the irregular distribution of the planeton, as Moberg (l. c.) has already suggested.

EAST LAKE (pl. 2)

East Lake is a long, narrow body of water extending southeast from the "Narrows" for some 17 km. It formerly was connected with Main Lake on the one hand and with Lamoreau Lake on the other, forming one continuous body of water, and is so represented on the present maps. It was separated from Main and Lamoreau Lakes about 1903. At the present time it has retreated about 2 km. from Lamoreau Lake, its former bed being occupied by a low, grassy swale in which are two nearly fresh water ponds, evidently spring fed.

With its separation from the other parts of Devils Lake the fall in East Lake has been rapid. When work was begun in 1911 it had a maximum depth of about 3 m., while at present it can hardly be more than a metre. The reasons for this are possibly threefold. In the first place the shores of East Lake are in general very low and flat and the drainage per unit of lake area is probably much less than that of the other parts. In the second place the supply from springs may be less, altho this source of supply is probably very small in all three bodies. Thirdly the shallow waters of East Lake are more disturbed by the wind than are the deeper waters of the other two parts, and hence the evaporation is greater.

The decrease in depth has naturally been accompanied by profound changes in its physics, chemistry and biology. I have but two color records for East Lake, both of which were made on samples which had been collected several days previously. One of these gave a reading of 86 for the surface and 64 for the bottom, and the other of 68 for the surface and 40 for the bottom.

The few turbidity readings taken show a range of from 25 to 46.

Some curves of temperature and dissolved gases are given in figures 10 and 11. They show differences between top and



Plate 8. Above, Lamoreau Lake.

Below, Mission Lake in left foreground, Mission Bay of Main Lake in right background.

bottom similar to those of Main Lake. The shallowness of the lake renders it more quickly responsive to the air temperature than the deeper waters of the other lakes. In the earlier years of the work (1911-14) there were the same differences, altho not so marked, between the shore and mid lake temperatures as noted for Devils Lake, but at present such differences are undoubtedly negligible, if existent. Its shallowness renders the temperature of the entire body higher in summer, while its greater salt content renders the freezing point, and hence the water temperature, somewhat lower in winter than the others. At present it freezes solid in winter.

The chemical character of East Lake is naturally similar to that of the main body, but has gradually become more concentrated with decreasing depth (table 3). Formerly East Lake showed the same zonation as Main Lake, but at present no such distinction can be made. Plankton records cover the period from 9/2/13 to 9/1/14, with a few prior thereto. They were taken at the shore and at depths of 0.6 and 2.0 m. The plankton species, at the time these records were made were similar to those of Main Lake.

Probably owing to poor preservation of material the data for *Micrococcus*, *Sarcina*, *Merismopedia* and *Dictyosphaerium* are inadequate and have accordingly been omitted. *Brachionus plicatilis* which appears in the collections of June 21 and July 12 only, is also omitted.

MISSION LAKE (pl. 8).

This is a small body of water resulting from the isolation of a bay of the main lake in 1909 or 1910. In spite of the fact that the lake probably receives a small amount of seepage from a fresh water lake situated on a terrace about a half kilometer distant, its history has been similar to that of East Lake, so that today it is only a shallow pool, nearly filled with foul smelling ooze. In winter it freezes solid and in summer is heated to 30° so that its life is subjected to a strenuous existence.

The chemical analysis and osmotic pressure are given in table 3. The life of Mission Lake in kind, distribution and abundance was formerly the same as that of the parent body, but with its separation, and consequent changes in its physico-chemical character, great changes have naturally also taken place in its fauna and flora. Only a few quantitative collections have been made, so that there are no records available of the seasonal distribution. Compared with collections from Main Lake these collections show a considerably greater number of zoöplanktons and much fewer phytoplanktons than collections taken at the same, or nearly the same time from the former water. Whether this difference is constant or not the collections are too few to determine, and if constant, the reason is

not obvious. It would appear that the Crustacea and rotifers, which constitute the great bulk of the zoöplankton, finding in Mission Lake a favorable environment, had multiplied rapidly; and, using the plants as food, had reduced the latter accordingly. At present, (1924) the Crustacea (except *Marshia*) and the rotifers have apparently disappeared.

LAMOREAU LAKE (pl. 8).

This was formerly the eastern end of Devils Lake, but about 1903 was separated from East Lake by the construction of a highway across the Odessa Narrows. Its size, depth, drainage area and possibly some supply from springs have sufficed to keep it in about the same condition as Main Lake, so that its life, in general, is similar to that of the latter. It covers an area of about 15 km. and in 1914 had a maximum depth of 7 m., slightly greater than Main Lake at the same time. The chemical analysis together with osmotic pressure is given in table 3, while O_2 , and temperature are shown in figure 12. Quantitative plankton collections are too few to have much significance. They indicate a smaller number of plankton animals (especially rotifers) than were present about the same time (8/6/14) in Main Lake, and a somewhat greater abundance of Crustacea than were present in the adjoining East Lake.

In the algae the most conspicuous differences between Lamoreau and Main Lakes at this time were the large numbers of the diatom *Cyclotella* in the former and its comparative rarity in the latter.

Nodularia, which is so characteristic of these lakes, was also much more abundant in Lamoreau than in Main Lake (Creel Bay) at this time, but much less so than in East Lake. These differences, however, may have been due to some local conditions and of no import in reference to the life of the lakes as a whole.

STUMP LAKE (pl. 5)

With the possible exception of Main Lake this is the largest body in the whole complex and its depth is greater than any.

As with Devils Lake, the shores are in places rocky, in others muddy and flat. On a flat at the southeastern end are the stumps, from which the lake derives its name. In places the old shore lines can be traced, marking the levels of glacial lake Minnewaukan.

The lake is mainly supplied by run-off, but in places, especially at the southern end, are some considerable springs, while near the northwestern end are a series of small ponds, seepage from which may reach the lake underground. There are no records of the levels of Stump Lake, but the old shore lines, and the character of the water tell a story similar to that of Devils Lake.

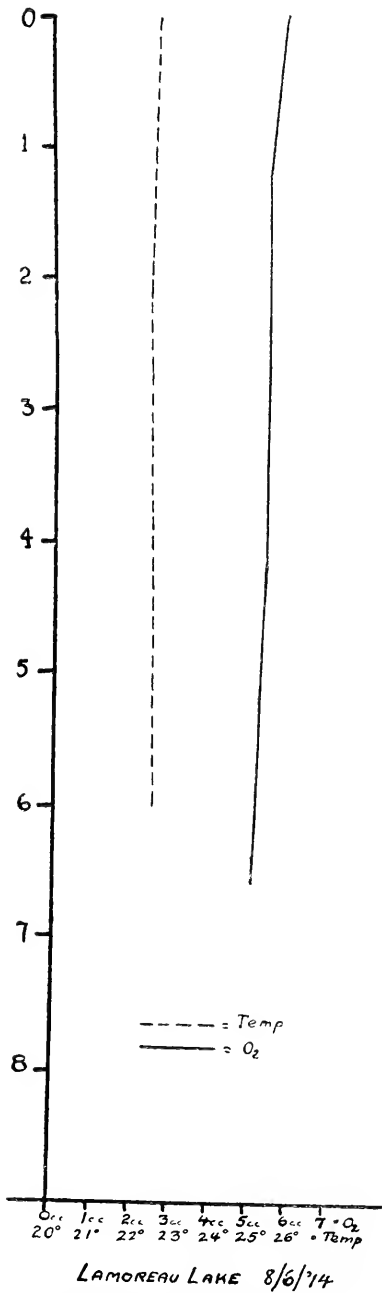


Figure 12. Temperature and oxygen curves for Lamoreau Lake, 8/6/14. Ordinates represent depths in metres, abscissas degrees of temperature (centigrade) and c. c. of O₂ pr. l.

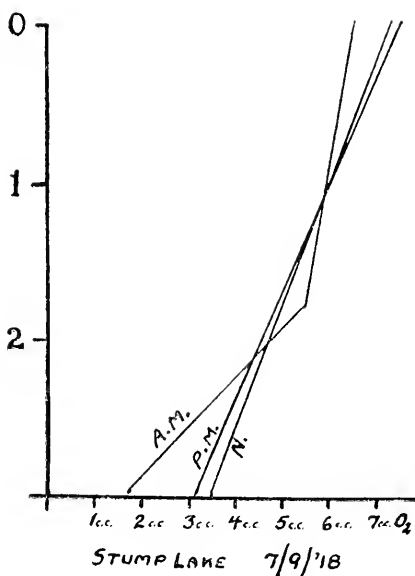


Figure 13. Curves of dissolved oxygen in Stump Lake (near west end), A. M., N. and P. M. 7 9 18. Ordinates represent depths in metres.

Studies of Stump Lake, as with all others of the complex, except Main and East Lake, have been confined mainly to the chemical

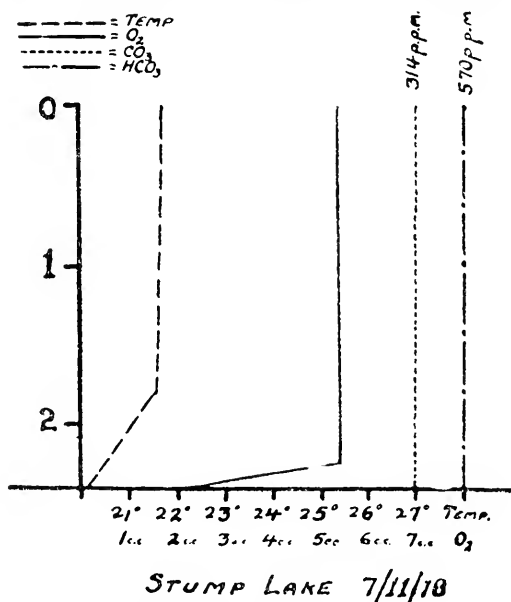


Figure 14. Curves of temperature and dissolved gases in Stump Lake (west end) 7 11/18. Ordinates represent depths in metres.

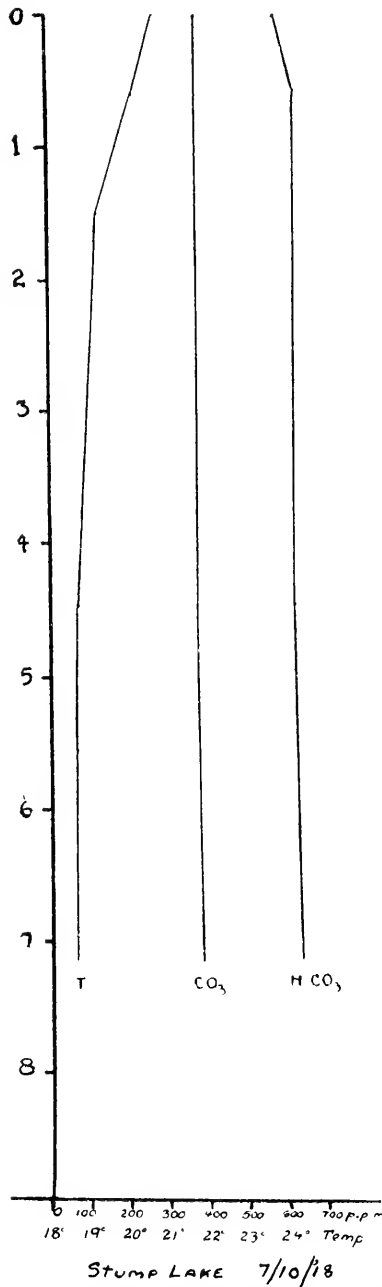


Figure 15. Temperature and CO₂ graph, for Stump Lake (middle) 7/10/18. Ordinates represent depths in metres, abscissas temperatures in degrees centigrade, c. c. of O₂ pr. l. and ppm. of carbonates.

analysis of the water and the determination of its inhabitants. A few records of temperature and dissolved gases for 1918, indicate very similar conditions to those of Main Lake (figs. 13-15).

The deepest part of the lake (7.6 m. in 1918) is near the southeastern end of the main body. Thence the lake gradually shallows in both directions, while the western arm in 1918 did not exceed a depth of 3 m. at any point. The bottom is covered with an ooze, similar to that on the floor of Devils Lake.

The chemical analysis and osmotic pressures are shown in table 3. There is a much greater amount of dissolved substances due to the higher chlorine and sulphate content, with a correspondingly greater osmotic pressure. A considerable part of the chlorine is present as NaCl, as evidenced by the distinctly salty taste of the water, which is lacking in Main Lake, or concealed by other ingredients.

The same life zones occur as in Main Lake, and the constituent organisms are similar. No extensive plankton studies have been made and there are no coincident records from Main Lake for comparison. The few collections made in 1918 indicate, however, a comparative scarcity of rotifers, a fairly average number of crustaceans and a considerable abundance of *Nodularia* and *Chaetoceros*. The distribution of the latter is evidently local however, as it appeared in large numbers (1000-1500 cells per cc.) at the eastern end of the lake on July 10, 1918, while only from 20 to 40 cells per cc. were present at the southwest end, about eight miles distant the following day.

The considerable abundance of *Nodularia* is of interest, as this alga appears to increase with increasing salt content, at least up to a certain limit. In East Lake also there was an enormous amount of *Nodularia* present in 1913-14, correlated possibly with the greater concentration of its water. But, on the other hand, no increase of this alga has been detected in Main Lake since 1911, while the concentration of its water has materially increased since that time,* so that the reason for its abundance in East and Stump Lakes is uncertain.

LAKE A (pl. 9).

This small lake was cut off from the main body about 1885. It is approximately 1.3 sq. km. in extent, with a maximum depth of about 2.5 m. While there has been a marked drop in the level of the lake since its isolation, it is, at present, fairly constant in level, due undoubtedly to a small supply from springs. At one point a very slight stream trickles into the lake, and there is probably some underground seepage. Run-off and rainfall can hardly be ade-

*Cp. the charts of distribution of *Nodularia* in Main and East Lakes (pl. 15 and fig. 20) with the chemical analyses (table 3.)



Plate 9. Above, Spring Lake.
Below, Lake A.

quate to maintain a constant level. Like other shallow lakes its temperature in summer probably reaches a maximum of 30° C.

It has a high salt concentration, as shown in the analysis (table 3), with a correspondingly high osmotic pressure.

Its inhabitants, so far as studied, are similar to those of Main Lake.

LAKE C

Lake C is about 0.3 sq. km. in extent with a maximum depth of 1.8 m. It was separated from what is now East Lake, about 1885. It lies in a shallow draw between two morainic ridges, and is probably spring fed, having apparently maintained its present level for some time.

In spite of its constancy of level, it shows a considerable concentration of dissolved solids as indicated by the analysis (table 3).

The study of Lake C has not been thoro enough to admit of any very definite comparison between its life and that of other lakes in the complex. In general this appears to be much less abundant both in species and individuals than that of neighboring ponds. A striking feature is the apparent absence of *Nodularia*, which is so characteristic of the more alkaline lakes of the complex. The same absence is noticeable in Spring Lake and Lakes N, O and P. The reason thereof is not obvious. Where comparatively few collections have been examined, as is the case with these lakes, it would not be safe to be too emphatic in making negative conclusions. A sufficient examination has, however, been made to reveal *Nodularia* were it common, as it is in the principal lakes of the complex, so that its absence is probably significant, tho of what, cannot at present be said. The salt content of lake C is rather low, about the same in amount and proportion as that of Main Lake in 1907. In 1909 *Nodularia* was observed as one of the most characteristic species in Main Lake. The other lakes, with the possible exception of Lake P, are all shallow, N and O being but temporary pools, and ranging in different seasons from nearly fresh to exceedingly alkaline ponds or mud flats. This may explain the absence of *Nodularia* in them, but no satisfactory explanation is at present evident for Lake C.

SPRING LAKE (pl. 9).

This is little more than a mud flat covered by a third to a half a metre of water. Were it not for a supply from springs it would undoubtedly have long since been dry. It has been separated from the main body for about 40 years.

In winter it freezes solid, while in summer it reaches a temperature of about 30°.

The chemical character of the water is indicated in table 3.

Spring Lake possesses several species of rotifers, not as yet reported elsewhere in complex, but in other respects, its characteristics are chiefly negative.

LAKE P (pl. 10).

This small pond was separated from Devils Lake about 1906. It is probably spring fed, as it maintains a fairly constant level from year to year, in spite of the lack of supply, apart from run-off and possible springs. Its maximum depth is between one third and half a metre.

The chemical analysis and osmotic pressure are given in table 3.

Lake P has several species of algae not reported elsewhere in the complex, which are of interest, coupled with the absence of *Nodularia* noted above.

One of the most interesting inhabitants of this lake is the larva of the dragon fly *Sympetrum*. This has not been found in any other of the brackish lakes of the complex, and is probably to be considered as a typically fresh water animal.

Triaenodes flavescens is another species occurring only in Lakes C and P and in neighboring fresh water ponds; all of these facts seem to relate Lake P rather more closely to fresh than brackish waters, and yet the analysis (table 3) shows the water to be highly brackish. I cannot at present reconcile these apparently irreconcilable facts.

LAKES N AND O

Both of these are shallow pools in spring and continue as such during wet seasons. They occupy parts of the old lake basin, from which they were separated about 1886-87. Like other pools they freeze solid in winter, when water is present, while in summer their temperatures must occasionally run to 30° or over.

Conditions in these lakes are too variable, and their study is as yet too incomplete, to justify any conclusions regarding their characteristics.

Besides the lakes already enumerated there are several fresh water ponds which at one time were a part of Devils or Stump Lake. These I have omitted from the discussion, because, being fresh water, they are very different, both chemically and biologically, from most of the cut-off lakes forming part of the Devils-Stump Lake complex.

Another lake has only recently (1923) been separated from Devils Lake by the construction of a highway, but its recent separation renders its consideration unnecessary here.



Plate 10. Above, Minnewaukan Bay in 1916.
Below, Lake P.

ANNOTATED LIST OF SPECIES BACTERIA

The bacteria of Devils Lake are abundant. Apart from the usual sources of infection thru wind and drainage, considerable sewage from the city of Devils Lake 5 km. distant, flows into Creel Bay thru a drainage ditch.

In the plancton collections the bacteria include one of the most common types. Naturally no attempt has been made to distinguish

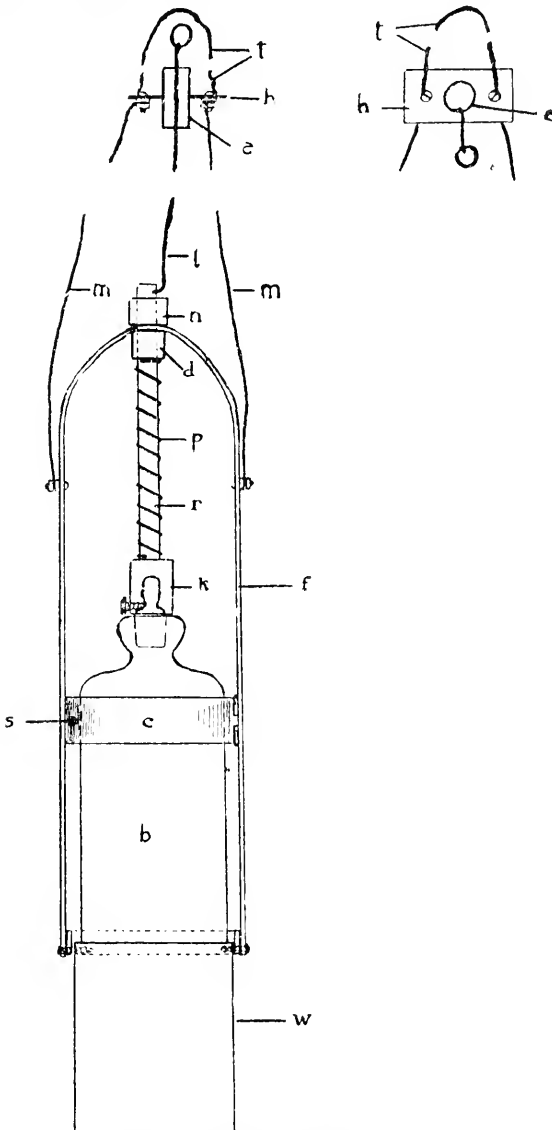


Figure 16. Water bottle for bacteriological samples, see p. 58 for description

species in the enumeration, and the form specified probably includes several. It is designated by form simply as *Micrococcus*. Besides these a less frequent type, *Sarcina*, is of common occurrence.

The bacteriology of Devils Lake was studied during the summer of 1916 by Mr. (now Dr.) F. W. Stevenson, a pre-medical student of the University, under the direction of Dr. L. D. Bristol, then director of the Public Health Laboratory of the State. The methods followed by Mr. Stevenson are those recommended by the American Public Health Association in their "Standard Methods of Water Analysis."

Samples for quantitative analysis were collected in the morning, shipped to the University in an iced container, and plated in the evening of the same day. With those intended for qualitative analysis only, especially with those from outlying parts of the lake complex, several days elapsed in some instances between time of collection and plating, and no attention was paid to keeping the sample at a low temperature. In collecting samples from points below the surface of the lake, the apparatus illustrated in figure 16 was employed. It consists of a metal frame *f*, weighted at the bottom with a block of lead, *w*. The frame carries a collar *c*, one side of which is hinged and can be swung open to admit a bottle, the latter being held in place by screwing the two parts of the collar together at *s*. The stopper of the bottle is held by a screw clamp *k*, at the base of a rod, *r*, which latter is attached to a cord, *l*, and surrounded by a spring, *p*. The rod, *r*, passes thru a collar, *d*, which is bolted to the top of the frame by means of a nut, *n*. The frame is suspended by two cords, *m*, which are attached to a small plate, *h*, thru a collar, *e*, at the center of which the cord, *l*, passes, and which is in turn suspended by a line, *t*. The apparatus is lowered into the water to any desired depth by the line *t*, when a pull on the cord, *l*, removes the cork and allows the bottle to fill. When the latter is full, the cork is replaced by releasing the tension on the spring, *p*.

The seasonal distribution of bacteria is indicated by the curves for *Micrococcus* platted from the planeton counts (pl. 11). They show, in general, an enormous development in summer, with a marked decrease or total disappearance in winter. Further than this, it is difficult to draw any general conclusions from the distribution curves, as they differ considerably in different years.

In 1912 and 1913 definite maxima occur about June 1 with indications of a mid-summer minimum and a small maximum near the end of August, at least in 1913. In 1911 a minimum is indicated about August 15, tho the records here are too few to warrant definite conclusions. In 1914 there is a June maximum without, however, any sharply marked peak, and a very distinct minimum about July 20, followed by a great increase in August. The 1914

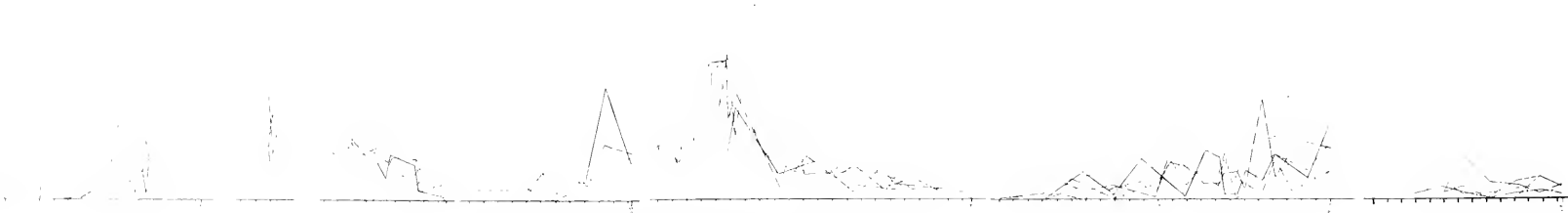
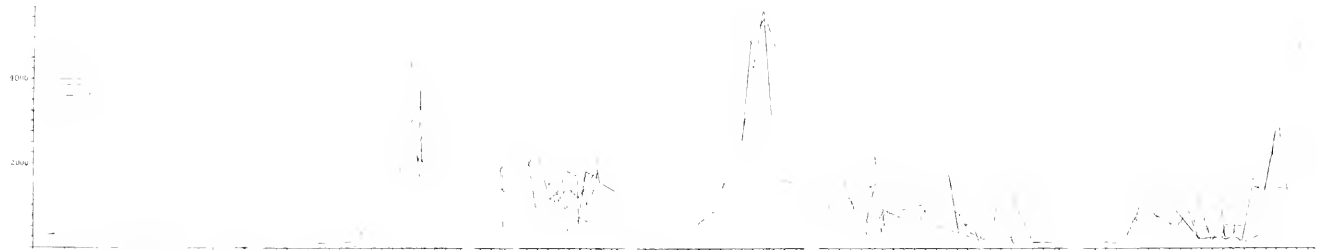


FIG. 11. Above: monthly distribution of *Macoma* in 1922. Below: monthly distribution of *Macoma* in 1923.

1923

material was in poor shape, however, when counted, and the form of the curve may be somewhat obscured as a result. In the records from December 3, 1922, to July 23, 1923, *Micrococcus* was disappearing from the plankton, when the records began. During the winter it was absent from most of the collections, tho present in every series in the shore samples. It increased rapidly in May and June to a large and well marked maximum about the middle of the month, falling off rapidly until the end of the collection period.

Much of the material included under *Micrococcus* may be *Clathrocystis*, which occurs commonly in the Devils Lake plankton, and which in preserved material "might closely resemble the coccus form of the bacterium and I doubt if it would be possible to separate the two".*

Micrococcus, while present in East Lake, had for the most part deteriorated when the counts were made.

Sarcina is much less abundant than either of the preceding, and the records in general are too scattering to admit of any conclusions regarding seasonal distribution other than that a marked decrease occurs in winter, with a corresponding increase in summer and autumn. Its distribution is approximately similar to that of the two preceding, altho it is conspicuously less abundant in spring. It is possible that some of it may have been included with *Micrococcus*.

The quantitative analyses covering the period from June 27 to August 9, 1916, and including 27 samples were designed to show rather the spatial than the temporal distribution of the bacteria in the Devils Lake complex. They showed quite clearly, as might be expected, the much greater abundance of bacteria in situations where there was a greater amount of decaying matter, such as the shore and bottom, compared with the surface, or the lake some distance out from shore, and the heads of shallow bays as compared with the middle of the lake. Especially numerous were the bacteria near the mouth of the Devils Lake sewer at the head of Creel Bay. The *B. coli* group were not limited to the former situations, but were widely distributed thruout the lake.

These results are of interest when compared with the organic analyses, in a majority of which (about 2 to 1) the organic content is higher at the bottom of the lake than at the surface.

The distribution of the bacteria in the various lakes of the complex has not been studied thoroly enough to warrant any definite conclusions.

During the summer of 1916 the Mauvaise Coulée was flowing into Devils Lake carrying with it large numbers of bacteria. This un-

*From a letter to the writer from Dr. Geo. T. Moore, who identified the Devils Lake algae.

questionably influenced the numbers of bacteria in Minnewaukan Bay and possibly to some extent in the main lake at this time.

None of the bacteria in Devils Lake occur uniformly in all of the collections, altho most of them occur frequently. In most cases their presence is apparently accidental and not characteristic.

The list of species identified is probably incomplete; which, coupled with the irregularity in their occurrence and the lack of adequate data regarding each, prevents a detailed discussion of them here.

Bacillus subtilis appears to be the commonest bacterium in the lake, but it is difficult to make any selection among the others.

The list follows:

Micrococcus *candicans*, *citreus*, *descidena*, *orbicularis*, *plumosus*, *radiatus*, *rosettaceus*, *simplex*, *Streptococcus* *albus*, *vermiformis*, *Sarcina* *alba*, *lutea*, *subflava*, *Bacillus* *aerogenes*, *albus*, *aquatilis*, *coli communis*, *convolutum*, *fluorescens*, *formosus*, *proteus vulgaris*, *reticularis*, *subtilis*, *vermiculosum*, *Bacterium* *aerogenes*, *desidiosum*, *flexuosum*, *nubilum*, *tiogense*.

ALGAE

Of the algae the blue-greens and diatoms furnish by far the greatest number of species, the three most characteristic genera being *Nodularia*, *Coelosphaerium* and *Chaetoceros*. Many of the species described do not occur, or cannot be recognized, in the plankton samples, due in part to their rarity, in part possibly to poor preservation, in part to the difficulty of recognition under the low magnifications used in counting and in part to their presence chiefly among attached algae, where the samples were not taken.

Dr. George T. Moore who has made a preliminary report on the Myxophyceae and Chlorophyceae of Devils Lake (1917) says: "The algal flora of Devils Lake can hardly be regarded as a rich one. The Myxophyceae are, it is true, fairly well represented, and the fact that they constitute practically 50 per cent of the genera and species present* may be regarded as one of the effects of the increasing salinity of the water. The almost entire elimination of the Conjugales, which so frequently constitute the greatest number of species in fresh-water lakes, is likewise to be attributed to the high content of salts, and perhaps the absence of this order is sufficient alone to account for the small total number of species. With the exception of *Spirulina nordstedtii*,* all the species listed are frequently, if not invariably, found in fresh water, so that the algal flora of the lake is to be regarded as typically a fresh-water one, showing no effect of the gradual concentration of the water.

*Not including the diatoms.

**Subtilissima* is also present. Moore describes it as "a salt water and sulphur spring form."

“Furthermore, of the species identified, it is worthy of note that with minor differences of measurement, they were all absolutely typical, with no indication of any effect of the, in many cases unusual, if not unfavorable, environment.”

The following list is compiled mainly from Dr. Moore's report, the notations being partly from his, and partly from my own data.

Myrophyceae—Most of the species recorded below are free floating and of general distribution thruout the lake, which may be assumed to be the case for each species, unless it is specifically stated to the contrary.

Aphanothece castagnei—This species occurs commonly in towings. In the quantitative samples numerous ovoid cells were found which probably belonged here. The colonies soon disintegrate however so that it is difficult of identification. It occurs from the end of May to December, but the records are too scattering to justify any conclusions regarding seasonal distribution.

Rhabdoderma sigmoidea has been reported from Main, East and Mission Lakes, and var. minor from Lake P.

Chroococcus limneticus and *minutus*. Both of these species are common and occur frequently in the plankton samples. In counting no attempt has been made to differentiate between them.

It is difficult to draw any conclusions regarding the cycle of *Chroococcus* from the distribution curves. It occurs in rather large colonies, and one count may show none or few, while another shows a large number. To this fact may be due, in part at least, the more or less zigzag form of the curve, which is especially noticeable in 1914. It is rarely very numerous in the collections, which, together with its colonial habit, and the liability of the colonies to disintegrate in preserved material, thus rendering it difficult to identify, tends to obscure the form of the curve. In its seasonal occurrence it is similar to other algae, appearing early in April and disappearing again toward the end of December. Its maximum falls between August 10 and September 15. Its occurrence in the East Lake collections is too scattering to warrant any conclusions regarding its seasonal distribution there (pl. 11 and fig. 18).

A similar irregularity is evident in Lake Mendota (Birge and Juday, 1922). *Chroococcus* is present here for about four weeks from the end of May to the end of June, then apparently disappearing until the middle of September, after which it occurs until winter. In 1916 it occurs from the first of May till mid-October, with the exception of a brief interval about August 1, but is not present later in the autumn.

Two other species of *Chroococcus*, *dispersus* and *turgidus*, occur in Lake P. and the latter has been reported from Main Lake.*

*Brannon (1910).

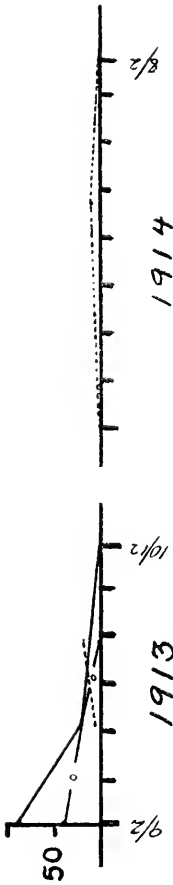


Figure 17. Seasonal distribution of Chaetoceros in cells in East Lake.

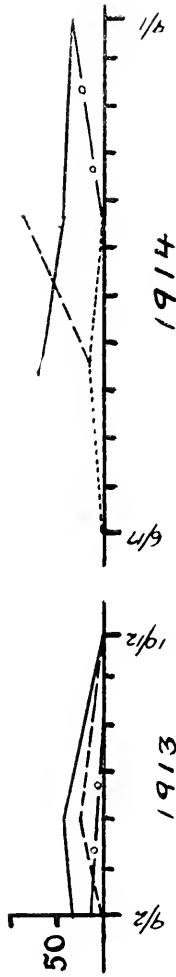


Figure 18. Seasonal distribution of Chroococcus in cells in East Lake.

○ = 0 m.
 — = 2 m.
 - - - = Shore

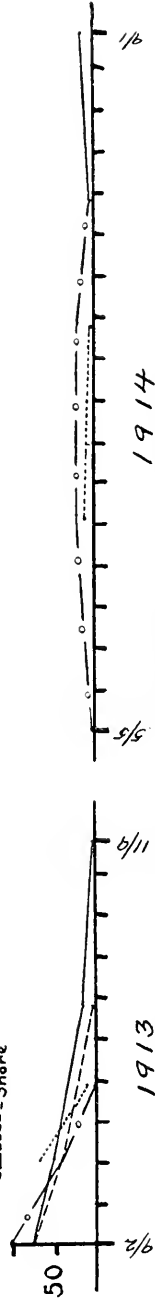


Figure 19. Seasonal distribution of Coelosphaerium and Gomposphaeria in colonies in East Lake.

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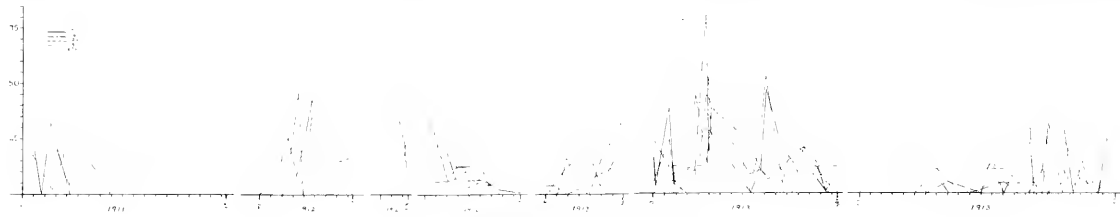
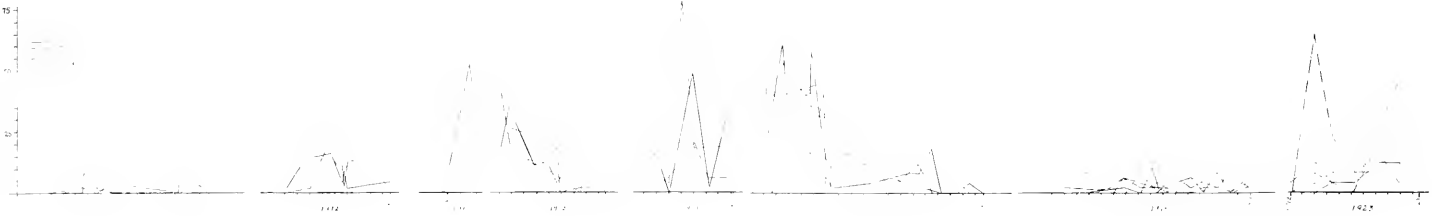


Fig. 12. 40 m. depth. (continued) Mean in galls by standard units, by May 1st.

Clathrocystis aeruginosa. Reported by Dr. Moore as "abundant in towings and associated with filamentous algae." In the quantitative plankton samples it has not been possible to distinguish this species. The cells are very small and the indefinite form of the colony renders it difficult, in preserved material and with low magnifications, to differentiate it from masses of zoöglea, so that some of it may be included under "Micrococcus" in the counts.

Microcystis incerta. Taken in Lake P only.

Coelosphaerium kuetzingianum. This is one of the most abundant forms in the lake. With low magnifications it is very difficult to distinguish it from the following species, so that both have been listed together in the counts. Reported from Main Lake and Lake C.

Gomphosphaeria aponina. A common and widely distributed species. Var. *cordiformis* has been found in Lake P. The seasonal distribution of this species is shown, together with that of the preceding, in the chart (pl. 12), which shows that they first appear in March or early April, and are present until after the freeze-up in December. The record for 1913-14 shows their presence thru the winter until March 1, followed by a brief absence and re-appearance about April 1. In 1911 a marked drop occurred in August parallel to that of *Nodularia*, *Merismopedia* and *Chaetoceros*, but not paralleled by *Chroococcus* or *Oöcystis*. This behavior does not correspond to the record of subsequent years. In 1912-14 there is apparently but a single maximum for each year, but this occurs at different times in 1912 (Aut. 25-Sept. 1), 1913 (Oct. 20) and 1914 (May 20-30). In the latter year a poorly marked minimum occurred July 25 to August 1, followed by a slight increase in August and September.

Coelosphaerium and *Gomphosphaeria* are much less common in East than in Main Lake (fig. 19).

The occurrence of *Coelosphaerium* in Lake Mendota (Birge and Juday, 1922) is less regular than in Devils Lake, for in the former, in 1915 it was absent or rare until June, developing in considerable numbers from July onward.

Merismopedia convoluta, *elegans*, *glauca* and *tenuissima*. Of these the latter "is by far the most abundant." No attempt has been made to differentiate between them in the counts, the results of which are shown in plate 13.

The curve corresponds rather closely to that of *Chroococcus*, with a distinct drop in mid-August in 1911 and a maximum at the same time in 1912 and 1913. In the 1914 collections probably most of the material had disintegrated before the counting was done, so no definite conclusions can be drawn for that year. In 1912 a small maximum is apparent about the end of May, and this is also indicated in the 1913 curve, altho the collections here are rather too scanty to admit of any definite conclusions. *Merismopedia* sp. oc-

curs occasionally in the East Lake collections, but the records are very few. *M. elegans* has been found in Mission Lake only.

Tetrapedia gothica. "Sparingly found in two collections, one from towings, the other associated with *Cladophora* near the shore in front of the laboratory. This, so far as is known, is the first recorded collection of this genus in the United States, and it is likewise the first time the species has been found since its original discovery by Reinsch in Germany."

Tetrapedia sp. has been found in Spring Lake.

Arthrospira jenneri. occurs occasionally in Main, East and Mission Lakes.

Oscillatoria. This genus is represented by ten species, one of them indeterminate. Of these amphibia is 'the most abundant and widely distributed.' Specimens of *Oscillatoria* occur occasionally in the plankton collections, but not often enough to warrant any conclusions relative to its seasonal distribution. Beside amphibia the following species occur, *brevis*, *chalybea*, *chlorina*, *geminata*, *jaunthiphora*, *limosa*, *subtilissima*, *tenuis* and sp., "a small form . . . resembling in a general way the descriptions of *O. subtilissima*."

Plectonema tenue. "Numerous filaments of this species were obtained from surface tow in one of the smaller bays of the lake. While it is probable that the material had become detached from stones, a search along the shore in shallow water failed to reveal any indication of from where the specimens had come."

Spirulina. This genus is also of sporadic occurrence in the plankton samples, and hence is not represented in the charts. Of the four species present, major, *nordstedtii*, *subtilissima* and *tenerima*, the first is the most common. *Nordstedtii* and *subtilissima* are of interest as being the only salt water representatives of either *Myxophyceae* or *Chlorophyceae* present in the lake.

Anabaena, represented by two species, *flos-aquae* and *spiroides*, occurs rarely. It is found occasionally in the plankton collections, but the data do not enable me to draw any conclusions regarding its seasonal distribution.

Lyngbya contorta was formerly one of the most characteristic forms of the plankton (pl. 14).

In 1911, 12 and 14 it was abundant from September on to the season's close*, while in 1913 it showed a great decrease in September and October. In both 1912 and 13 a distinct maximum occurred at the end of May and early June, while in 1914 this maximum, tho present, was very small. In 1913 a very large and well marked maximum occurred about the middle of August, and apparently a similar maximum occurred about two weeks later in 1912. In 1914

*In 1914 this was on September 14.

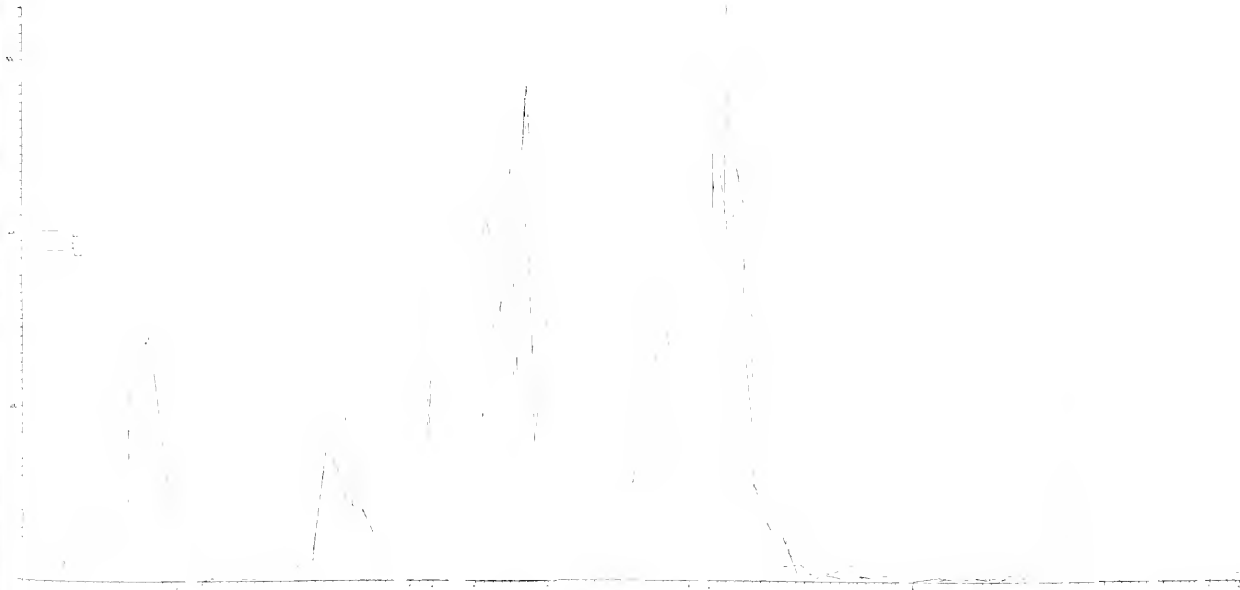


Plate 14 Seasonal distribution of precipitation in millimeters in Main Lake

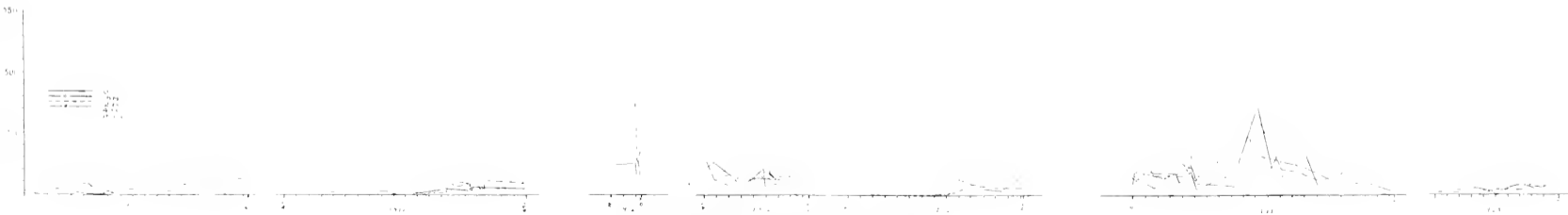
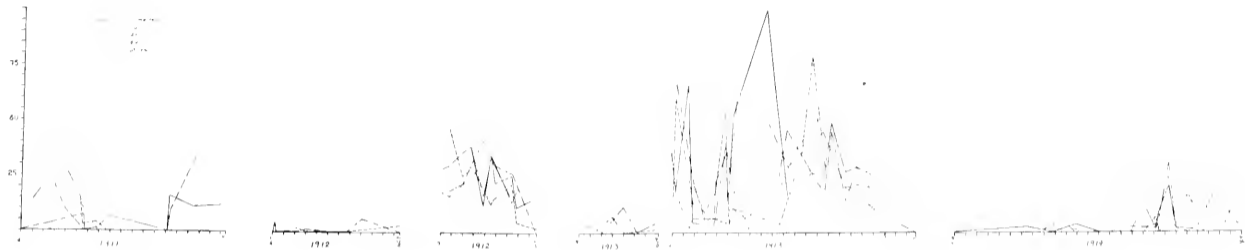


Plate 15. Above: seasonal distribution of *N. infans* in milligrams in Mich. Lake.
 Below: seasonal distribution of *D. pulex* in hundred eggs in Mich. Lake.

there was a marked increase about September 1, which apparently corresponds to the mid-August maximum of 1913.

In 1911 the records are too few to warrant any definite conclusions.

In 1923 there are only a few scattering records of *Lyngbya*. Apparently it is much less numerous now than formerly, correlated possibly with the increasing concentration of the lake. It appears to be absent from Stump and Lamoreau Lakes and very scarce in East Lake. It was abundant in Main Lake in 1916 and present in some quantity in 1918, altho the records for this year are too few to warrant any conclusions as to its relative abundance at this time. It is of interest that in 1916, when still abundant in most of Main Lake it was apparently absent from Minnewaukan Bay which was nearly fresh at this time*. Its absence or scarcity in Stump and East Lakes supports the hypothesis of its dependence on a certain degree of concentration (10000-15000 ppm.); but its apparent absence from Lamoreau Lake, which has about the same chemical character as Main Lake, negatives this conclusion and renders the cause of its erratic distribution in the complex uncertain. It was, moreover, common in two collections from Mission Lake in 1916, altho the concentration of the latter was 32640 ppm. at this time.

Lyngbya martensiana has been reported from Lake O.

Nodularia spumigena. Excepting *Coelosphaerium* and *Lyngbya* this is the most common alga in the lake. It is frequently driven by the wind into extensive masses along the lee shore, while other regions may be comparatively free from it. It develops in considerable quantity rather later than most of the other algae, appearing sparingly during April and May and showing a rapid increase in June, with a maximum about the end of July and a more or less distinct minimum about the middle of August. This was particularly striking in 1913 in which it fell from an average for the several depths of collection of 1720 on August 1 and 2 to an average of 285 on August 20-26. But it occurred also in 1911 (August 8-22) and 1914 (August 17). In 1912 the data are too few at this season to warrant any conclusions.

In 1914 a marked minimum occurred July 20-22, but the suddenness of the previous drop and the succeeding rise renders this minimum open to question. Prior to July 20 *Nodularia* developed mainly along shore and at the surface, so it is possible that a shift in the wind, driving it into other parts of the lake, may have caused this apparent drop (pl. 15).

Nodularia appeared to be much more abundant in East than in Main Lake, in 1913 and 1914 (fig. 20), but the records are too few to permit of any definite conclusions*. It was abundant in

*See table 3.

*See p. 54.

Mission Lake in 1923, tho the total solid concentration of the latter at this time was 32600 ppm.

Var. major has been reported from Lamoreau Lake.

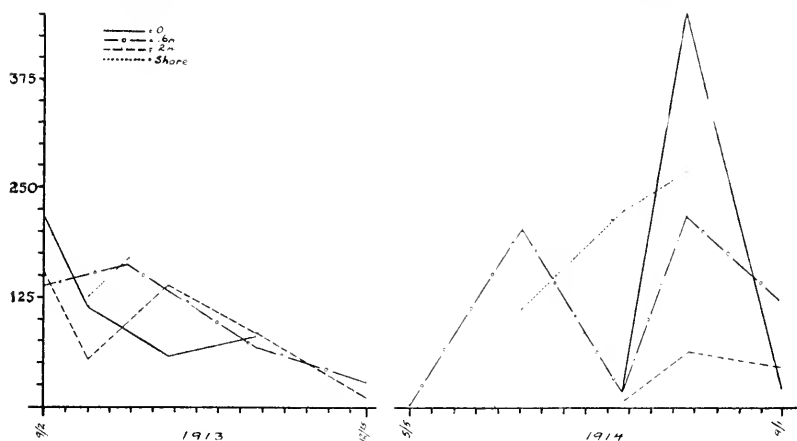


Figure 20. Seasonal distribution of *Nodularia* in millimeters in East Lake.

Tolypothrix lanata. "Found in two collections growing with other algae attached to twigs near shore."

Calothrix braunii. "Collected but once, growing on a single large boulder."

Calothrix fusca. Reported from Main Lake.

Calothrix parietina. "Slightly incrustated, forming brownish patches on small stones near shore."

Gloetrichia natans. "Several large masses in one towing."

CHLOROPHYCEAE

Closterium occurs occasionally in the plankton samples from Main Lake from July 1 to October 24,* but the species has not been determined. Both *C. diana* and its variety (*areuatum*) have been found in Lake P.

Cosmarium. Three species of this genus (*formulosum*, *scopularum* and *sub-costatum*) have been taken in Lake P.

Staurastrum *sp.* occurs occasionally in the plankton of Main Lake from May 31 to Dec. 13. The dates for both *Closterium* and *Staurastrum* are significant only in so far as indicating an extensive seasonal distribution for both.

Mougeotia *sp.* "Found near shore in three collections . . . with *Tolypothrix* and *Anabaena*."

Pandorina morum. Reported from Main Lake.

Pandorina *sp.* An indeterminate *Pandorina* has also been reported from East Lake.

*See below, under *Staurastrum*.

Botryococcus braunii. "Abundantly present in one towing. Doubtfully present in two other towsings." Also in neighboring fresh waters.

Ankistrodesmus falcatus. Found infrequently in planeton collections from Main Lake.

Characium hookeri. Occurs abundantly as an epiphyte on Crustacea and filamentous algae. Found frequently but irregularly in the planeton samples at all seasons. Its irregularity renders it difficult to draw any definite conclusions as to its seasonal distribution. Numerous detached cells are found in the collections but normally it is probably always epiphytic, mainly on Crustacea.

"Apparently the first record of this species in America."

Coelastrum microporum. "Rare in towsings."

Dictyosphaerium. This, in common with *Characium* and *Oöcystis*, is the most characteristic of the green algae in the planeton. It readily disintegrates in preserved material so that the records are incomplete. Especially is this true for most of the 1914 collections, which could not be counted until 1919. No attempt has been made therefore to plot a distribution curve for this year. The records for 1913, which are complete except for the period from June 24 to August 1, show practically none in winter, with a rather uniform rise from none on May 1 to a maximum about October 10, and a return to zero by the end of December.

In 1923 *Dictyosphaerium* appeared on May 12 and gradually but slowly increased up to July 23 when the collecting ended (pl. 15).

Both *ehrenbergianum* & *pulchellum* occur in the complex.

Nephrocytium naegeli. "Occurring rather frequently in towsings."

Eudorina elegans. A rare species reported only from Main Lake.

Oöcystis is one of the characteristic genera, but very irregular in its presence in the planeton samples. In 1913 a small maximum occurred about September 1, while in 1914 there was a very marked rise on September 14, when the collections were ended (pl. 13).

Judging from the diagrams of Birge and Juday (1922) *Oöcystis* is rather more regular in its occurrence in Lake Mendota than in Devils Lake, but here too marked irregularities occur.

It is represented in the complex by five species, *crassa*, *lacustris*, *naeglii*, *pusilla* and *solitaria*, of which the latter is the most numerous.

Scenedesmus bijugatus and *quadricauda typicus*. "Both species rather common in towsings, also associated with filamentous algae along shore," and of occasional occurrence in the planeton samples.

Zoöchorella conductrix. "In *Stentor* from towsings."

Actinastrum hantzschii. Reported from Main Lake and fresh waters.

Pediastrum angulosum and *boryanum*. "Both species rather frequent in towings." No attempt has been made to differentiate them in the counting of the plancton collections, and their occurrence here is too irregular to warrant the construction of a distribution curve. *Pediastrum* appears sporadically from April to December.

The following attached forms are characteristic of the shore and *Ruppia* zones. Of these *Cladophora* is the most characteristic, altho *Enteromorpha* is very common in several scattered localities.

Microspora loefgrenii. The cell wall of this species may be occasionally .006 mm. thick, which is perhaps an adaptation to its saline environment, altho without a change in permeability mere thickness would hardly be adequate to prevent plasmolytic action of the water on the cell contents. The increase in thickness moreover only occurs in some specimens, which is a further argument against its adaptive character.

Ulothrix zonata. "With *Cladophora* along shore."

Enteromorpha. "Although *Enteromorpha* is ordinarily regarded as a marine form, *E. prolifera* has been reported from several fresh water lakes in the west." *Intestinalis*(?), *prolifera* and an indeterminate species occur in the complex.

Protoderma viride. "On stones along shores."

Stigeoclonium nanum. "Attached to *Cladophora* and associated with *Enteromorpha*."

Cladophora. The most characteristic littoral genus in all the lakes of the complex. Both *kuetzingiana* and an indeterminate species occur.

Rhizoclonium hieroglyphicum has been found in Lakes P and N. *Vaucheria* sp. One record from Main Lake (6/24/15).

Oedogonium sp. Taken in Lake P. only.

DIATOMACEAE

The diatoms of Devils Lake have been studied by Professor C. J. Elmore of William Jewell College, both at the lake and in collections sent to him from time to time. They are the most numerous in species, altho not greatest in numbers of any class of plants in the lake. Serving as food for many species of animals they play a very important part in the biology of the lake. They include a total of 80 species,* 46 of which are fresh water types with two doubtful forms additional; 18 inhabit both fresh and brackish water; 1 fresh, brackish or marine; 4 marine or brackish, while four are brackish and four marine types only. There is one new species (*Navicula mimewankonensis*).

*Including one subspecies (*Navicula cryptocephala veneta*).

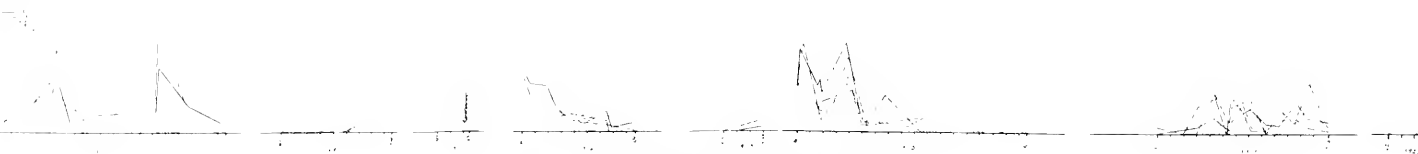
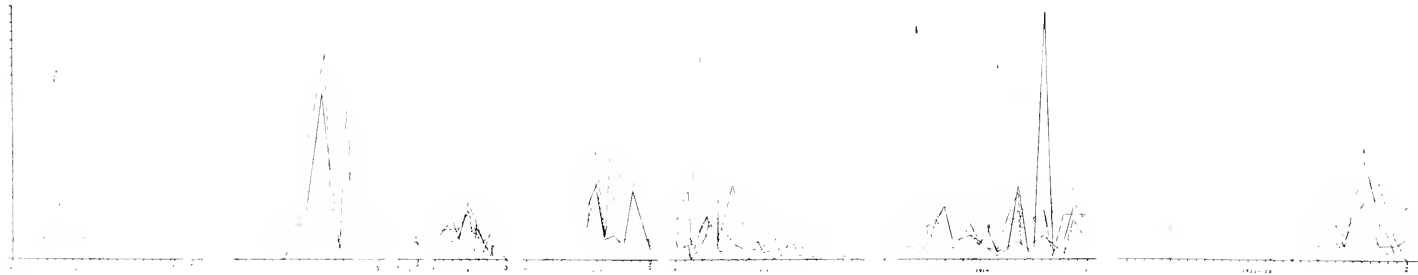


Plate 16 Above, seasonal distribution of diatoms, except Chaetoceros, in individuals in Main Lake
 Below, seasonal distribution of Chaetoceros in cells in Main Lake

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Of the 46 species, which are typically fresh water forms, "there is nothing in their appearance to indicate that they have been in any way modified by their changed environment." That many species of diatoms are very insensitive to changes in their environment is shown by a comparison of the flora of Minnewaukan Bay in 1916 with that of the main lake. In that year by reason of heavy snow fall the preceding winter, and of heavy rains in the spring the Mauvaise Couée, draining a wide extent of country north and west of Devils Lake, was flowing for the first time in many years. The construction of a highway grade across the mouth of the bay, leaving it connected with the main lake by a culvert, thru which water was flowing at the rate of about 7750 cu. m. daily, converted the former into a lake with about 1/3 of the salt content of the main lake (4464 as compared with 12920 ppm.). Of the fourteen species found in the bay in this year thirteen were identical with those in the main lake, while only one (*Stephanodiscus niagrae*) was new, evidently brought down by the couée. It is not unlikely that a more thoro study would have revealed a larger number of species common to both places, but the data suffice to show that many species at least are very tolerant of great changes in their chemical environment.

The *Ruppia* zone is the chief source of the diatoms in the lake, partly because it furnishes suitable attachment for the sessile species, and probably because of the greater amount of dissolved food-stuffs in this zone. They occur in considerable numbers in the pelagic zone, however, and especially in the shore zone at certain times. They may be carried into these zones from the *Ruppia* by currents, or they may develop there independently of the latter. Probably both factors are involved in their presence in these zones.

Their occurrence in the plaucton samples is very erratic. That this is due to improper preservation, or to errors in sampling and concentrating the material is unlikely. It is possibly to be explained by the action of currents, just mentioned, especially in the case of the shore samples, where the diatoms may be present in large numbers at one time, and soon after absent or very rare in the same place.

The following genera occur more or less frequently in the plaucton collections: *Amphora*, *Amphiprora*, *Cyclotella*, *Cymbella*, *Cystopleura*, *Gyrosigma*, *Navicula*, *Rhoicosphenia*, *Surirella* and *Synedra*, of which *Cyclotella*, *Navicula*, *Surirella* and *Cymbella* are the commonest.

The individual distribution of all of these has been plotted as well as that of the diatoms collectively, but only the latter chart and that of *Chaetoceros* are reproduced here.* Apart from the

*Plate 16 and figs. 17, 21.

irregularity of their distribution, and their frequently greater abundance in the shore collections, to which attention has already been called, the charts show little except that, like other algae, they are much more abundant in summer than in winter. That this is due to temperature is unlikely, because in some instances at least there is a marked increase in early spring or late autumn. Similar

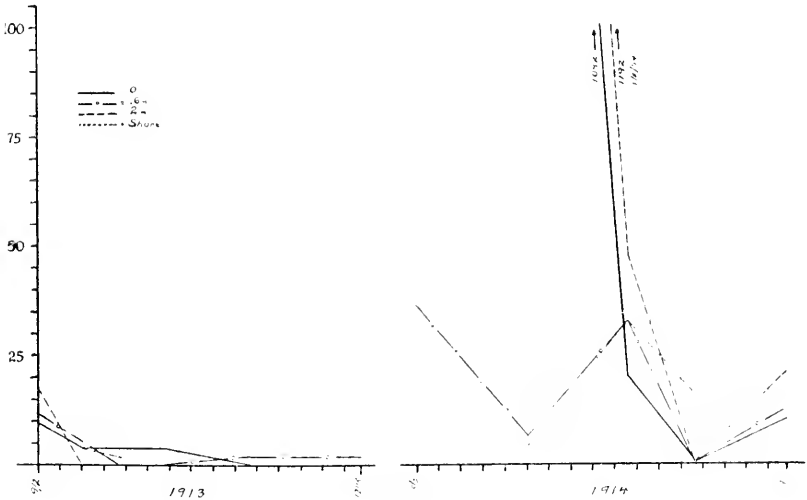


Figure 21. Seasonal distribution of diatoms in individuals in East Lake.

conditions are described by Needham and Lloyd (1916, pp. 302-3) and Marsh (1900, p. 176). In a letter to the writer from Grand Island, Nebraska, (Dec. 31, 1920) Professor Elmore says, "Here, diatoms are much more abundant in the winter, when the water is partly frozen over." Their infrequent occurrence then in the winter collections from Devils Lake is probably due to other factors, such as reduction in amount of light or dissolved food-stuffs.

In shore collections, especially in bays of the lake, the numbers of diatoms, especially *Navicula* and *Synedra*, may run very high, the maximum number recorded being found at the head of Creel Bay, near the mouth of the sewer ditch from Devils Lake City, on August 13, 1912, as follows: total 1292, *Navicula* 748, *Synedra* 376, *Cymbella* 128, scattering 40, per cc. Other high records are from the same place: total 292, *Navicula* 144, *Synedra* 140, scattering 8, date?, and total 168, *Navicula* 152, *Synedra* 16; Aug. 9, 1916, and from the mouth of Minnewaukan Bay on July 13, 1916, *Navicula* 116, *Synedra* 4. These are the only records of more than 100 diatoms per cc., but there are a few others of 90 or more.

Other species of occasional occurrence in the plankton are *Odontidium elongatum*, *Mastigloia elliptica* and *Campylodiscus*

elypeus, tho it is likely that all of the species in the lake are occasionally driven from their natural habitat in the *Ruppia* zone into the open water.

The list of species follows.

Chaetoceros clmorci. One of the characteristic phytoplanktons of the lake. It also frequently serves for the attachment of other planktonic organisms such as *Characium*, *Vorticella* and *Cothurnia*. It is of interest to note that this representative of a marine genus should find in this brackish lake so favorable a habitat that it now forms one of its characteristic species.

The curve of seasonal distribution is given in pl. 16 which shows that it is more limited in its occurrence than most of the algae, seldom appearing before June, and disappearing about December first. It has a distinct minimum about mid-August, with maxima about the end of July and August, while in 1914 a second sharp minimum occurred July 20. The few records from East Lake show a much smaller number in Main Lake (fig. 17).

Cyclotella. Three species of this genus, *meneghiniana*, *striata* and *comta* occur in the Devils Lake complex. No attempt has been made to differentiate them in the plankton counts. *Cyclotella* occurs occasionally, tho rarely in winter, and rather frequently at other seasons. In only one year (1913) is there evidence of a rather definite maximum, which occurred in early September. *Meneghiniana* has been found in Main, East and Spring Lakes and in fresh water. *Striata*, which is typically a marine and brackish water species, is reported from Main and East Lakes and Lake P. Professor Elmore writes me that Devils Lake is the only place where he has taken the latter species, altho it is reported by Boyer from blue clay near Philadelphia.

Stephanodiscus carconensis is widely distributed in the complex, being reported by Elmore from Main, Mission, Stump and East Lakes and Lakes C and P, altho he tells me that this is the only region in which he has found it. He further states that it is not given by Van Heurek (1896), and I have not found it in Schonfeldt (1913), so it is evidently a rare species. Professor Elmore reports it as common in Devils Lake in the plankton samples.

Gyrosigma. Three species of *Gyrosigma* occur in Devils Lake, of which *kutzingii* is common and the others rare. *G. kutzingii* is reported by Elmore from East and Mission as well as Main Lake, and *G. acuminatum* from Main and Spring Lakes; while *G. spencerii* is reported from Main Lake only in three collections. No attempt has been made to differentiate the three species in the plankton counts. The genus appears sporadically from April to November, but the data are inadequate for drawing any conclusions as to its seasonal distribution.

Mastigloia. Two species of *Mastigloia*, *elliptica* and *smithii*, occur in the complex, of which the former is common and widely distributed; while of the latter there is but one record (Main Lake 12/29 15), altho Professor Elmore reports it from a fresh water lake in the vicinity. The genus appears sporadically in the plancton collections.

Scoliopleura peisonis. In his "Diatoms of Nebraska" Elmore (1921) gives Devils Lake as his only record for this species. It is not mentioned by Schonfeldt (1913), while Professor Elmore informs me that Van Heurek (1896) records it as marine. Elmore's only record from Devils Lake is Minnewaukan Bay, 7 20/15.

Navicula. No attempt has been made to differentiate the various species of *Navicula* in the plancton samples. The genus occurs irregularly in the collections thruout the year. It has a fairly well marked maximum in May-June and two other rather indefinite maxima in July-August and October-November. It frequently appears in large numbers in the shore collections* while absent or rare in the others. This irregularity renders it difficult to draw any very definite conclusion regarding its seasonal distribution.

Notwithstanding the irregularity of its occurrence it is, as might be expected, the richest in species, and one of the richest in numbers of the genera inhabiting the lake complex. The following species have been identified by Professor Elmore: *ambigua*, *anglica*, *brebissonii*, *cincta*, *crucicula*, *cryptocephala*, *hungarica*, *iridis*, *lacustris*, *lanceolata*, *fulva*, *gastrum*, *major*, *minnewaukonensis*, *oblonga*, *parva*, *pygmaea*, *rostrata*, *scandinavica*, *sculpta*, *sphaerophora* and *sub-capitata*.

Amphora. Of the two species of *Amphora* present in the complex *ovalis* is common and widely distributed, occurring in fresh and alkaline waters alike; while *proteus* is much rarer, being reported by Elmore only in Main and Mission Lakes.

Amphora occurs occasionally in the plancton collections, but no attempt has been made to chart its seasonal distribution.

Cymbella. Four species of *Cymbella* occur in the complex (*aequalis*, *cistula*, *parva* and *pusilla*), of which the latter is the most common and widely distributed. *Parva* occurs in fresh waters as well as in Mission Lake, while *aequalis* is reported only from Lake P.

The genus occurs sporadically in the plancton collections from the first of May to the middle of November, but the data are insufficient for drawing any conclusions regarding its seasonal distribution.

*See p. 70.

Gomphonema is represented by three species, *gracile*, *montanum* and *parvulum*, of which the two latter are the commonest, *gracile* being reported only twice, 8 21 13 and 8 28 13, both from Main Lake. *Gomphonema* appears but rarely in the plankton samples, hence no attempt has been made to determine its seasonal distribution.

Rhoicosphenia curvata is common in Main Lake, tho not often taken in the plankton collections. Reported also from Lamoreau Lake.

Amphiprora alata. Taken occasionally in the plankton collections from Main Lake, and reported once from Lamoreau Lake.

Cocconeis. Two species of *Cocconeis*, *pediculus* and *placentalis*, are common and widely distributed in the complex and in neighboring fresh waters.

Achnanthes is represented in the complex by three species, *delicatula*, *lanceolata* and *microcephala*, none of which are common, and there is a doubtful record of a fourth, *hungarica*.

Homococcladia is represented in the complex by eight species, *angustata*, *amphioxys*, *commutata*, *hungarica*, *lanceolata*, *palea*, *tryblionella* and *vermicularis*, with one uncertain record (Main Lake, 8 28 13) of another species, *stagnorum*. Of these *hungarica* is the most common, followed, in the order named, by *palea* and *amphioxys*.

Campylodiscus clypeus is fairly common in Main Lake, tho of infrequent occurrence in the plankton samples. Reported also from Mission and Spring Lakes and Lakes A and P.

Surirella occurs frequently in the plankton catches, appearing about the first of April and disappearing about the middle of November, somewhat earlier than most of the algae. The irregularity of its occurrence renders it difficult to draw any conclusions relative to its seasonal distribution. Of the two species in Devils Lake, *striatula* and *ovalis ovata*, the former is the more common.

Denticula elegans. A rare species, reported only from Main Lake.

Fragilaria construens. Reported in one collection 8 19 20 from Lake P.

Odontidium elongatum. Reported from Main Lake only. A fairly common species, but too irregular in the plankton collections to warrant any conclusions regarding its seasonal distribution.

Synedra. Four species of *Synedra* occur in the complex, *pulehella*, *tabulata*, *tenuissima* and *ulna*, with a doubtful record (Main Lake 8 28 13) of a fifth, *amphicephala*. Of these *pulehella* is common, while the others occur rather rarely. No attempt has been made to differentiate the several species in the plankton

counts, which show that the distribution of the genus follows rather closely that of *Navicula*. It occurs rarely in winter and has one or two rather definite maxima in May and June. Its irregular occurrence, especially in the shore collections, renders it impossible to make any statements regarding maxima at other times. It sometimes appears in the shore collections in large numbers.*

Cystopleura. There are six species of *Cystopleura* in the complex, *argus*, *gibba*, *ocellata*, *sorex*, *ventricosa* and *zebra*, of which *gibba* is common and the others rare. It appears erratically in the plankton samples and is usually too infrequent to justify any conclusions regarding its seasonal distribution. Occasionally, however, it appears in large numbers (80 per c. c. surface Creel Bay, 8/10/14).

Eunotia lunaris. There is but one record of this species for the complex (Main Lake, 6/27/14).

Sphinctocystis librilis. There is but a single record of this species in the complex (Main Lake, 8/28/13).

FUNGI

Spores of a mold occasionally occur in the plankton collections, but are probably accidental.

SPERMATOPHYTES

The only flowering plant of importance in Devils Lake is the ditch grass (*Ruppia maritima*) but in periods of high water sedges (*Cyperus* sp.) may occasionally be found in shallow places close to shore.

The *Ruppia* probably plays a more important role in the life of the lake than any other organism. It has already (p. 33) been mentioned as characterizing one of the life zones of the lake, which derives its name from this plant. It not only functions in the interchange of chemical substances in the water, but contributes a considerable part of the annual deposit of ooze on the lake floor. It also furnishes shelter and attachment for many smaller animals and plants. It is widely distributed, occurring in most of the lakes of the complex, both brackish and fresh water.

It grows in from 0.6 to 2.4 m. of water, forming a zone, which naturally varies in width at different points, depending on the configuration of the lake bottom. During winter much of the leafy parts of the plant die. Enough of the stems survive, however, to renew the growth the following year. During the break up of the ice in spring considerable masses of *Ruppia* are carried by floating ice cakes from point to point, or thrown on shore to die (pl. 4).

It flowers chiefly from July to September.

* See p. 70.

The sedges, which occasionally occur in the edge of the lake, play an insignificant part in its life, and may accordingly be dismissed with brief mention. In 1916, however, as a result of the abundant supply of fresh water thru the Mauvaise Couée, Minnewanau Bay extended over a wide expanse of old lake floor, and numerous sedges and rushes were found growing in its waters (pl. 10).

PROTOZOA

The data on the Protozoa in Devils Lake are largely the result of studies by Professor C. H. Edmondson, in 1914 and 1917. Some data have, however, been taken from my own notes.

As a result of his studies Edmondson (1920) found that: "The protozoan fauna of the Devils Lake complex . . . in many respects, was such as one might expect in a fresh water lake of similar depth, yet some very pronounced differences were disclosed . . . A most noticeable feature is the apparent total absence of numerous forms universally found in fresh water. . . .

"Experiments of a preliminary character indicate that certain protozoa having adjusted themselves to fresh water conditions are not in all cases at least, readily adaptable to the waters of Devils Lake."

Just how large a part the Protozoa play in the bionomics of Devils Lake cannot be estimated. They are of relatively infrequent occurrence in the plankton catches, and then mostly attached peritrichs, such as *Cothurnia* and *Vorticella*. Any collection of *Ruppia*, however, after standing in the laboratory for a few days, contains large numbers of Protozoa of several species, and it is this material which is the chief source of Protozoa in the lake. No attempt has been made to estimate the number of the Protozoa as a whole, nor the relative abundance of the different species, except in a general way.

Many of the forms are so minute as to escape thru the sand filter in the Sedgwick-Rafter tube, and even if retained in the preserved sample, they are so distorted as to prevent identification. They are comparatively rare, so that the only way to obtain them in considerable numbers for study is to allow a culture of ditch grass and algae, or of ooze to stand in a culture jar for several days, when many of them develop in enormous numbers. In this way it is possible to obtain them at any season, even in winter, when they doubtless occur encysted in the ooze.

The vitality of some of the Protozoa is quite remarkable. Apart from the results of Professor Edmondson's experiments, mentioned above, which show the ability of some species to withstand sudden transfer from lake water to fresh, I have observed an

Oxytricha which was still living, altho inactive, after a 25-26 hour confinement beneath a cover glass in a sealed Petri dish.

Many Protozoa occur in the lower levels of the lake and in the ooze at the bottom, where dissolved oxygen (as shown by the Winkler test) is absent. This is discussed elsewhere in this report.*

One hundred and six species are recorded from the lake, a list of which follows.

Ameba proteus. Found occasionally at several points in the main lake. Also reported from East Lake.

Ameba radiosa. Rare. Taken in Ruppia in Minniewaukan Bay. Also reported from Lake A.

Ameba Uinar. "Associated with Ruppia and algae at the head of Creel Bay . . . and the east side of the main lake (numerous)", also taken ("numerous") in Lake A and Mission Lake (1917).

Ameba verrucosa. "Observed but once."

Ameba guttula. Of fairly common occurrence in the lake.

Amoeba striata. One specimen noted in a plant infusion from Stump Lake.

Ameba vitrea. Rare.

Diffugia pyriformis. Taken in Lake A near seepage from a fresh water spring.

Diffugia constricta. Found near the outlet of the Devils Lake sewer in Creel Bay, and in Lake A near seepage from a spring.

Arcella vulgaris. Found in ooze in Creel Bay, and abundant in Lake A near seepage from a spring.

Cyphoderia ampulla. "One specimen only has been observed." Taken in Ruppia.

Euglypha alveolata. "Observed but once" in the overflow of a tank of lake water. It is possible that this species does not occur in the lake, its presence in the lake water overflow may have been accidental.

Actinophrys sol. Rare, in Ruppia from Minniewaukan Bay.

Cercomonas sp. "Probably *Cercomonas longicauda*. . . . Observed in infusions from Stump Lake only."

Monas sp. Three different species have been found in the ooze from Creel Bay.

Heteromita globosa. "In dredged material from Creel Bay."

Heteromita sp. "Probably . . . ovata." Taken from ooze on rocks near the Station. Also taken in Lake A.

Trepomonas agilis. Common in ooze and Ruppia cultures from all parts of the lake.

Euglena viridis. Occurs occasionally at various points in the main lake. Also taken in Lake A.

*See pp. 406-7.

Euglena deses. Common and of widespread occurrence in ooze and Ruppia, in the main lake. Also taken in Mission and East Lakes and Lake A.

Phacus pyrum. Common, and widely distributed in the main lake. Also numerous in Lake A.

Eutreptia viridis. "From the surface among Ruppia" in Lake A.

Astasia tricophora. Common in Ruppia and algae. Widespread in the main lake. Reported also in Lake A.

Petalomonas mediocancellata. Occasional in ooze in the main lake, and the surface of Lake A.

Petalomonas sp. "From the ooze of Creel Bay."

Helicronema acus. "From Six-mile Bay and from the ooze of Creel Bay."

Anisonema grande. "Among Ruppia and algae at the head of Creel Bay."

Notosolenus sp. Occasional. Taken in Main and Stump Lakes.

Tetraselmis cordiformis. "Taken from Stump Lake only."

Polytoma urella. Occasional in the main lake.

Chlamydomonas pulvisculus. "Taken from the head of Creel Bay."

Glenodinium pulvisculus. "Taken from the surface and from the ooze at the bottom of Creel Bay."

Holophrya orum. "Among algae from Creel Bay."

Urotricha labiata. Common in the main lake.

Proterodon teres. A fairly common and widely distributed species in the main lake in Ruppia and algae. Also in Lake A.

Proterodon edentatus. Occasional in Ruppia. Taken in Minnewaukan Bay and Lake A.

Euchlys sp. Noted by Edmondson in ooze of the main lake and in overflow from a tank of lake water. What was probably the same species was observed by me in the shells of rotifers in a shore collection, July 20, 1914.

Spathidium spatula. "Among algae from the head of Creel Bay."

Two indeterminate species of *Spathidium* were taken by Prof. Edmondson, one in a Ruppia infusion from the head of Creel Bay and one from "ooze of the main lake."

Chacnia teres. "Among algae from the head of Creel Bay."

Mesodinium pulcr. One of the most common Protozoa in the lake, found in infusions of Ruppia, in surface tows and in the ooze of the main lake. Undoubtedly occurs in other lakes of the complex, but has not yet been observed other than in the main lake.

Didinium nasutum. Occasional and of wide distribution in Main Lake.

Lacrymaria olor. "Among Ruppia in Creel Bay."

Lacrymaria truncata. "Among Ruppia from the north end of the main lake."

Lacrymaria lagenula. "In ooze from the main lake."

Lacrymaria cohnii. "In an infusion from Stump Lake."

Lionotus fasciola. Common and widely distributed in main lake. "Also taken from Stump Lake", and Lake A.

Lionotus sp. "Among algae from Creel Bay."

Amphileptus meleagris. "From algae at the head of Creel Bay." Also in Stump Lake.

Nassula rubens. In overflow of lake water from tank.

Nassula ornata. Taken from Lake N only.

Chilodon cucullulus. "In infusions of algae from Creel Bay" and Lake A.

Chilodon caudatus. "Among Ruppia from Minnewaukau Bay."

Aegyria pusilla. "Among algae near the Station."

Glaucoma scintillans. In an infusion of algae from the west end of the lake.

Glaucoma margaritaceum. "Very abundant" and widely distributed in Main Lake both at the surface and in the ooze. Reported also from Stump Lake.

Leucophrys patula. "One specimen only observed from . . . the Main Lake."

Frontonia leucas. Common and widely distributed in Main Lake, and reported from East Lake.

Loxocephalus granulatus. "Taken only in the ooze of Lake A near the insepape of fresh water."

Uronema marinum. "One of the most common species in the lake. Abundant everywhere both at the surface and in the ooze."

Uronema is also reported by Edmondson among algae in Stump Lake. Presumably this species.

Colpidium putrinum. "From algae at the east side of Creel Bay."

Tillina saprophila. "Taken only in the overflow of lake water from fish-tank."

Paramaecium trichinum. Occasional.

Paramaecium caudatum. "Taken from Lake A near the insepape of fresh water."

Cyclidium glaucoma. Abundant everywhere in Main Lake at the surface and in the ooze.

Cyclidium litomcesum. "Numerous in infusions from the head of Creel Bay and in the ooze from the main lake."

Pleuronema chrysalis. "Observed in infusions from Stump Lake only."

Metopus sigmoides. "Common in dredged material from Min-

newaukan Bay, Creel Bay and the main lake. Abundant in East Lake."

Spirostomum ambiguum. "Observed in dredged material from Creel Bay."

Stentor sp. Reported by Moore (1917) from Main Lake.

Halteria grandinella. Common and widely distributed in Main Lake, both in ooze and infusions of *Ruppia* and algae.

Uroleptus agilis. Occasional in ooze in Main Lake.

Uroleptus rattulus. Occasional in *Ruppia* in Main Lake.

Oxytricha. This genus is probably the most characteristic genus in the lake, both in respect to variety of species and number of individuals, almost every infusion of *Ruppia* containing them. Four species have been determined, but it is Professor Edmondson's opinion, that further study would reveal others. These four are fallax, pellionella, parvistyla, and bifaria, of which pellionella is the commonest. The latter is reported from Lake A also. The others from Main Lake only. Bifaria? has been seen with contained diatoms (*Navicula*?).

Histrio erythystieus. In *Ruppia* in Creel Bay.

Stylonichia notophora. "With algae from Creel Bay."

Holosticha vernalis. "Among *Ruppia* from the main lake."

Pleurotricha lanceolata. "Taken at the head of Creel Bay."

Tachysoma parvistyla. "Observed in infusions from Stump Lake only."

Euplotes charon. This species and *E. patella* are among the most abundant Protozoa in the lake. Charon is reported from East Lake also, while patella occurs in Stump, East Lake and Lake A.

Aspidisca costata. Abundant in *Ruppia* infusions thruout the main lake.

The genera *Vorticella* and *Cothurnia* are the only Protozoa which occur with any frequency in the plancton. This may be due to the fact that they are carried out of their natural habitat in the *Ruppia* by animals or plants to which they are attached. No attempt at specific determination has been made in the plancton counts. *Vorticella* occurs frequently at all seasons while *Cothurnia* appears more rarely, but it is probably perennial also. My records run from June 22* to December 30.

Six species of *Vorticella*, two of them indeterminate, have been observed by Professor Edmondson as follows: teleoseopiea, convallaria, octavo, microstoma and two sp. Of these convallaria is reported from Lake A. also.

Gerda annulata. "Among algae and *Ruppia* from the north end of the main lake."

Epistylis plicatilis. "From . . . Creel Bay."

*June 21 in East Lake.

Epistylis branchiophila. "Among algae near the head of Creel Bay."

Carchesium epistylidis. "Among algae from Creel Bay."

Zoöthamnium alterans. "Among Ruppia and algae from Stump Lake."

Zoöthamnion sp. Fairly common and widely distributed. Among Ruppia in Main, Stump and East Lakes.

Vaginicola crystallina. "Numerous among algae from East Lake, also taken from Stump Lake and from the north end of the main lake."

Cothurnia imberbis. "Commonly attached to floating diatoms, from dredged material and also among Ruppia in Creel Bay. Also taken from Stump Lake."

Cothurnia curva. "Among Ruppia at the north end of the main lake."

Podophyrya libera. "Numerous at east side of the main lake."

Podophyrya sp. "Attached to algae from the main lake."

Sphacrophrya magna. "From Stump Lake and the east side of the main lake."

Acineta sp. "From floating material in the main lake and also among algae from Stump Lake."

Acineta sp. "Attached to algae from Stump Lake. Commonly feeding on Uronema."

Species incertae sedis

Trimastigidae gen. "Numerous among Ruppia from Creel Bay."

Fam. and gen. An undetermined ciliate was found by Professor Edmondson at the "surface of the main lake and among Ruppia and algae."

Genus sp. A small green flagellate sometimes occurs in large numbers attached to Pedalion, and probably to other rotifers. It is flexible but not ameboid; in form ovoid, stipitate. It bears a single anterior flagellum, which is vibratile thruout its length, and which about equals the body in length, and is inserted near the bottom of a depression, one side of which projects forward as an overhanging lip, and which in depth about equals one third the length of the body.

There is a single vacuole situated posteriorly. Staining with magenta brings out a number of dark granules, but I have not been able to differentiate any definite nucleus. Nor have I determined the form of the chromatophore, the entire cell appearing filled with chlorophyl. There is no eye spot. Measurements of three specimens (exclusive of the stalk) follow: .0049x.0033, .0057x.0024, .0057x.0024 mm

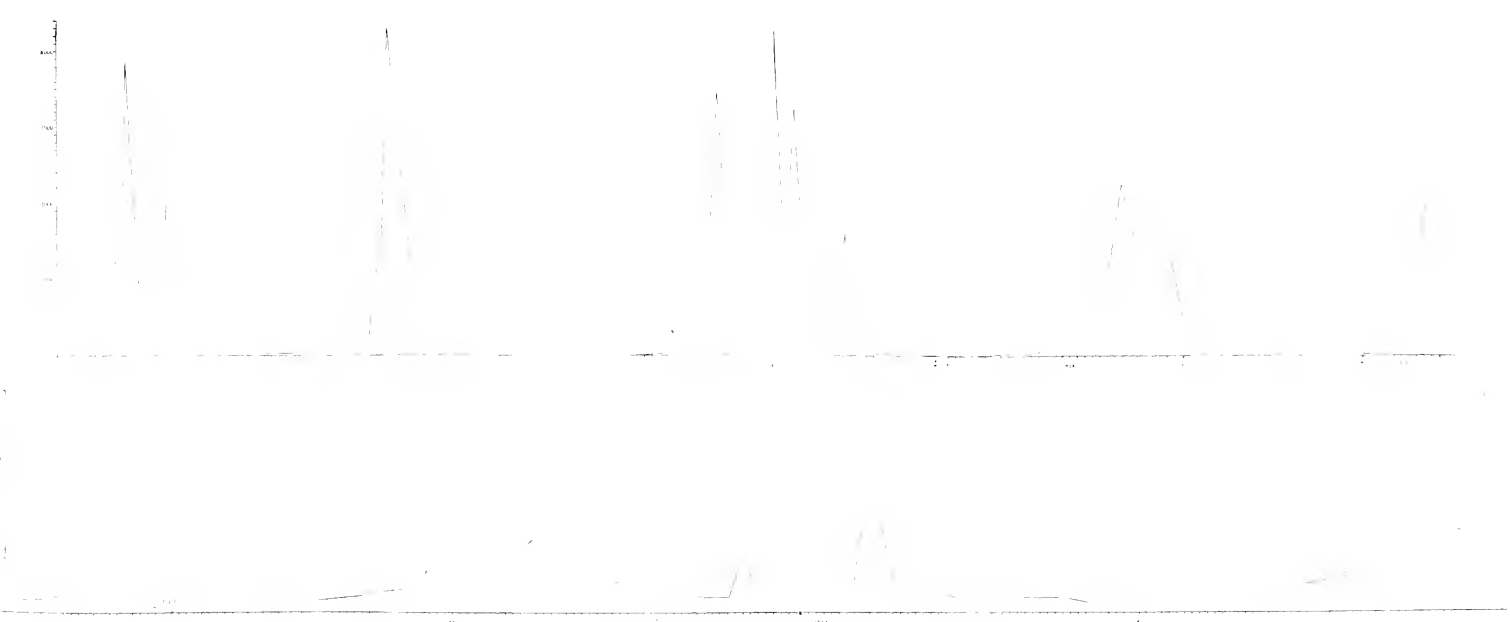


Plate 17 Above, seasonal distribution of Rotifera in Man Lake.
 Below, seasonal distribution of Crustacea in Man Lake.

PLANARIA

But a single species of this group (*Gyratrix hermaphroditus*) has been found in the Devils Lake complex, an occasional specimen being taken in collections from *Ruppia* in the main lake.

NEMATODA

The nematodes of the complex are numerous in individuals and undoubtedly in species, but as yet complete identifications are not available. Dr. N. A. Cobb of the U. S. Department of Agriculture has kindly given me the following list, based on fresh material which reached him, for the most part, in poor condition.

Monohystera sp. "Very common."

Monohystera sp. "Not common."

Diplogaster sp. "Common."

Achromadora sp. "Rare."

Ironus sp. "Not common."

Plectus sp. "Not common."

Dorylaimus sp. "Rare."

Dorylaimus sp. "Rare."

Cephalobus sp.

Chromadora americana n. sp. "Rather common."

The nematodes occur mainly in the *Ruppia* zone and in the ooze, but are occasionally present in the plankton catches. They occur at all seasons of the year, both in winter and summer, but no attempt has been made to determine their relative abundance at different times.

ROTIFERA

Both in respect to numbers and variety the rotifers are the most important animals in the Devils Lake plankton. Thirty-one species and one sub-species occur, two of them, *Brachionus satanicus* and *Pedalia feminea*, at certain times in great numbers.

The attached forms naturally are found in the *Ruppia* zone, which also shelters a number of the rarer, free swimming forms. All of the latter are probably of widespread distribution thruout the lake, but the rarer forms occur so infrequently that but little can be said regarding their distribution, either spatial or temporal.

Reproduction is almost entirely parthenogenetic, males of any species having been seen in very few instances. The difficulty of recognizing males in preserved material may, however, partly account for this.

The seasonal distribution of the rotifers as a whole is shown in pl. 17 and figure 22, anent which the same remarks apply as those made anent that of the Crustacea.* The distribution of those species which occur in the collections in numbers large enough to

*See p. 87.

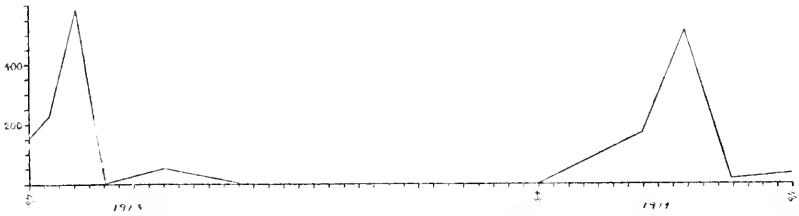


Figure 22. Seasonal distribution of rotifers in East Lake.

be significant is shown in plates 18 to 21 and will be discussed briefly in the annotated list.

Absent, or practically so, in winter, the rotifers develop rapidly in early summer and may reach their maximum for the entire year by the first of June. There are usually two maxima, one in June or July and another in August, but in 1913 there are three such periods, the last one appearing about October 6, which is unusual. The curves show very sharp breaks, indicating rapid development and equally rapid disappearance.

While the rotifers of Devils Lake are mostly fresh water types, like rotifers in general elsewhere, there are a few which are marine as well as fresh water. These are *Colurella adriatica*, *colura*, *Brachionus plicatilis*, *Notholea striata thalassica* and *Pedalia fennica*. *Collotheca cornuta*, *Brachionus calyciflorus pala*, *Polyarthra trigla*, *Keratella cochlearis*, and possibly *Asplanchna silvestrii** occur in both fresh and brackish water, while *Brachionus satanicus* and *B. pterodinoides*, both of them new species, belong in the latter class, judging from their distribution in the complex and its adjoining waters.

The widespread distribution of so many species in both the brackish and fresh water lakes of the complex indicates the adaptability of the group to widely varying environments; the apparent restriction of some to one or a few lakes, being due possibly to the incompleteness of the investigation. The rotifers show marked light reactions, a discussion of which has already been given.**

Rotifers occur occasionally in oxygen free water.***

The annotated list follows:

Cephalodella catellina. Occurs occasionally in the main lake, where it is of widespread distribution. Reported also from East Lake.

Diaschiza stercora. Widely distributed in main lake. Reported also from East and Mission Lakes.

*The character of the Chilean lake from which this species was first taken is not known.

**See p. 46.

***See p. 107.

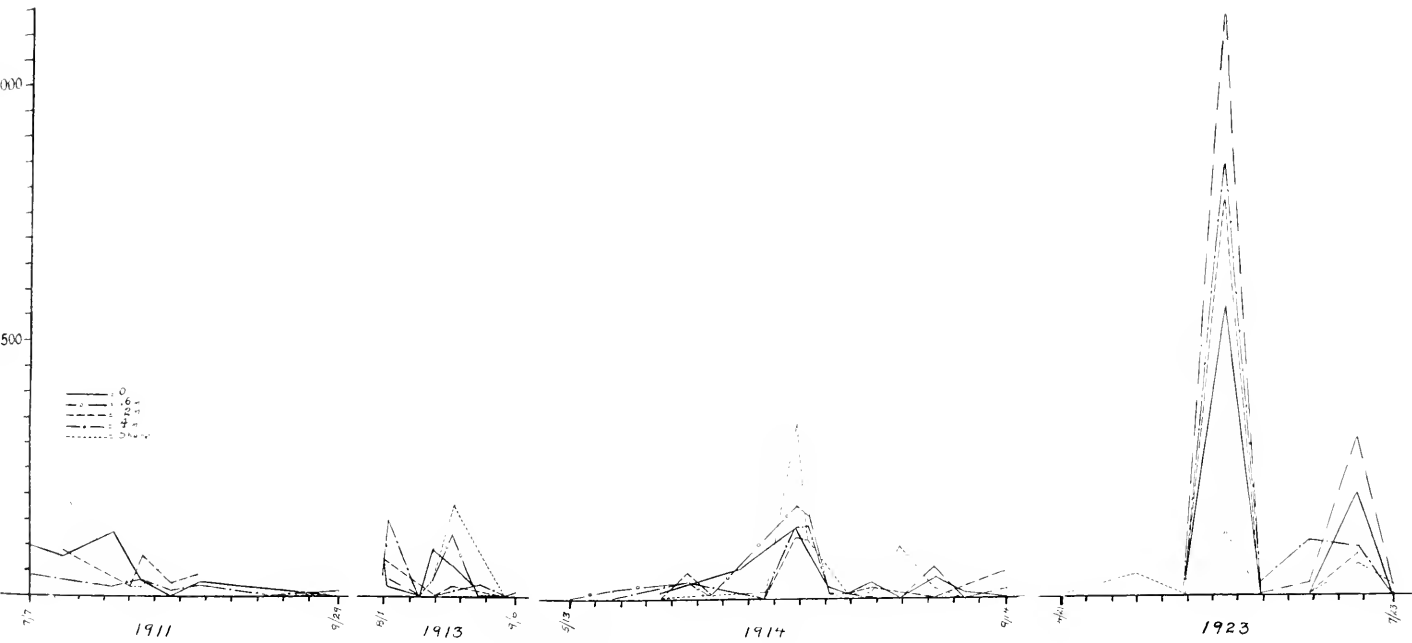
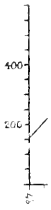


Plate 18 Seasonal distribution of *Brachionus plicatilis* in Main Lake



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D. megalocphala. One record only, a single specimen in a collection from Creel Bay (8/31/14).

Brachionus plicatilis. A very common and widely distributed species but not usually as numerous as either *Pedalia* or *Brachionus satanicus*; occurring in Main, East, Mission, Lamoreau, Spring and Stump Lakes, Lakes A, C, and O, and in certain fresh water lakes of the complex as well. Owing to the close similarity between this species and its variety *spatiosus* no attempt has been made to distinguish them in the plancton counts. Typical *spatiosus* is sufficiently distinct, but intergradations render it impossible to determine where every specimen belongs. Accordingly I have included both the species and variety in the chart (pl. 18), which illustrates the seasonal distribution. This shows its presence thru a comparatively short period. In 1911 a few were present up to the end of September. In 1912 the records show their practical absence prior to June 26, one or two records being all that I have before this date. A few were present later in the season, but the records are too scanty to represent as a curve. In 1913 they were absent prior to June 24, when the spring collections ended, occurring in small numbers from August 1 to September 6. The 1914 records cover a longer period (May 15 to September 14) but even here they were present in considerable numbers during July only. In 1918 on August 7 a rough comparison of the numbers of various species of rotifers taken in a tow showed 63 *Brachionus p. spatiosus* and 1 *plicatilis?* to 36 *Pedalia* and 3 *Brachionus satanicus*. August 12, 1918, a similar comparison showed 103 *B. p. spatiosus*, 47 *Pedalia*, 2 *B. satanicus* and 1 *Colurella?* With remarkable suddenness, however, the *plicatilis* disappeared, for on August 21, I found but one specimen, as compared with 86 *Pedalia* and 9 *B. satanicus*.* Usually two maxima with an intervening minimum occur in a season. In 1913 there is a very definite minimum on August 11 followed by a definite maximum on the 20th and preceded by a maximum sometime in July or early August. In 1914 there was a distinct maximum on July 20, and another, less well defined, between August 17 and 26, with a very distinct minimum on August 2. In 1911 the records are not adequate for interpretation. The records for East Lake are too scattering to have much value.

Brachionus plicatilis spatiosus. The spatial distribution of the variety described by Rousset (1912) is similar to that of the parent species, altho there is no record from Lake P. from which the parent species is recorded. In the main lake, where the most extensive collecting has been done, *spatiosus* is much commoner than *plicatilis*. In his description of this form Rousset says (p. 374)

*See p. 45.

"I was in doubt at first whether this form should not be called a variety of *B. Mülleri* with which structurally it is undoubtedly more nearly allied than with any other species; but after comparing it with the mounted specimens in my collection from various localities I have decided to give it specific rank on account of its striking shape." My reason for classing it here as a variety of *B. plicatilis* are the occasional intermediate forms which occur in my material as already noted.*

Brachionus capsuliflorus quadridentatus. Of occasional occurrence and widespread in the main lake, and reported in one collection each for East Lake (1913) Stump Lake, Spring Lake, and Lakes A., C., O., and P. It occurs also in several fresh water lakes of the complex.

Brachionus urceolaris. Taken near the head of Minnewaukan Bay in 1916. Also in fresh water lakes in the vicinity. As already noted the former was nearly fresh at this time.

Brachionus pterodinoïdes. This species, described by Rousset (1913), is fairly common and widely distributed in the complex and in fresh waters. While common, it appears only sporadically in the plankton collections, and hence there are not sufficient data for plotting its seasonal distribution. It occurs first in early May, disappearing again early in November.

Brachionus calyciflorus pala. Reported from Minnewaukan Bay.

Brachionus dolabratus. Reported from Minnewaukan Bay (June 6, 1921) and Spring Lake (July, 1920).

Brachionus satanicus (pl. 19, 20). This species, described by Rousset (1911), is one of the most abundant and characteristic species in the lake. The curve of its seasonal distribution in Main Lake shows that two cycles, one major and one minor, occurred prior to June 26 in 1912. Three of them are evident in 1913, with maxima about June 11, August 1, and September 1, and in 1914 there are also three, with maxima between June 10 and 24 and on July 2 and September 2.

It is not only one of the commonest, but naturally also, one of the most widely distributed species in the complex, occurring in all the lakes examined except N and in fresh water as well. Lake N is merely a temporary pool which possibly explains the apparent absence of *B. satanicus* there.

In a letter to the writer (July 17, 1912) Mr. Rousset says "I have found two distinct seasonal varieties of this species, evidently winter forms, which during the warmer weather of July will produce the normal type . . . These . . . are not immature . . . forms, for they carry eggs. These two seasonal varieties

*See p. 83.

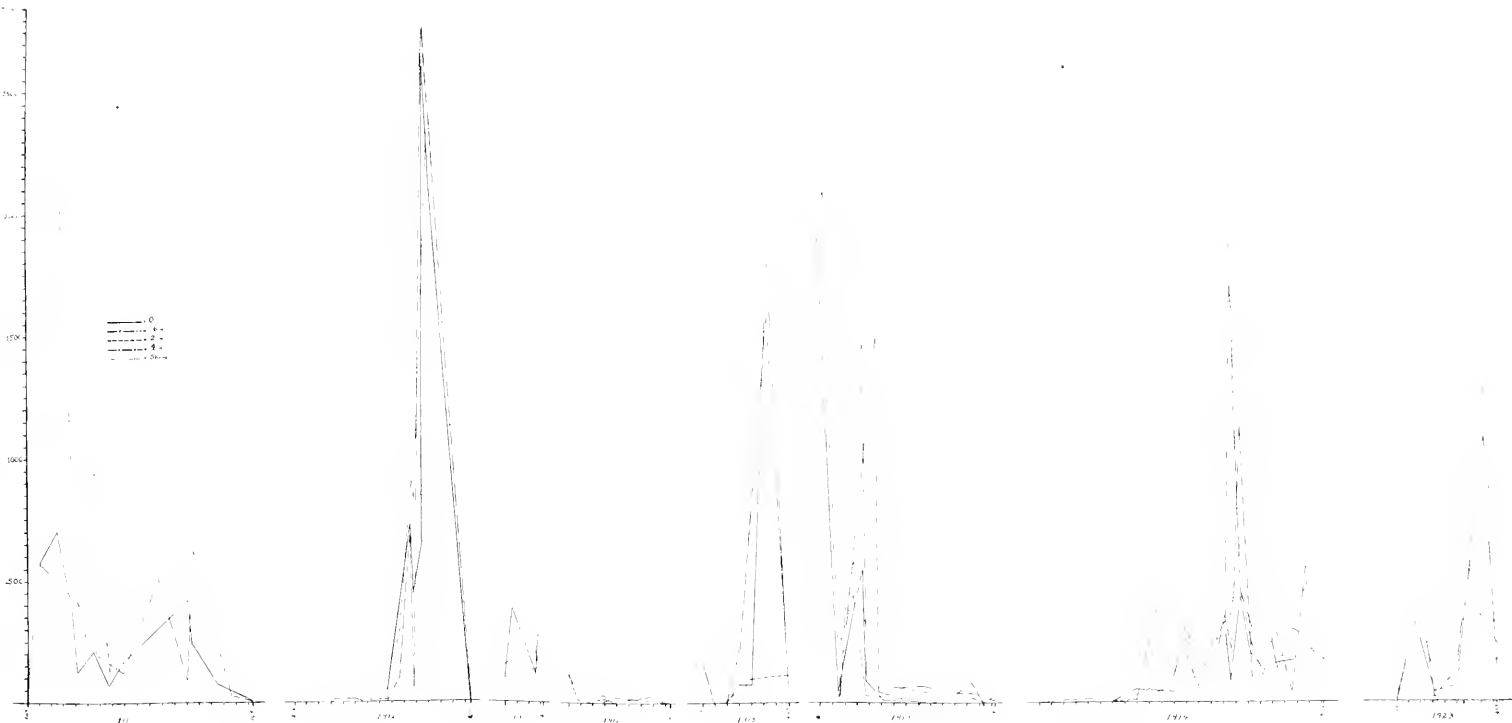


Plate 19 Seasonal distribution of *Brachionus satanicus* in Main Lake

of *B. satanicus* present some remarkable features for not only are the posterior spines reduced and curved inwards, but the foot opening is situated on the dorsal side, which does not occur in any other known *Brachionus*." Further investigation, however, has shown the presence of both short and long-spined forms in summer (August 22, 1913), so that it is doubtful if these varieties *are* seasonal ones.

Platygias quadricornis. Reported from Main, Stump, and Spring Lakes and fresh waters. It occurs in all of the zones of the lake except the ooze.

Keratella cochlearis. Present in Spring Lake—also in fresh waters.

Keratella quadrata. Reported from Stump Lake and fresh water lakes.

Natholea striata thalassica. There are a number of records from Main Lake, where it is widely distributed but not common. Reported also from Mission Lake (1914), Lamoreau Lake, and Lakes C and P and in fresh waters.

Mytilina ventralis brevispina. One record only for Main Lake. Recorded also in Spring Lake and in fresh water lakes of the complex.

Lecane incrimis. Of occasional occurrence and widely distributed in Main Lake, and reported from East Lake and Mission Lake and Lake C.

Lecane luna. Reported in two collections from Main Lake. Also in Stump, East and Spring Lakes and fresh waters.

Monostyla cornuta. Recorded only from Spring Lake and fresh waters.

Monostyla bulla. Present in a surface tow from Creel Bay (8/13/12). Also in Stump and Spring Lakes and fresh waters.

Monostyla lunaris. Two specimens in a surface tow from Ft. Totten Bay (10/2/17) is the only record for Main Lake. Also in Lake N and fresh water.

Monostyla quadridentata. Reported from Minnewaukan Bay (Main Lake) Spring Lake and fresh waters.

Lepadella patella. Present in a few tows from Main Lake. Also in fresh waters.

Squatinella mutica. One record, from Ruppia, Creel Bay, (8/26/14).

Colurella adriatica. Occurs occasionally and is widely distributed in Main Lake. Present also in Mission Lake (1914-15) and in Lakes A and P.

Colurella colura. Occurs occasionally and is widely distributed in Main Lake. Reported also for Mission Lake (1914).

Filinia longiseta. In September and early October 1909 this species was of occasional occurrence in the plancton collections from the main lake. Since with increase in salt concentration of the water above 1‰ it appears to be absent there, but was present in two collections from Minnewaukan Bay in 1916, when this Bay was reduced about 2/3 in salinity and greatly increased in area, due to the influx from the Mauvaise Coulée, it appears to be unable to adapt itself to as great concentration of salts as several other species in the complex.

It has also been reported in Spring Lake. It is in general very rare in the complex but in the Minnewaukan Bay samples of 1916 Mr. Harry K. Harring of the United States National Museum reports it as "abundant" and "common" in two collections. My last record from the Main Lake is May 17, 1912.

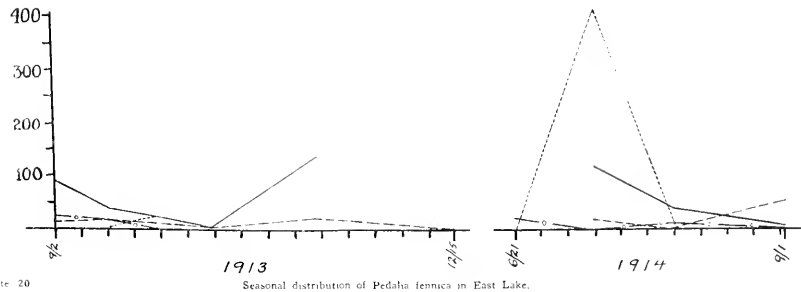
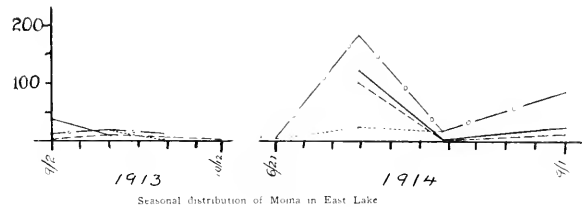
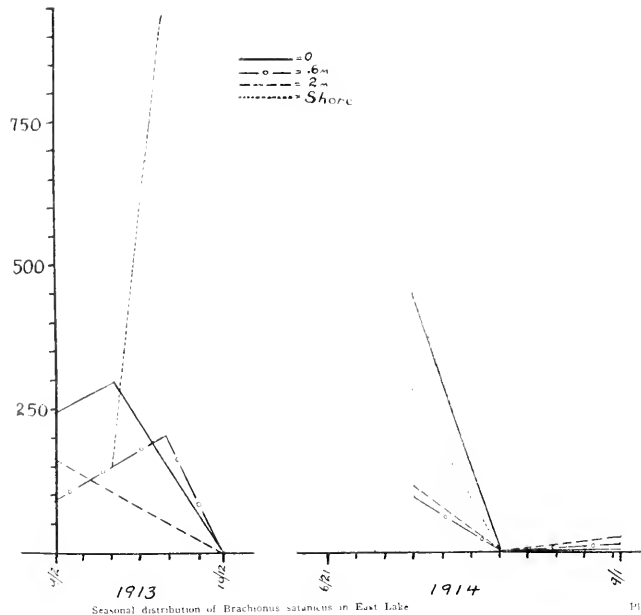
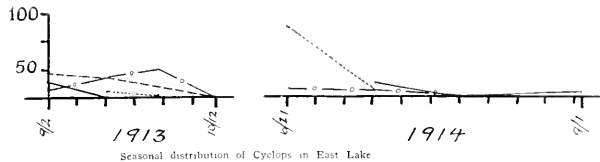
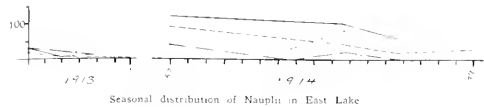
Pedalia fennica (pl. 20, 21). Abundant and widely distributed in the complex and in fresh waters. It is evidently readily adaptable to a great variety of habitats.

Its distribution curve for Main Lake shows that in 1911 three rather poorly defined maxima occurred, one about mid-July, one in early and one in late August. In 1912 a distinct maximum occurred about May 25. The records for this year, altho incomplete, suggest also another smaller one about the end of August. In 1913 a small maximum occurred the last of May, and three well marked maxima from August to October (8/12/20, 9/3/10, and 9/29-10/6), altho the latter consists chiefly of a great development at shore on the last date, which may have been due to a swarm and not indicate a time maximum at all.

Occurs rarely in winter, but is in active reproduction very early in spring, gravid females having been taken as early as April 8 (9) when the lake was still frozen.

In a letter to the writer of July 17, 1912, Mr. Rousset says, "It is remarkable that *Pedalia fennica* should be found in active reproductive stage - - so early in the year (May 17) . . . in Europe *Pedalion mirum* is a summer form and is hardly ever seen before June."

Asplanchna silvestrii. During summer *Asplanchna* occurs rather frequently in the plancton samples and occasionally in considerable numbers (100 pr. l. 0.6 m. depth, 6/24/12). It is too erratic however to justify any attempt at an analysis of its seasonal distribution. It usually occurs in numbers of 50 pr. l. or less. It appears rather suddenly in considerable numbers, about the end of June, disappearing again in September or early October. My earliest record for Main Lake is 4/20/12 and the latest 10/15/10. Present also in Mission Lake (1914), in Spring Lake, in Lakes A, and C. and in fresh water lakes of the complex. Numerous in a collection from Creel Bay (6/24/10) in which several males were



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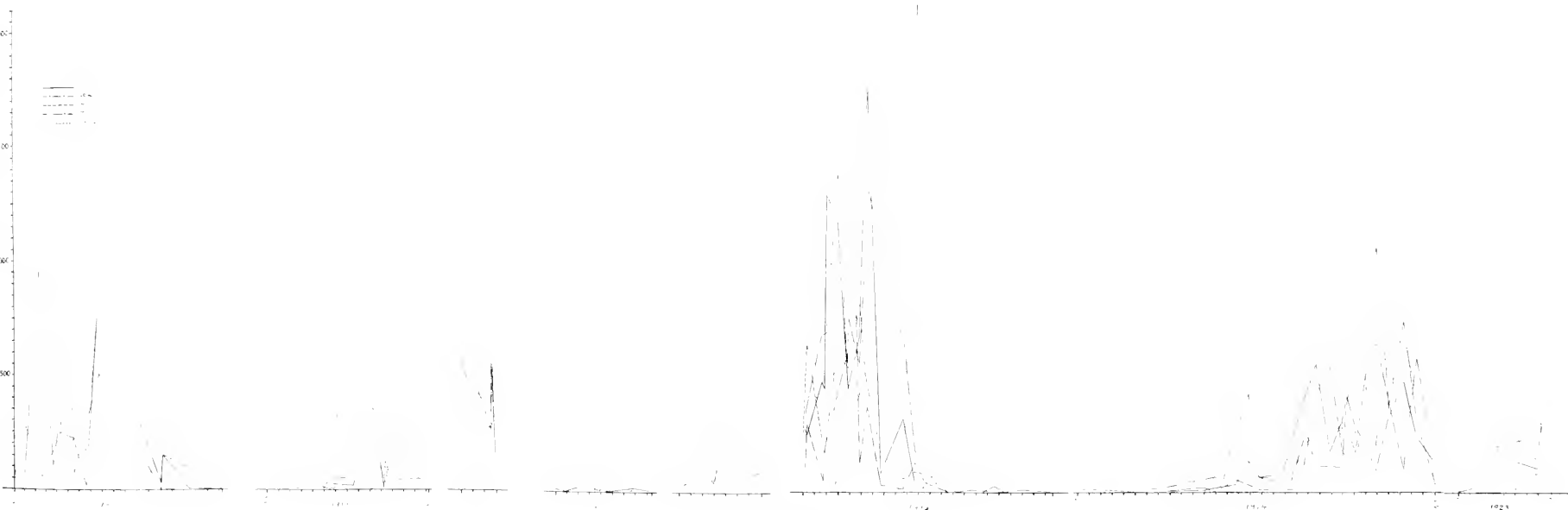


Plate 21 - Seasonal distribution of Peptide termites in Main Lake

present. Prior to its discovery in the Devils Lake complex it had only been reported from Chile, which is doubtless due to incomplete study of our waters.

Testudinella patina. One record only for Main Lake (10/18/14). Reported also from Spring Lake, and there are several records from fresh water lakes of the region.

Ptygura sp. Two specimens in a collection from Mission Lake (8/18/14).

Collotheca cornuta. Infrequent. Reported only from Main Lake.

GASTROTRICHA

Chaetonotus maximus. Occasionally noted in collections from the Ruppia zone in Main Lake.

CRUSTACEA

In plate 17 is shown the annual records of the Crustacea for Main Lake, from 2/6, 1911 to 9/14, 1914 and 12/3, 1922 to 7/23, 1923, and in figure 23 those for East Lake for 1913-14. There are gaps in the records for 1912 (6/25-8/6, 8/28-10/7), 1913 (6/24-8/12) and 1923 (1/27-3/11). The curves represent the average of all collections from different depths on a given day or for a period of successive days. The shore collections have not, however,

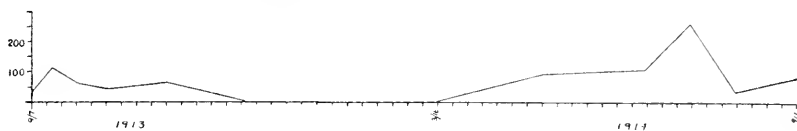


Figure 23. Seasonal distribution of crustacea in East Lake.

been included until 9/3/13 because of their scarcity prior thereto. The number of collections have varied from time to time, so that the probable accuracy of the record is not the same thruout. Especially is this true of 1911, in which year comparatively few collections were made. In spite of these defects the records are fairly consistent thruout, except for 7/13/23 when great numbers of nauplii appeared, averaging over 1000 per l., to disappear again as quickly as they came. Furthermore, the 1923 records in general are very much higher than for former years. What the explanation for this is I cannot say. There was a marked development of *Coelosphaerium* about the end of June in this year, but not conspicuously more than in 1914, while the diatoms and other algae showed no unusual development. *Lyngbya*, however, was greatly reduced in 1923 as compared with former years. Birge (1897) considers an abundance of this genus prejudicial to the Crustacea since the latter do not feed on it. I doubt very much whether this hypothesis holds good for Devils Lake because the filaments of the

former are so extremely delicate that they could scarcely be shunned by the Crustacea because of their inability to feed upon them, as Birge believes; altho, as he suggests, there may be factors other than size which cause them to avoid it. He undoubtedly refers to another species (*L. birgei?*), with filaments about 20 μ wide, from that occurring in Devils Lake (*L. contorta*), which has filaments about 1.5 μ in width.

As to whether or not the Crustacea do feed on *Lyngbya*, I cannot say, as I have paid little attention to their feeding habits.

The only other obvious difference between conditions in 1911-14 and 1923 is the increase in concentration of the lake water, which, a priori, one would expect to be inimical to fresh water animals, rather than the reverse. Differences in plankton abundance in different years are of frequent occurrence elsewhere and have been previously discussed in this paper.* The curves in general, show two maxima, one in May-June and another larger one in August-September.

The sex ratio in the Crustacea presents some interesting features. In *Diaptomus*, during the summer,** when reproduction is most active, the females outnumber the males in the ratio of 662:118, while the ratio for the remainder of the year is 905:942. In *Cyclops* the summer ratio is 167:112, and for the balance of the year 32:10. While the numbers of the latter ratio are too small to have much significance, there is evidently here not the same difference for different seasons as occurs in *Diaptomus*. When *Moina* first appears it is represented almost exclusively by females, males usually appearing about the end of August. In 1911 and 12 the numbers of *Moina* are too small to have much significance. In 1913 males first appeared on August 27, from which time until the last appearance of the genus on October 26 the ratio was 131 females to 66 males. In 1914, out of a total of 59 individuals taken from August 2 to September 14, no males were observed.

The above data are based on collections from Main Lake only, and, of course, on sexually mature specimens.

Kofoed (1908) finds similarly large variations in the sex ratio of various species of Entomostraca of the Illinois River.

Diaptomus. There are several species of this genus in the complex, but most of them are of only occasional occurrence, *D. sicilis* being by far the most common. No attempt has been made to differentiate the various species in the plankton counts (pl. 22 and fig 24).

Diaptomus is one of the most characteristic forms of the plankton. It occurs in considerable numbers thruout the year, and is,

*See page 44.

**The data for the "summer" periods are as follows: 1911, 7/7-9/11; 1913, 6/21-9/30; 1914, 6/8-9/14 (end of collecting period).

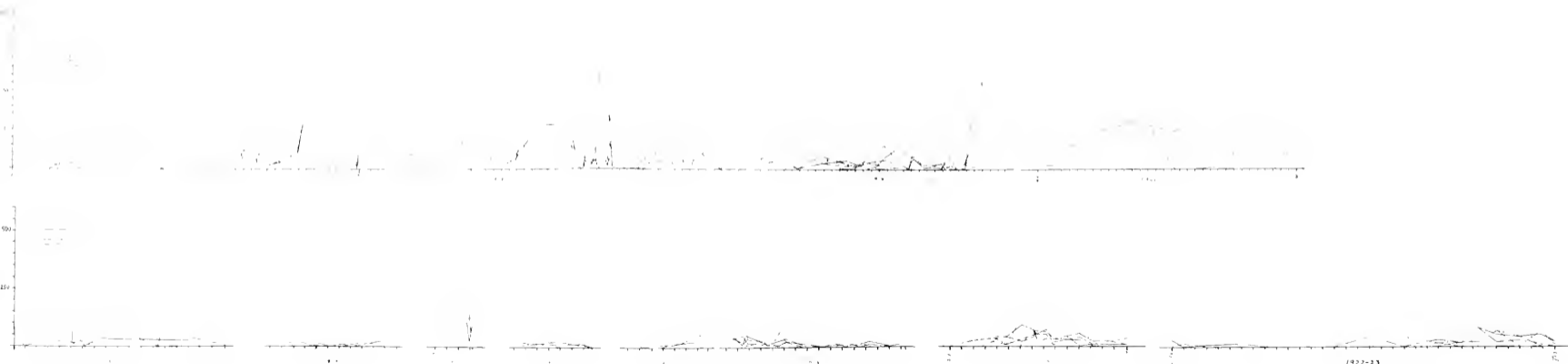
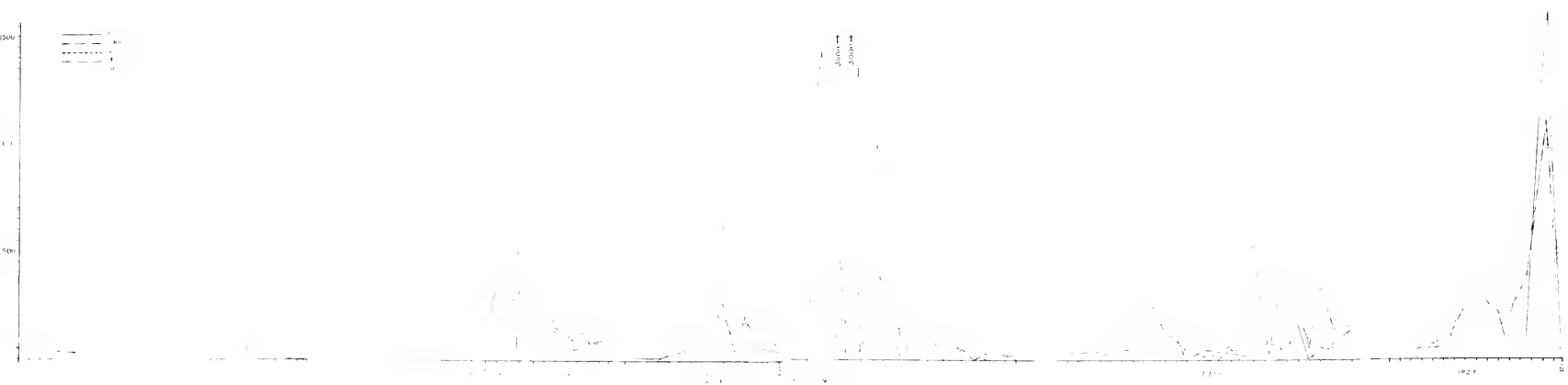


Plate 22. Above: seasonal distribution of Diptera larvae in Main Lake
 Below: seasonal distribution of Diptera pupae in Main Lake



in fact, the only species, either animal or plant, which is not wholly absent from, or very rare in the plankton catches in winter time. The other important genera, Cyclops and Moina, may, at times outnumber it, but are on the whole of secondary importance.

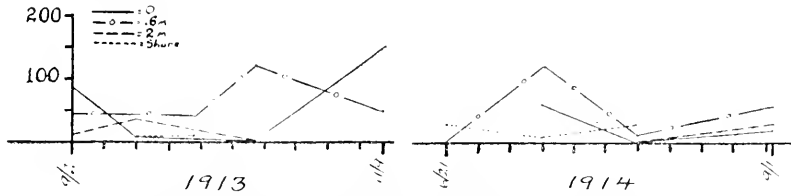


Figure 24. Seasonal distribution of Diaptomus in East Lake.

Its distribution curve shows rather poorly marked maxima and minima. In general, there is a minimum in April-May, succeeded by a maximum in May-June, a minimum in July-August, a maximum in August-September and a minimum in September, with one or more less well defined waves in October-November. Its abundance in fall and winter is in general greater than its minimum number in summer, therefore temperature is not the controlling factor in its distribution. Its waves alternate in a general way with those of the nauplii (pl. 20 and 23), as might be expected, tho in midsummer, when both Diaptomus and Cyclops show maxima, this relation is not very clear.

Diaptomus is interesting as the only genus, either plant or animal, which is common in winter. While its reproduction decreases materially at this season, immature individuals, nauplii (probably of this species) pregnant females and eggs occur occasionally beneath the ice.

From the occurrence of a winter maximum of *D. graciloides* in lake Plön and a summer maximum of the same species in Dobersdorfer lake Apstein (1896) concludes that temperature is ineffective in influencing the development of Diaptomus, and Marsh (1896-97) reaches a similar conclusion. Birge, (1897) on the contrary, considers temperature the chief factor determining the seasonal distribution of Diaptomus (*oregonensis*) in Lake Mendota. Its maxima here occur in the warmer months (May-September) with a great reduction in winter. He states that "it is the first of the perennial Crustacea to slacken its reproductive activity in the autumn and this occurs when food is at its maximum. I can attribute this check only to the fall in temperature. Indeed, my observations show that the reproductive activity of *D. oregonensis* is more promptly checked by the decline of temperature than is that of any other of the perennial species." (p. 326).

My own observations on Devils Lake indicate that the development of Diaptomus is in inverse ratio to the temperature because of

its greater abundance in winter and early spring than in mid-summer. What the factor is which determines the relatively large number present at the former season is impossible to say. After the lake becomes ice-bound there is almost a total absence of algae so that food is very scarce. In Lake Mendota, on the contrary, Birge (l. c. page 320) states that "the food supply is ample." In Devils Lake I believe that the winter population consists of individuals which have developed in the preceding summer or fall; that, due to decrease of temperature and food, there is no active reproduction in winter, but this, on the other hand, reduces metabolism and lowers the death rate and that consequently the numbers remain fairly stationary. The diminution in spring, which in 1923 occurred before the lake opened, is probably due to the death of many of the individuals which have lived thru the winter, possibly due to lack of food. Some of these survive, however, and give rise to a large number of nauplii and adults in May or June.

This genus is frequently colored a deep red, due, apparently, to the presence of a highly colored oil derived from its food, probably diatoms. This was especially noticeable on one occasion (7/13/16) when the water above the grade across Minnewaukan Bay was literally colored red by great masses of *Diaptomus* driven on shore by the wind. This material may be present in the nauplii even before hatching.

Diaptomus sicilis elsewhere is a cold water species, which might explain its greater abundance in winter than in mid-summer in Devils Lake, were it not for the August-September maxima of 1913 and 1914. In 1913 this occurred between 9/1 and 9/8 a period of *high* and *rising* temperature, culminating in a surface temperature of 23 C° at 1 p. m. on 9/6. In 1914, on the contrary, it occurred a week earlier (8/24-8/31) when the temperature was falling* (17° at the surface at 6 p. m. 8/26). It is impossible therefore, from my experience to find any close correlation between temperature and the seasonal distribution of this species. There is probably no *one* factor which determines it, as Robert (l. c.) has pointed out.

Diaptomus sicilis is a widely distributed form, adapting itself readily to a great variety of environments. Hence it is not strange that it should occur even in so brackish an environment as Devils Lake. It occurs more or less commonly in all of the bodies of the Devils-Stump Lake complex and is ubiquitous in its distribution, being present in all parts of the lake, with the exception of the ooze.

Diaptomus shoshone has been reported in one collection (7/27/20) from Main Lake and from Lake P and Spring Lake, and a neighboring pond, not included in the complex.

*See pl. 22.

Diaptomus leptopus piscinac. Reported in one collection from Lake A (9/23/17).

Diaptomus siciloides. This species has been recorded from Main and Stump Lakes and Lake A; in Stump Lake since 1922 only. Prior to this time *D. sicilis* was common as elsewhere in the complex, but appears to have given place to *siciloides* at this time. That this is a case of seasonal succession is unlikely, since the 1922 and '23 collections were made at times (8/25/22 and 7/21/23) when *sicilis* was formerly common. In 1922-23 *siciloides* was apparently as common as *sicilis* had been formerly.

Cyclops viridis americanus. (pl. 20 and 22). *Cyclops* is generally present in much smaller numbers than *Diaptomus*, and, with the exception of the shore records, which are erratic, for reasons already noted, shows little evidence of waves of abundance thru the season. It is almost wholly absent in winter, appears first in the collections in April or May, the time of its appearance varying in different years, and disappears again in November. In 1914 it appeared much later than usual, the earliest record being May 30. The reason for this is not evident. There was no corresponding scarcity of other zoöplaneton this spring and the temperature was similar to that of preceding years. *Cyclops* is seldom abundant and the number present in the spring months is always so few as to have little significance. Their total absence in the early spring of 1914 is nevertheless notable.

It is difficult to locate the time of maximum production of *Cyclops*, because of its general scarcity and the influence of the erratic shore collections. The curves are fairly regular from May to November, with the crest about August 1. In Lake Mendota Birge (l. c.) found *Cyclops brevispinosus* reproducing under the ice. This I have not observed in *C. v. americanus* in Devils Lake. He traces the decline of the former from its spring maximum to lack of food. In Devils Lake there is no evident relation between food supply and abundance of Crustacea, and I suggest as one possible factor in determining the summer maxima and minima, a brief life cycle accompanying rapid metabolism, which in turn is dependent on temperature.*

It is similar in its spatial distribution to *Diaptomus*.

Cyclops leuckarti. I have one record of this species from Lake A, 9/23/17.

Cyclops serrulatus. There is only one record for this species in the complex—Main Lake, 10/2/17. It has also been taken in a neighboring fresh water coulée.

Moina macrocopa (pl. 20 and fig. 25). Appears in the plancton samples about August 1, rises to a maximum about four weeks later,

*See pp. 45 and 90.

disappearing again in October; altho I have a single record for November 4, 1909, and one from a towing on June 24, 1914. This was a female with three nearly developed young in her brood pouch. *Moina* was also numerous in Minnewaukan Bay on July 20, 1916. It forms a relatively small part of the plancton, tho occurring at times in dense swarms in the warm water close to shore.** Generally distributed throughout the lake with the exception of the ooze, where however the ephippia occur in winter. Reported also for Stump, East, Lamoreau and Mission Lakes. In Lake A an indeterminate *Moina* has been reported which is probably this species.

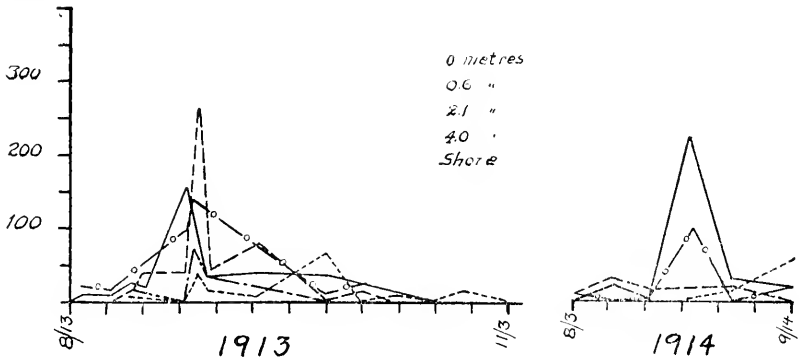


Figure 25. Seasonal distribution of *Moina* in Main Lake.

Daphnia magna. Reported from Minnewaukan Bay in 1916, probably due to the fresh water supply which the latter received in that year. It occurs also in Spring Lake and fresh waters.

Daphnia psittacea. Occurs infrequently in widely separated lakes. One record each from Main, Stump and Spring Lakes.

Daphnia longispina var.? This species has been found occasionally in Main Lake, but the variety has not been determined.

Daphnia pulex? An immature specimen was taken in Main Lake (10/2/17). It occurs also in fresh waters in the vicinity.

Daphnia sp. *Daphnia* occurs in Lamoreau Lake and Lake O, but the species are indeterminate, as only ephippia have been found. One male, sp.?, has also been reported for East Lake (1917).

Ceriodaphnia pulchella, *Simocephalus retulus*, *Alona rectangu-
gula*. *Chydorus sphaericus*. There is one record only for each of the above species—Main Lake, 10/2/17. The last species, however, has been taken in neighboring fresh waters.

Bosmina longirostris. One record from Lamoreau Lake, and one from a fresh water lake in the neighborhood.

**As many as 70,000 per l. See Moberg (1918).

Diaphanosoma brachiurum. Present in East and Mission Lakes in 1911, and one record from Main Lake 10, 2-17.

Marshia albuquerqueensis. Of occasional occurrence. My records show its presence in Main, East, Mission, A and O Lakes, as well as in fresh water. Present in Main Lake occasionally from July 20 to Sept. 6.

There are but three previous records of this species, that of Herrick (1895), Dodds (1920) and Willey (1923a).⁸ Doubtless the examination of other brackish lakes in the western United States would reveal its presence elsewhere. In the Devils Lake complex it occupies a wide variety of habitats, showing its adaptability to widely different conditions. It occurs but rarely in Devils Lake proper, but recently has developed in considerable numbers in East and Mission Lakes.

Marshia appears occasionally in the plankton catches from East Lake, but too infrequently to warrant very definite conclusions regarding its seasonal distribution. My earliest record is May 5 and my latest August 2.

Laophonte calamorum. I have but one record of this species for the Devils Lake complex, from Lake C, Sept. 1917. It has recently been reported by Willey (1923a) as a new species from the Quill Lakes, Saskatchewan, which are quite similar in their chemical character to those of the Devils Lake complex, and in Lake St. John, Quebec. According to Willey the other species of the Laophontidae are strictly marine, but this species has adapted itself to both brackish and fresh water.

Hyallcla azteca. A common form, but not of sufficient numbers to appear, other than occasionally, in the plankton. It occurs in all zones and at all depths of the Main Lake, and is widely distributed thruout the complex, and neighboring fresh waters. It is notably phototropic in its reactions, but, as with other zoöplankton, does not appear to show any relation to light in its distribution. Stereotropism appears to be an important factor in its distribution, for it is frequently found crawling over submerged objects, such as timbers. It is more or less of a scavenger, and is found in large numbers on the bodies of dead birds. In their moist feathers it will live for several days after removal from the water. I have observed it copulating as early as April 15, while the lake was still frozen.

Cypris pellucida. This species has been definitely determined from Main Lake only, but doubtless occurs in other parts of the complex also.

Ostracods occur but rarely in the plankton catches; consequently no attempt has been made to follow their seasonal distribution.

⁸From Devils Lake complex.

They are seldom found in the open water, being restricted mostly to the *Ruppia* zone near shore.

Crustacea may occur in oxygen-free water, together with other animals.*

INSECTA

The aquatic insects of Devils Lake and adjoining waters have been studied by Mr. C. K. Sibley of the Department of Entomology of Cornell University, assisted by Miss Helen Stegenga formerly of the University of North Dakota. A few data have been supplied by Professors C. J. Needham, R. Matheson, Mr. C. R. Plunkett and C. H. Kennedy. Many of the forms, however, are still awaiting specific determination.

With the exception of the corixids and occasional chironomids, the insects of Devils Lake are found in the shore and *Ruppia* zones and in the ooze. While they occasionally occur in the planeton catches, they do so too infrequently to warrant any conclusions regarding their seasonal distribution. Much remains to be done, not only in their classification, but also in a study of their food, reproduction and reactions. The present report can be considered only as a beginning.

Most important, in respect both to variety and number, are the chironomids. Their larvae are present at all times in the year in the ooze, while in summer the most conspicuous insects about the shores are members of this family, which fill the air with their swarms in the evening, and during the day lie hidden in the grass and brush.

Second in importance to the chironomids are the corixids, of which at least two species inhabit the lakes, and which are common everywhere, especially in the *Ruppia* zone.

On the whole, however, the insect fauna of Devils Lake cannot be said to be rich in species, tho plentiful in number of individuals.

Its constituent species are characteristically those of fresh water, tho a species of *Ephydra*, which is a salt and alkaline water form, is common in Main and Mission Lakes.

Several species of dragon and damsel flies naturally occur in the Devils Lake region, but only one, so far as known, breeds in the main lake. This is an undetermined (probably new) species of *Enallagma* with a two-segmented gill, which according to Professor Needham is "unlike anything in our eastern fauna."

Damsel fly nymphs are very common in the shore and *Ruppia* zones of Main and Stump Lakes, and have been taken in Lake O.

*See p. 107.

They probably occur in most of the lakes of the complex, but these are the only records.

Sympetrum corruptum breeds in Lake P, but apparently not in other parts of the complex.

Arctecorixa sp. Common and widely distributed in all lakes of the complex and in fresh water.

Corixa sp. A common species. Reported from Main, Stump, East and Spring Lakes and Lakes A and P.

Corixids are both thermo—and phototropic. I have found them numerous in the open water along shore in spring, when most of the lake was frozen and the shore water was several degrees warmer than that beneath the ice. They are attracted by the light of a lantern, but their manner of response appears to be that of trial and error, not direct.

They are present at all seasons of the year, but while occasional in the plankton samples are not sufficiently numerous to admit of any definite conclusions regarding their seasonal distribution. While occurring in all zones and at all levels, they appear to be more numerous near shore and in the *Ruppia* zone. I have observed them copulating in August and September and have found immature specimens in July and August. In a laboratory they do not live long. Whether this is due to a natural brevity of life, or to the artificial conditions of their environment I cannot say.

Notonecta sp. Prior to 1914 the back-swimmer was occasionally taken in Main Lake. It was present thru the summer and beneath the ice in March.

Notonecta undulata. Reported in Lake O, also in fresh water.

Buenoa margaritacea. A single specimen from Lake P about September 5, 1919, is the only record of this species.

Trienodes flavescens. Larvae were found in Lakes C, O and P and in fresh waters.

Limnophilus rhombicus L. This widely distributed species is the commonest caddis fly in the region. Present in Minnewaukan Bay and in fresh waters (1921).

Phryganea sp. A few caddis fly larvae were found among algae near shore in Main Lake in 1922 by my assistant, Miss Stegenga. This record is of considerable interest because of the very unusual occurrence of caddis larvae in other than fresh water.* Apparently these larvae are not of regular occurrence in Devils Lake, for this is the only record of their presence here. Larvae of *P. interrupta* occur rather rarely in fresh water lakes in the vicinity of Devils Lake.

*See p. 102.

Chironomus. At least three species of this genus occur in Devils Lake, the specific determination of which has not yet been possible.

Midges, including both *Chironomus* and *Protenthes*, are the most characteristic insects in all part of the Devils Lake complex. Of these *P. punctipennis* is probably the most common. They may be seen swarming about the lake shore any still evening in summer or early autumn until after the middle of September. During the day they seek the shelter of the herbage on the shore. Some species as larvae inhabit the *Ruppia* zone, while others live in the ooze, but determination of the exact distribution of the various species, naturally awaits the determination of the latter. Those which inhabit the ooze in the deeper parts of the lakes are frequently in an environment free from oxygen.* Occasionally the ooze inhabitants are found in the upper levels of the lake, probably as the result of wind action. In the ooze the larvae live in tubes.

Midge larvae of probably more than one species occur rarely in the plancton samples, not being normally inhabitants of the open water. The cast pupal skins frequently occur in large numbers on the surface of the lake, and especially on shore where they are driven by the wind.

Thienemann (1918-20) has classified lakes faunistically as 1) *Chironomus*, 2) *Chironomus* plus *Corethra*—and 3) *Tanytarsus* lakes; the first being characterized by the presence of the red *Chironomus* larvae at the bottom, the second by the presence of *Corethra* larvae in addition to those of *Chironomus* and the 3) by the absence of the two former and the presence of the larvae of the *Tanytarsus* group of chironomids (i. e. *Lauterbornia*). In the first of these the oxygen content of the bottom water in summer ranges from 35 to 50% of saturation; in the second it lies below 37% and in the third above 50%.

Thienemann asks whether his classification is of universal application or not. It appears to apply nicely to Devils Lake, which belongs in the first group above mentioned (i. e. *Chironomus* lakes). Neither *Corethra* nor *Tanytarsus* occur here, and the oxygen content is probably often zero in the ooze where these midge larvae live. This ooze is probably frequently aerated by wind action in summer, but the oxygen content quickly drops upon subsidence of the wind, in consequence of the oxydation of the large amount of organic material which it contains. In early spring also, before the melting of the ice, the bottom water may be oxygen-free as already noted.*

Tanytus sp. Recorded only from Lake P and a fresh water pond in the vicinity.

*See pp. 106-7.

*See p. 30.

Procladius sp. Several specimens, examined by Prof. Needham, were taken in a surface tow in Creel Bay on July 6, 1911. "Apparently a new species," but impossible of determination because of poor condition.

Sayomyia sp. One specimen was taken in a surface tow near Bird Island, July 31, 1911.

Odontomyia sp.

Stratiomyia sp.

Soldier flies include two indeterminate species, both of which are common as larvae in shallow water near shore among decaying vegetation, and as pupae in decaying vegetation and under logs and stones along shore. They have been taken in Main, Lamoreau and Stump Lakes and Lake P, as well as in fresh waters.

Nemotelus sp. Taken in Main Lake, Lake P and a fresh water pond near Stump Lake.

Tabanus sp. Adult horse flies are common in the Devils Lake territory. "Larvae and pupae were quite common in the sand at the waters edge" in Main and East Lakes and a fresh water pond near Stump Lake.

Chrysops sp. Deer flies are exceedingly common in all of the Devils Lake territory. The larvae occur in "sand at the water line." They are not common in the alkaline waters of the complex, and probably develop mainly in fresh waters.

Eristalis tenax Rat-tailed maggots are common in decaying vegetation along the shores of the main lake and Lake P.

There are several species of beetles in the complex, but it has not been possible to obtain identifications of most of them.

Octhebius sp. is common and widely distributed thru the complex.

Bidessus lacustris. This and the following genus has been determined by Dr. R. Matheson of Cornell. I have one record from a surface tow near the station on July 14, 1911.

Coelambus. Two undetermined species were taken in the same collection as the above. *C. nubilus* has been taken in Lake N.

Deronectes sp. Common thruout the Devils Lake complex. Occurs also in fresh waters.

Berosus sp. "Larvae were numerous" at the grade across Minnewaukan Bay, "and in a fresh water pond north of East Lake." (1921).

Hydrous triangularis. "Larvae were common at the Minnewaukan grade" and in fresh waters (1921).

Tropisternus sp. "Larvae were found at the Minnewaukan grade." and in Six-Mile Bay, also in fresh waters. (1921).

Agabus sp. There is one record only (Creel Bay 4/21/23).

Philhydrus sp. This is the common hydrophilid of Devils Lake. All stages were found. The species was also present in Lake A, Lake P, Stump Lake and a fresh water pond.

HYDRACARINA

There are several species of mites in the Devils Lake complex, as yet only partly identified. Dr. Karl Viets has determined *Hydrachna schneideri* and *H. valida*, both from Main Lake, the former from Spring and C Lakes also. One specimen of *Diplodontus despiciens* from Spring Lake has been identified by Prof. Ruth Marshall, while Prof. R. H. Wolcott has found a third species of *Hydrachna*, as yet undetermined, in Main Lake. *Eylais* sp. occurs rather commonly in Main Lake and *E. extendens* has been taken in Lakes Spring and P. A single specimen of *Hydryphantes* was found by Prof. Wolcott in a collection from a shore pool close to the lake edge. The latter was probably formed in part by rain and partly by wash from the lake, from which the *Hydryphantes* undoubtedly came.

Mites are fairly common in Main Lake but do not occur in sufficient numbers in the plankton samples to give definite records of their seasonal distribution.

Other than Main Lake I have recorded mites from Spring Lake and Lakes C and P only, but they doubtless occur elsewhere in the complex.

FISH

At present there is but a single species of fish inhabiting Devils Lake, the stickleback (*Eucalia inconstans*), altho previously it is reported to have swarmed with pickerel (*Esox lucius*?), and Lord (1884) reports the "shiner," and Pope (1908) the minnow (*Pimephales phomelas*) as occurring here.

The reasons for the disappearance of fish from Devils Lake are probably primarily the increase in concentration of the lake water, and secondarily the loss of suitable breeding grounds for the pickerel, thru the cutting off of the coulée which formerly flowed into Minnewaukan Bay, but which in recent years has only done so exceptionally. The ruthless destruction of the pickerel by the fishermen was probably a contributing cause, and there is some evidence (but very uncertain), from the accounts of early observers, of an epidemic among the fish.

Since 1908 numerous experiments have been made in the introduction of various species of fish (chiefly yellow perch—*Perca flavescens*) into Devils Lake, but without any permanent success, and on the tolerance of fish for several different salts in varying concentrations.*

In another part of this report** I am discussing briefly the

*See Pope (1908), Brannon (1911, 1913) and Young (1923).

**See p. 106.

great difference in tolerance for salt concentration shown by various species of both plants and animals in the Devils Lake complex, and need not consider it further here.

The stickleback occurs in both Main and Stump Lakes and probably in other lakes of the complex, as well as in fresh waters. It was formerly common in Main Lake, but appears to be much less so at present. In the summer of 1914 several were found dying in the lake, for a reason which could not be ascertained. The temperature of the water at the time was not higher than probably occurs frequently in lakes where the stickleback abounds, and bacteriological examinations made a few hours after death gave no evidence of pathogenic bacteria in the fish.

In 1912 also the sticklebacks were found dead in large numbers on shore in spring about the time of opening of the lake. The cause of this fatality also is obscure. It is possible, altho it seems unlikely, that the fish may have been trapped in the ice and frozen to death. Lack of oxygen will hardly account for it, since it always appears to be ample, thru the greater part, at least, of the water stratum.

The freezing of a layer of water a metre thick in a lake only 6 or 7 metres deep necessarily causes a great concentration of salts in the remaining water, and it is possible that the weaker sticklebacks were unable to withstand this increased concentration; and further that their death in summer may have been due to salt concentration, coupled with high temperature.

In recent years their death has not been noted, altho they appear to be present in considerably diminished numbers.

They breed in the *Ruppia*, nests with eggs having been found during late June and early July.

AMPHIBIA

Two amphibians occur in Devils Lake, the pickerel frog (*Rana pipiens*) and the salamander (*Amblystoma tigrinum*).

The former of these is occasionally common about the edges of the lake and has been taken in Stump Lake, while the latter is a regular inhabitant of its waters. Neither species, so far as known, breeds in the lake.

The salamander was reported by Pope (1908) as *Cryptobranchus allegheniensis*, and later reported by me (Young 1912) as *Amblystoma*. They occur both as larvae and adults. Some of the adults are unusually large, measuring 25 to 28 cm in length.

There are numerous small fresh water ponds, ditches and swamps in the Devils Lake complex, which in spring are usually full of water, and which probably serve as breeding grounds for both frogs and salamanders. In one of these, near the south end of Stump Lake, the salamanders breed abundantly.

The ability of frogs and salamanders to tolerate the highly concentrated water of Devils Lake, is of great interest, in view of the inability of most species of fish to live therein. Further consideration of this question is given below.*

AVES

In his recent report on the birds of North Dakota Wood (1923) lists 67 species of water birds at Devils Lake, divided among the following orders: Colymbiformes, 6; Ciconiiformes, 5; Anseriformes, 23; Charadriiformes, 33.

While birds are not, properly speaking, a part of the life of a lake, they nevertheless play an important part in its bionomics by feeding extensively on the insects and other organisms which it contains.

MAMMALS

The only mammal present in Devils Lake, other than accidentally, is the muskrat, (*Fiber zibethicus cinamominus*). This is frequently seen swimming in the lake, and what are undoubtedly its burrows may be found occasionally on the shore, but I have never seen any of its "houses" in the lake. It is not numerous, and plays a minor role in the biology of the lake.

PARASITES

There are of course several parasites infecting various members of the Devils Lake fauna, but no study has been made of them. While, in a broad sense, they might be considered members of the fauna, in a stricter sense, they are not, since their habitat is determined for them by their hosts, and is not, at least so far as known, influenced by the physico-chemical environment of the water in which the hosts may happen to live.

DISCUSSION OF RESULTS

Devils Lake is interesting as well for what it does not, as for what it does contain. Derived from an originally fresh body of water, it probably at one time contained representatives of all the larger groups of fresh water animals. At present there are no members of the sponges, celenterates, nemerteans, annelids, bryozoans, molluscs or reptiles in the alkaline waters of the complex, altho sponges, leeches and molluscs and turtles occur in some of the fresh water ponds, which at one time were part of Devils Lake. Thus far no hydroids, nemerteans or bryozoans have been found in any part of the complex, either alkaline or fresh. Large numbers of snail shells, including several species occur along the shores of Devils Lake, but apparently no living species at present inhabit its waters. At one point, in a gravel bed, many mussel shells occur, evidently remains of a former fresh water fauna.

*See p. 106.

Among the plants all of the larger groups are represented, but the flowering plants by practically only a single species. While both fauna and flora have more fresh than salt water affinities, there is one genus (*Chaetoceros*) and several species, which are typically marine or brackish water forms.

But while the fauna and flora are characteristically fresh water, a comparison with those of fresh waters elsewhere reveals several striking differences. Here, as in brackish water elsewhere, the blue-green algae play a predominant role, while the diatoms and desmids, which often form so important a part of the plancton, are here, with the exception of the marine genus *Chaetoceros*, very irregular in occurrence and comparatively small in number, altho of the diatoms a large variety of species occur. *Nodularia*, which at certain seasons is one of the most abundant plants in Devils Lake is seldom met with in fresh water, while forms such as *Aphanizomenon*, *Aphanocapsa*, *Clathrocystis* (*Microcystis*), *Oscillatoria*, and *Anabaena* are either absent or of wholly minor importance.

Of the Protozoa there are none of importance in the plancton, and some forms, such as *Ceratium*, *Synura* and *Dinobryon* which in other waters are often so abundant, appear to be wholly absent here: while the scarcity of shell-bearing rhizopods is noteworthy.

The number of important species of rotifers and Crustacea is comparatively few, there being but three of each. Among the former *Brachionus satanicus* and *B. plicatilis spatiosus* are new, while *Pedalia fennica* has hitherto been reported from only a few localities. The rotifers which are usually most important in fresh water are here either absent or of secondary importance. In their examination of a large number of lakes in the northwestern United States Kennerly et al. (1923), report *Pedalia** from only one—Medical Lake, Washington, which is so "distinctly alkaline" that "no fish will live there for any period of time."

The Crustacea are likewise signalized by the absence or rarity of several animals, chiefly Cladocera (*Daphnia*, *Bosmina*, *Leptodora*, etc.) which are characteristic of the plancton of fresh water lakes in general.

Of the nine orders of insects which Needham and Lloyd (1916) give as common in inland waters four (Plecoptera, Ephemera, Neuroptera and Lepidoptera) have not been found in the Devils Lake complex, while the Odonata and the Trichoptera are represented by a single species each.

Comparatively little work has yet been done on the alkaline lakes of North America, so far as I am aware. Recently Huntsman (1922), Willey (1923a) and Bailey (1922) have made a brief survey of the Quill Lakes in central Saskatchewan, which shows a striking

*Species not given.

similarity of fauna and flora in these lakes, as compared with Devils Lake, in correspondence with their similarity in physical and chemical characteristics.

Like Devils Lake, the Quill Lakes are shallow and of high salinity (about 11000 ppm. of total solids in Little Quill and 16500 in Big Quill). The study of the Quill Lakes has been too brief to permit of any comparison between their life and that of Devils Lake, either as to quality or quantity, but a few points may be noted. In both *Diatomus sicilis* appears to be the principal crustacean with *Hyalella azteca* a common species. *Cyclops viridis* is represented in Devils Lake by var. *americanus* and in the Quill Lakes by *pareus*. *Laophonte calamorum*, a new species from the Quill Lakes, occurs in the Devils Lake complex, altho it has not yet been found in the main body of Devils Lake. The Odonata are represented in Devils Lake by *Enallagma* sp. and in the Quill Lakes by *E. calverti*? It is interesting to note the presence of caddis fly larvae (*Phryganea interrupta* in the Quill Lakes and what is probably the same species in Devils Lake) as these are characteristically fresh water inhabitants.

The presence of numerous gastropod shells along the lake shores, but the absence of their occupants in the water is noticeable in both regions.

Sticklebacks are the principal species of fish in both waters, but the presence of other species in the Quill Lakes and their absence from Devils Lake is a noticeable difference.* In both regions the sticklebacks are frequently infected with large tapeworms in the celome, the identity of which has not been determined.

The algae reported from the Quill Lakes are, in most cases, species occurring in Devils Lake. Of particular interest is *Nodularia spumigena* which is abundant in the Quill Lakes and is one of the characteristic forms in Devils Lake, but is not common elsewhere. Of much interest also are the diatoms. Seven of these, which are characteristically marine types, are reported by Bailey (1922) from the Quill Lakes, of which three, either identical or closely related forms (*Chaetoceros*, *Surirella striatula* and *ovalis*) are common to both regions.

Among the sandhill lakes of Nebraska are found waters of similar character to Devils Lake, the algae of which have been studied by Andersen and Walker (1920).

Detailed analyses of these lakes are not available, but they range from comparatively fresh waters (111 ppm. of "alkali") to highly alkaline ones (1129 ppm.). While the depth of only one is given, they are apparently all shallow (under 3 m.) Since the periods and localities of collection were not the same in all, an exact

*For a further discussion of this question see Young (1923, pp. 387-8).

comparison of their algae is impossible, but, in general, the alkalinity appears to be a limiting factor in the distribution of these plants, the higher the amount of alkalinity the smaller the number of species. Big Alkali lake with 622 ppm. of "alkalinity" is probably most like Devils Lake, but as this was visited only once, only a very superficial comparison of their algae is possible. Of 26 species recorded from this lake 16 occur in Devils Lake and every genus is represented except *Chara*.

Recently Moore and Carter (1924) have extended the survey of the former (Moore, 1917) to include about 70 lakes in central North Dakota, including both fresh and alkaline types. As a result of this study these authors conclude; "that as far as the Myxophyceae are concerned the 'alkaline' lakes are considerably richer in species than the 'freshwater' lakes. On the other hand a definite 'bloom' was rarely developed in strongly alkaline waters, whereas in several of the 'freshwater' lakes there was frequently a copious 'bloom' consisting of *Clathrocystis aeruginosa*, or sometimes of *Aphanizomenon flos-aquae*, one or other of these species being dominant, and often the only representative of the Myxophyceae in the sample. In the alkaline lakes there was never such a pronounced development of a single species of *Oscillatoria*, *Nodularia spumigena*, *Arthrospira Jenneri* and *Spirulina* spp. The tiny species *Rhabdoderma sigmoidea*, described here for the first time, also occurred in some of the alkaline lakes as a dominant constituent.

With regard to the Chlorophyceae, the condition is reversed. Many of the species seem to be very intolerant of increasing concentration of salts, and are therefore eliminated from the flora of the strongly alkaline lakes. On the whole the Conjugatae are very poorly represented, as pointed out by Moore (l. c., p. 302), although a few species are able to thrive under the unusual conditions. The genus *Oocystis* seems to maintain itself satisfactorily in the alkaline waters, as do also some species of *Scenedesmus*, *Pediastrum*, and *Dictyosphaerium* spp. Many of the Protoceceles commonly found in freshwater plancton are not represented at all, however, in lakes of the 'alkaline' group.

The 'alkaline' lakes were conspicuous by reason of their paucity of species, the richest lakes of this type containing only 5-9 species, whilst some of the 'freshwater' lakes had as many as 12-17 species.'

While the number of species inhabiting Devils Lake is rather restricted, especially in certain groups; the number of individuals of a few species is large. This is especially noticeable in the case of the rotifers *Brachionus* and *Pedalia* and in that of the Myxophyceae, *Nodularia* and *Coelosphaerium*. It is quite possible that the paucity of certain species, thereby restricting competition, has permitted a greater development of others than would otherwise have occurred. More important factors, however, are probably the favor-

able physical environment, the shallowness, and the lack of inlet or outlet to the lake. Shallow lakes, in general, are better plancton producers than deeper ones, and Devils Lake is no exception to the rule. It is well known, also, that certain temporary pools, may, at times, be swarming with life, while in bodies of changing water, especially rivers, the number of organisms is frequently much less.

A comparison of the amount of plancton in lakes and rivers is difficult to make because of the great individual differences between different bodies of water, due to various factors. Thus Birge & Juday (1922) in their study of three Wisconsin lakes* found that the total amounts of dry net plancton in milligrams per cm. ranged from 491 for Mendota to 2182 for Waubesa, while the corresponding amounts for centrifuged material ranged from 3090 to 5665. Apstein (1896 p. 92) found variations running from 4.5 cc. pr. cm. to 454.3 cc. and similar variations have been found by other authors.

A comparison between the amount of plancton in lakes and rivers made by Whipple (1914, p. 20), in spite of great individual variation, shows clearly enough the relative paucity, of plancton in many streams as compared with lakes.

Kofoid (1908), however, records amounts of plancton for the Illinois River,* which compare favorably with the figures for most lakes. So much depends on the individual character of the water in question that it is unsafe to generalize too broadly.

A comparison between the plancton production of Devils Lake and that of other waters is difficult to make because different workers have used different methods of expressing their results, and in many cases, moreover, the period of observation is too brief to enable one to draw any conclusions concerning maximum, minimum or average productivity of the water in question. Some data are, however, available and may be of interest. The average number of Crustacea (incl. nauplii) in Devils Lake for the periods of collection from 1911 to 1923 inclusive is 228,000 pr. cm. From table B in Birge (1897) I have computed the average for Lake Mendota in 1895-96 as 37,350 pr. cm. In each case the average was obtained by adding all the collections for a given date and dividing by their number. From the data given by Birge & Juday (1914, '21) I have computed the averages for Canandaigua, Cayuga, Hemlock, Otisco and Seneca Lakes, N. Y. and Green Lake, Wis., the maximum of which is 67,800 pr. cm. in Otisco Lake on August 16, 1910. It should be borne in mind that these averages are for very few collections; for Hemlock, Green and Otisco Lakes, only one; and for the others three each.

The rotifer average for Devils Lake for the same period is 350,000 pr. cm., while, for the reproductive season only, the average

*Mendota, Monona, Waubesa.

*See Kofoid, p. II, p. 16.

is 560,000. The maximum for the lakes studied by Birge & Juday was about 40,000 pr. cm. for Cayuga Lake, while the others were distinctly lower.

In a recent paper by Kemmerer et al. (1923) there are data for 51 lakes in the northwestern United States. I have computed the averages for a few of these, chosen more or less at random, but including both deep and shallow lakes. The maximum number of Crustacea was 212,400 for Calvert Lake, Washington, a small lake about 12 m. deep. The other lakes ran very much lower than this. The rotifer maximum for these lakes was 34,000 pr. cm. in Cottage Lake, Washington on August 13, 1913. Here, too, it should be remembered that these averages are, in most cases, for only a single series of collections.

The data for the nanoplaneton have, in most cases, been based on net collections, and hence are much below their true values. Birge & Juday (1923), however, give some data from centrifuged collections. Neither method, however is closely comparable with the Sedgwick-Rafter method, which stands between the other two in respect to the amount of nanoplaneton recorded by it.

The average number of diatoms in Devils Lake for the years 1911-14 inclusive is 50,000 pr. cm. which is higher than most of the figures recorded by Kemmerer et al. (l.c.),* altho in a few instances their figures are very much higher. It is in every instance far below the figures given by Birge & Juday (1921) for their centrifuged samples, and in several cases lower than their results for the net planeton.

I have attempted no comparison for the other algae for the additional reason that many of my results are in "standard units,"** or mm., while other authors state their results in colonies or filaments.

Devils Lake may be compared to a large pool, where, finding conditions favorable to existence, and little competition, and there being no flow to carry them away as they multiply, certain types of life have developed extensively; while others have developed slightly, or not at all, in an environment, which is unfavorable to them. Rate of reproduction enters here, of course, as an important factor, and the whole question is complicated and obscure.

The study of the lake has revealed new species as follows: Protozoa—*Urotricha labiata*, *Gerda annulata*, (Edmondson 1920); Diatoms—*Chaetoceros elmorei*, *Navicula minnewaukonensis*, (Elmore 1921); Rotifiers — *Brachionus satanicus*, *B. spatiosus* and *B. pterodinoides*, (Rousselet 1911, 12 & 13); while several hitherto known

*In Upper Klamath Lake, Oregon, on July 29, 1913 there was the large average of more than 20,000,000 pr. cm. This is a shallow lake in most of its area, with a maximum depth of about 11 m.

**See Whipple (1914).

only from other continents have been found to occur here. These include: *Tetrapedia gothica*, previously known only from Germany, *Characium hookeri* from Europe and *Asplanchna sylvestrii*, previously recorded only from Chile, so far as I know.

The difference in tolerance of different types of life to waters of various salt concentration opens up a wide field of interesting experiment and speculation. I have already (Young 1922) discussed this question at some length in connection with experiments on fish. These, and other experiments indicate, not only considerable specific, but also individual differences in resistance to unfavorable environment.

In his paper on the African Lakes Cunningham (1920) has pointed out the absence or rarity of certain species of animals and plants in Tanganyika and Kivu, which occur in other lakes of Central Africa, or even in tributary streams.

Thus, with the exception of an occasional isolated specimen there are no Cladocera in the two former lakes, altho they occur in the Lofu River, one of the tributaries of Tanganyika, and in Lakes Nyasa, Victoria, Albert and Edward Nyanza. Rousselet* records 23 species of rotifers from the river and only 10 from the lake, only one of which was common to both lake and river; while West* found 30 species of phytoplankton in the river, but one of which was present in the lake.

Cunnington seeks an explanation for these facts in the saline character of the water of both Tanganyika and Kivu. He gives no analyses of either, but states that the amount of magnesium salts is high, altho Tanganyika water is "fresh."

In the absence of adequate data no satisfactory comparison can be drawn with the water of Devils Lake. The character of the three waters is probably somewhat similar, however, since in all of them magnesium salts are present in considerable quantity. In Devils Lake, however, these salts have not excluded the Cladocera, nor apparently restricted the rotifers. Some species are, however, so restricted. The scarcity of the Conjugales** and the shell-bearing rhizopods is noteworthy,** and there are several groups present in Tanganyika which are wholly unrepresented in Devils Lake.*** It is doubtful then if salinity alone will explain these deficiencies in the fauna of the African Lakes and what the explanation is remains obscure.

The presence of animals in the oxygen-free ooze at the bottom of lakes is a discovery of great physiological interest, since it has generally been regarded that oxygen is a sine qua non for the exist-

*Fide Cunningham.

**See Moore (1917) and Edmondson (1920).

****Gastropoda*, *Lamellibranchiata*, *Polyzoa*, *Maerura*, *Brachyura*, *Brauchiura*, *Oligochaeta*, *hirudinea*, *Hydrozoa* and *Porifera*. Of the above those italicized occur also in Kivu.

ence of animal life. Recently, however, Juday (1908) has found many species of animals living in the bottom of Lake Mendota, including several Protozoa, rotifers, annelids, crustaceans, insect larvae, a nematode, and a mollusc. Juday has shown very clearly the absence of dissolved oxygen in the bottom water of Lake Mendota at certain seasons, both by boiling and titration tests.

In my own work on Devils Lake I have used exclusively the latter method, which, as already noted,* is probably not very accurate in alkaline water. The decaying character of the ooze, which has a very foul odor, is strong presumptive evidence, however, which, together with the titrations and the results of Juday's work, renders it practically certain that the bottom ooze of Devils Lake is frequently oxygen free.

In this ooze I have found several species of Protozoa and a red Chironomus larva, while in the water immediately overlying the ooze, which showed no oxygen by titration, I have found Diaptomus, Moina, Cyclops and nauplii, in addition to the Protozoa. These animals may, however, have been temporary invaders of this layer, which is never very thick.

As yet we have no satisfactory explanation of the way in which these animals live in an oxygen-free environment, the various explanatory theories have been advanced, which have been discussed at some length by Cole (1921).

In any study of distribution of either animals or plants, one finds some wide-spread, adaptive species, and others of restricted distribution. The latter may not necessarily be non-adaptive, however, since the question of ease of dispersal enters into any problem of distribution.

The questions of adaptability and dispersal lead up to that of the source of the life of Devils Lake. While it is possible to trace with a fair degree of probability the origin of land floras and faunas, from the distribution of both living and extinct forms; this is much more difficult in the case of aquatic organisms, especially those of the plankton; because of their ease of dispersal and consequent wide spread distribution; their great adaptability, in many cases, to widely different environments, and especially to our lack of knowledge concerning the distribution of many of them.

Thus, in at least three cases, in the present study** organisms have been recorded for the first time in North America, and in a recent paper on the algae of several other North Dakota lakes by Moore and Carter several other species are recorded as new to America.

Diaptomus sicilis has hitherto been considered as a cold water species. Thus, according to Marsh in Ward & Whipple (1918) it oc-

*See p. 30.

**See p. 106.

curs commonly in winter in Green Lake, Wis. but is rare in summer; but is found in the cold waters of the Great Lakes thruout the summer. In the Devils Lake complex, however, it is common at certain times in summer at high temperatures.** *Brachionus plicatilis* is given as a marine and brackish water form in Brauer (1912), but here it occurs in both fresh and alkaline waters. These instances might be multiplied, but are sufficient to illustrate how much we have yet to learn regarding the distribution and adaptation of aquatic life.

It is unsafe therefore to attempt at present any delimitation of life zones, or to draw conclusions regarding the origin of any fauna or flora, based upon their planeton components.

This opinion agrees with that of other workers in this field. Thus Jennings, in Ward & Whipple (1918), emphasizes the essentially cosmopolitan character of rotifers, whose distribution is determined by the character of their environment, rather than its geographical position; while the former factor is ineffective in the case of many species, which can inhabit fresh and brackish, or even sea water alike. And Edmondson (1912) in his account of the Protozoa from some high mountain lakes in Colorado, says (p. 67) "By comparing the following list with the protozoa reported from sea-level in tropical Tahiti (*Science*, September 9, 1910), there will be seen not only the latitudinal but also the great altitudinal range which many of our species have." In a letter to the writer (August 21, 1923) Prof. C. J. Elmore who has worked on the diatoms of Devils Lake says:

"I have never been able to find that certain species of diatoms are northern and others southern. A good many species that are common in this region (Nebraska) were first described as Arctic diatoms . . . As to locality, I have found just the same species in collections from India that I find at home."

Birge, in Ward & Whipple (l. c.), says (p. 687) of the Cladocera, "The geographical distribution . . . offers little of interest that can be stated in a brief sketch, chiefly because the species are so widely distributed. Some are . . . cosmopolitan. A majority (of those) found in this country are found also in Europe." *The study of our forms has not gone far enough* to enable us to speak of the local distribution of each species within the area which it covers, but it is known that the rare species are very irregularly distributed. On the whole the fauna of the various regions of the country is strikingly similar, but with some forms peculiar to each region.

Sharp in the same place says (p. 800) "Owing to the variations in habitat, and the vicissitudes to which most fresh water

**Over 20° C.

Ostracoda are subject and because of the variable and inconstant nature of their surroundings, it is almost impossible to work out their exact distribution."

So far as I am aware the only attempts which have been made thus far to compare the zonal distribution of plancton with that of higher animals have been those of Dodds (1920, 1924) in his papers on Entomostraca and life zones in Colorado, who found (1920, pp. 104, 5) that "The zonation is definite, even though the present collections do not enable us to discriminate between all of the colder zones. It is equally difficult, on the basis of our present knowledge to sharply differentiate these same zones in their continental extent in Canada and northern United States . . . Though these zones have been established and defined on the basis of organisms other than Entomostraca, yet the agreement is striking and real and extends even to common species inhabiting the same zones in localities hundreds of miles apart and separated by many degrees of latitude."

Marsh also in his chapter on the copepods in Ward & Whipple (1918) points out the influence of temperature in limiting the distribution of certain species, but not of others.

If we attempt to determine the life zone of Devils Lake or the origin of its fauna on the basis of its entomostracan population we find that the majority of its species are wide spread or cosmopolitan in their distribution. These include the three species of Cyclops (*viridis*, *leuckarti* and *serrulatus*) and the Cladocera, *Bosmina longirostris*, *Moina macrocopa*, *Daphnia longispina*, *psittacea*, *pulex* and *magna*, *Diaphanosoma brachyurum*, *Ceriodaphnia pulchella*, *Alona rectangula*, *Chydorus sphaericus* and *Simocephalus vetulus* and the ostracod *Cypris pellucida*. *Diaptomus sicilis* has hitherto been considered a cold water type restricted to the Great Lakes and adjoining waters. Recent studies, however, have extended its area westward to Devils Lake and northward into central Saskatchewan (Huntsman, 1922).

D. leptopus piscinae occurs thruout the northwestern United States, Alberta and Manitoba. *D. shoshone* occurs in mountain lakes of the western United States and southern Canada. "The occurrence in Devils Lake is interesting in that it is out of the mountains and is the most easterly location that has been reported."* Its presence here brings it into the transition zone.

D. siciloides. Its occurrence in the Devils Lake complex is the most northerly yet recorded bringing this species into the transition zone from the south.

*Letter from Dr. C. Dwight Marsh to the writer.

Marshia albuquerqensis has hitherto been reported only from New Mexico** (Herrick and Turner 1895) and Colorado (Dodds, 1920). Our present knowledge regarding its distribution is too limited to consider it in attempting to determine the zonal position of the lake or the origin of its fauna.

Laophonte calamorum. This species, recently described by Willey (1923 a), is evidently widely distributed in both fresh and alkaline waters, having been found thus far in the Quill Lakes, Saskatchewan, Devils Lake, N. D. and Lake St. John, Quebec.

The origin of the fauna and flora of Devils Lake must be traced back to the days of the old glacial lake Minnewaukan when the latter was a part of the Mississippi drainage basin. At this time it was possible for both northern and southern forms to have entered directly, and without any carriage by birds or any air blown dust, etc. Later, with the loss of this connection and the establishment of one into Lake Agassiz, only northern elements could enter directly, and this condition remained after the retreat of Lake Agassiz and while Devils Lake was draining through the Sheyenne River into the Red River. The loss of this outlet has been comparatively recent. Since then additions to the fauna and flora must have been thru outside agencies.

The foregoing facts indicate then that the fauna and flora of Devils Lake are in general widespread in their distribution and undoubtedly have come from many sources.

At present the life of the lake is distinctly fresh water in character with, however, a considerable admixture of brackish water forms. The species are for the most part cosmopolitan in their distribution. Of those types with restricted distribution it is difficult to say whether northern or southern ones predominate, until we have fuller information regarding the distribution of aquatic animals and plants.

The fauna and flora, moreover, are not static, but are changing from year to year with the changing character of the various lakes in the complex. Thus, as already pointed out,* *Filinia longiseta* has apparently disappeared from Main Lake with the gradual increase in concentration of its water. Similarly the Crustacea, with the exception of *Marshia*, have apparently disappeared from East and Mission Lakes in recent years, while the latter, on the contrary, has increased in numbers (1922).

No careful study has been made of these changes, but the above data are sufficient to demonstrate clearly the great changes that are taking place.

**In his publication Herrick apparently does not mention the locality. Marsh, however, in Ward & Whipple (1918, p. 780) gives it as New Mexico.

*See p. 86.

CONCLUSIONS

1. The Devils Lake complex comprises a series of large shallow pools of alkaline water; which were originally parts of a large, deep, fresh water lake; in which certain organisms, finding conditions favorable for their existence, develop at certain times in enormous numbers: while other organisms, though present in adjacent waters, are rare or absent.

2. Conditions in the different parts of the complex vary, especially in respect to depth and chemical character. In response to these changing conditions marked changes in their faunas and floras have occurred and are progressing.

3. The character of these latter is that of fresh water, being distinguished therefrom rather by the absence of many fresh water species, than by the presence of many brackish or marine types, tho a few of these occur.

4. The source of fauna and flora is manifold. They are not characteristic of any particular region, but are rather cosmopolitan in aspect.

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