TRANSACTIONS

OF THE

WISCONSIN ACADEMY

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VOL. XXXIII

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Contents

THE GEOLOGY, GROUND WATER AND LAKE BASIN SEAL OF THE REGION SOUTH OF THE MUSKELLUNGE MORAINE, VILAS COUNTY, WISCONSIN

W. A. Broughton

Introduction

The material for this report was gathered under the direction of the Wisconsin Geological and Natural History Survey. The field work was done during the months of July and August, 1937 and during August, 1939. The work was confined mainly to that part of Township 40 North, Range 7 East which lies south of the Muskellunge Moraine and north of Arbor Vitae Lake. In 1937, the investigation was supported by a grant of funds from the Wisconsin Alumni Research Foundation.

This report considers the glacial geology of the area, lake water and ground water analyses, lake elevations and the character of the deep drift. A discussion of the possibility of lake basin seal and the source of the calcium carbonate content of some of the lake waters is given. The elevations of the lakes were determined, under the direction of the writer, by students of the Armour Institute of Technology who were in training at the summer camp at Trout Lake. The chemical analyses of the water samples were made by chemists at the Wisconsin Geological and Natural History Survey Laboratories at Trout Lake.

Helpful suggestions and criticisms were received from the State Geologist of Wisconsin, E. F. Bean, and Professors W. H. Twenhofel, F. T. Thwaites and C. Juday.

Geology of the Area

There are no bedrock exposures in the area and the surface everywhere is underlain by glacial material. The bedrock underlying these glacial deposits is probably almost entirely crystaline rock of Pre-Cambrian age. (Thwaites 1929.)

5

Moraines

The area studied is bounded on the north by the Muskellunge Moraine, which is a high, narrow, elongate, recessional moraine extending in an east-west direction. It rises about 200 feet above the surrounding outwash and its highest part is 1847 feet above sea level. It is made up of large and small coalescing knobs. Numerous small kames and deep kettles are scattered along the moraine. Road cuts show the till to be composed mainly of a heterogeneous mixture of coarse and fine fragments of pink and grey granite, rhyolite, basalt, gabbro, gneiss and schist. A large quantity of vein quartz and lesser amounts of quartzite, sandstone, jasper, red slates and iron formation are also present. There are occasional cherty pebbles, but no limestone or dolomite, which indicates that this is a part of the "non-calcareous drift". Lying on the surface are occasional boulders up to 10 feet in diameter, composed of coarse grained granite and gneiss.

Several of the small kames have been opened and are used as local sources of road material for surfacing fire lanes. These kames show irregular, steeply dipping beds of sand and fine gravel and the bedding shows much small-scale slump faulting. The kettles are steep sided, with a large variation in size, and those that contain water are not necessarily confined to the lower parts of the moraine.

This moraine touches the northern edge of Section 5 and a narrow arm of it extends southward along the boundary between Sections 1 and 2 of the area studied. This is the only moraine in that area. Thwaites (1929) suggests the possibility of isolated spots of moraine in Section 16, along the C.M.St.P. & P. Railroad tracks. From test pits dug in these deposits and from railroad cuts through them, it is the writer's opinion that the material is outwash of the "crevasse filling" type or more specifically speaking the "outwash filling between ice blocks" type. The large granite boulders that occur at the surface appear to be mainly erratics dropped by the melting of the stagnant ice blocks and occur mainly along the sides or in the bottoms of the kettles. The railroad cuts and test pits showed stratified sands and gravels beneath 1 to 3 feet of soil and slump materials.

For the positions of areas of moraine see map, Figure 1.

FIG. 1. Map of the area studied.

OUTWASH

Except for the small parts of the Muskellunge Moraine in Sections 1, 2 and 5, the glacial deposits are of several types of outwash of which all can be included under the general, broad term of sandy and gravelly, pitted outwash. There are all degrees of pitting. Only the outwash features that are outstanding are described here. Over much of the area, road cuts show the "cut and fill' structure of typical stream deposited outwash. This structure is shown in Figure 2.

The western half of Section 2, all of Section 3, and the eastern part of Section 4 are covered by very sandy outwash which is intensely pitted with high, irregular hills and ridges between the kettles. The topography suggests moraine, but the stratified character of the sands proves outwash.

◄──────── Direction of flow
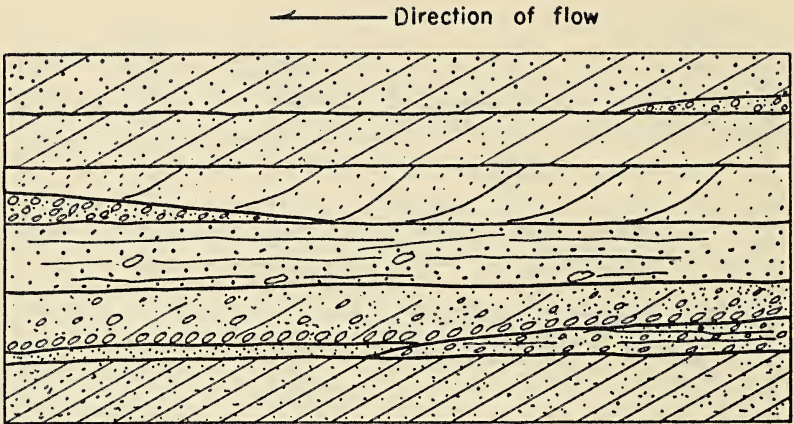
Fig. 2. Sketch of typical cut and fill structure of outwash showing ir-
regular cross-bedding of sands and gravels deposited by outwash streams.

In the SE¼ and the southern part of the NE¼ of Section
5 and in the SW¼ of Section 4 there is a most striking example
of typical "textbook" pitted outwash. The surface is essentially
a plain that is "pockmarked" by numerous, nearly circular ket-
tles, most of which are between 15 and 20 feet deep.

There is what appears to be a glacial drainage system that
trends north-south through the SW¼ and the NW¼ of the
SE¼ of Section 4 and continues south into the NW¼ of the
NE¼ of Section 9 and turns southeast to the SE corner of the
NE¼ of Section 9. From here it extends southeast to the shores
of Ross Lake where it expands into numerous northwest-south-
east trending ridges. Along the east shore of Klondike Lake,
this old drainage system takes the form of a high, steep-sided,
gravel ridge.

The area between Bug Lake (Section 17) and Arbor Vitae
is a very flat, sandy outwash plain. The surface lacks deep
kettles and steep ridges so characteristic of the rest of the out-
wash area. Along the southern edge of the plain, on the north
shore of Arbor Vitae Lake, there are two small deposits of gravel
that resemble beach or bar deposits. In each case the gravel is
very well sorted. In the largest deposit the maximum sizes of
the gravel particles are about 2 inches and in the smaller deposit
they are less than 1 inch.

The outwash in the vicinity of Scaffold Lake (Section 9) is

distinctly "filling between ice blocks" type. High, pitted plain forms the north shore of the lake and it is underlain by stratified sands and gravel with some material of cobble size. South of Scaffold Lake is a low, swampy tract that connects this lake with Benedict Lake. Along the southern edge of Scaffold Lake, and originally separating it from the above swamp, is an E-W trending ridge of stratified sand, topographically resembling an esker. This ridge is not an esker, but is made up of outwash material that was washed into the space between the ice blocks that formerly occupied the sites of Scaffold Lake and the swamp. At the point of its lowest elevation, the ridge of sand has been cut through, so that Scaffold Lake is now connected with the swamp to the south by a narrow neck of shallow water. The positions of the former major ice blocks of this vicinity are now occupied by Klondike, Scaffold, Benedict, Roach and Hurrah Lakes.

In the flat, sandy outwash plain west of the village of Arbor Vitae, there is a NE-SW trending valley. It extends from the south-west edge of Arbor Vitae Lake, through the southern parts of the NW¼ and the NE¼ of Section 30, diagonally through the northwest corner of the SW¼ of Section 30 and into the SE¼ of Section 25, Tp. 40 N, R. 6 E. This valley was cut in the outwash by a post glacial stream which probably flowed northeast into Arbor Vitae Lake. The valley sides are composed of very sandy outwash with only occasional pebbles and cobbles. The valley bottom is covered with coarse sand and gravel to a depth of at least 6-7 feet. This gravel is a residual concentration formed by the removal of the sand by a stream. The gravel grades laterally across the valley into sand.

CHARACTER OF THE DEEP DRIFT

The surface materials that cover this area are characteristic of the "non-calcareous drift". The road cuts and gravel pit materials show no calcareous material such as dolomite and limestone pebbles or calcareous concretionary materials around pebbles. However, there is a buried "calcareous drift" beneath the surface deposits. The usual method of studying the older drift deposits is by the examination of well cuttings. During the summer of 1937, there were no new wells drilled within the area included within this report, but three were drilled in surround-

ing areas, one at the Ranger Station at Wildcat Lake, one at the Forestry Headquarters at Trout Lake and one at the Lake Tomahawk Community Hall. Samples of the well cuttings were taken by the writer and their descriptions are given below.

Wildcat Lake Ranger Station Well

1'—Sandy, gravelly soil.
10'—Red, silty sand medium to fine grained, igneous cobbles, a few sandstone and quartzite pebbles.
8'—Medium to coarse sand, coarse gravel, red clay.
7'—Sand and red clay, fine gravel and black sand.
4'—Coarse to fine basic gravel, medium to fine sand, red clay and black sand.
8'—Brown clay, medium to fine sand, black sand and muscovite.
8'—Fine gravel, medium to fine quartz sand, brown clay.
4'—Coarse sand high in basic minerals, fine to coarse gravel, a little red clay (calcareous), dolomite pebbles.
8'—Gray, calcareous clay, dolomite pebbles, black sand, garnets medium to fine rounded quartz sand.
8'—Red, calcareous clay, dolomite pebbles, much fine gravel, medium to fine quartz sand.
20'—Brown, calcareous clay, dolomite pebbles, medium grained quartz sand, fine to medium gravel, much black sand and some cyanite crystals.
6'—Gray calcareous clay, dolomite pebbles, fine to medium grained sand and fine gravel.
3'—Calcareous red clay; dolomite pebbles; medium to fine sand and gravel.

——
95'

Well at Forestry Headquarters Residence, Trout Lake

3'—Sandy soil with some brown clay.
6'—Yellow quartz sand, medium grained; much black sand.
5'—Sand and gravel high in quartz.
14'—Brown sand and clay. Rounded medium grained sand.
6'—Brown, medium to coarse sand with some clay and pebbles.
1'—Very coarse sand.
5'—Medium to fine rounded sand.
6'—Fine brown sand with clay. Much black sand.
2'—Sandy gravel.
21'—Fine gravel beds alternating with fine and coarse sand. Very little coarse gravel.
2'—Fine sand and gravel.
5'—Medium grained sand, fine gravel, redish clay.

——
76'

Lake Tomahawk Community Hall Well

3'—Reddish, clayey, sandy top soil.
13'—Fine quartz sand, very little clay, black sand.
13'—Medium to fine sand and fine gravel.
16'—Medium to coarse sand and coarse gravel. Dolomite pebbles and fossiliferous pebbles.
6'—Medium to fine sand and fine gravel. Dolomite pebbles.
4'—Fine sand and red clay. Very few pebbles.

8'—Fine sand and red clay, more gravel than above.
2'—Fine sand.
5'—Medium to fine sand with much red clay. Few pebbles.
5'—Medium grained sand with very little clay and some fine gravel.
--
75'

In the Wildcat Lake and Lake Tomahawk wells, calcareous pebbles and clays were encountered at depths of 45 and 34 feet, respectively. The figures show the thickness of the non-calcerous drift at these places. No calcareous material was found in the well cuttings at the Trout Lake Forestry Headquarters, which probably indicates that the calcareous deposits were not penetrated here. Thus, at this place the non-calcareous drift is at least 76 feet thick. One might disagree with this on the basis that the probability of a six inch hole showing the presence of calcareous pebbles is very slight and they may have been missed in the Forestry Headquarter's well, but the calcareous pebbles in the other two wells were entirely lacking down to the above depths and then were very abundant. If any beds of calcareous clay were penetrated they would have shown in the cuttings. Fossiliferous pebbles were obtained from the 45-50 foot depth in the Lake Tomahawk well. The fossils were colonial corals and brachiopods of possible Silurian age, but with preservation too poor for more definite determination. The last samples obtained from the Wildcat Lake well were fragments of crystaline rock resembling granite. This granite is either a large boulder embedded within the drift or else the underlying bedrock. The well driller, after drilling for some time in this material, said that it "felt" like bedrock.

Fries (1938) reports on several well drillings in the Trout Lake district and they are here listed with the depths from the surface to the calcareous drift.

East end of Crystal Lake .... 80'
South of Allequash Creek along Trout Lake .... 35'
Trout Lake .... 35'
Point Camp Site, Trout Lake ....200'

From these figures it can be seen that the non-calcareous drift has a thickness of at least 35 feet to 200 feet, and a greater range is possible.

As one might expect, the surface of the old drift was quite irregular before the deposition of the younger drift. It had a topographic relief of at least 165 feet. At some places, the

calcareous material of the older drift very likely comes close to the present surface and in such cases it would increase the hardness of the ground water. Some of this ground water, relatively rich in $CaCO_3$, could make its way to the streams and be carried into the lakes, thus increasing their corbonate content. The streams act as collecting agents for the $CaCO_3$ and the lakes act as reservoirs for the accumulated carbonates. This fact suggests why drainage lakes of this area are so much harder than the so-called seepage lakes.

Lakes and Lake Water Analyses

The lakes of this area are nearly all kettle lakes, occupying depressions formed by the melting of large isolated ice blocks which were left as the glacier receded and were covered or surrounded by outwash materials. These lakes vary in size from intermittent ponds in the smaller kettles to large bodies of water such as Arbor Vitae Lake which has a shore line of about 7½ miles.

Three types of lakes are recognized; bog lakes, seepage lakes, and drainage lakes. The bog lakes are generally the smallest and contain the softest waters of the three. They are considered to receive practically all of their water from precipitation and direct runoff from the surrounding hills. Due to the extremely pitted character of the outwash, the water-sheds furnishing direct runoff to these lakes are small in area and no surface streams empty into the water bodies. Sphagnum, swamp, and lake vegetation is rapidly encroaching on these lakes. Klondike and Bug are the bog lakes in this area. Several small, unnamed bogs were studied and in this paper they are referred to by number.

The seepage lakes receive water from direct precipitation, runoff and, presumably, from the seepage of ground water through the surrounding outwash. They have no surface inlets or outlets such as streams. The waters are generally intermediate in hardness between those of the bog lakes and the drainage lakes. Seepage lakes of this area are Witches, Roach, Vandercook, Scaffold, Hurrah and Benedict.

The drainage lakes contain the hardest waters of the three types and they receive water from surface streams as well as

from direct runoff and precipitation. The surface drainage in the form of streams is probably the reason for the higher carbonate content. Drainage lakes of the area are Arbor Vitae, Little Arbor Vitae, Erickson, and Ross. During very wet seasons, Scaffold and Benedict Lakes have a surface connection through the line of small ponds and swampy land that extends between them, but they should not be classed as typical drainage lakes.

The surface elevations of some of these lakes were determined by students of the Armour Institute of Technology Summer Camp at Trout Lake. These elevations are given in Table 1.

TABLE 1. Lake elevations given in feet above sea level.

Lake	Elevation
Bog #1	1643.57
Bog #2	1638.71
Witches	1642.58
Roach	1652.83
Klondike	1645.05
Scaffold	1639.95
Bug	1636.25
Hurrah	1635.65
Benedict	1644.85

Samples of the lake water were analyzed by chemists at the Trout Lake Laboratories and the results are shown in Table 2.

TABLE 2. Chemical analyses of lake waters given in parts per million.

Lake	Date, 1937	Bound CO_2	Ca	Mg	Fe	SiO_2	pH
Bog Lakes							
Klondike	7/12	1.0	1.93	trace	0.13	0.2	6.3
Bug	7/12	3.0	2.66	trace	0.29	0.6	6.3
Box #1	7/7	2.7	0.87	0.2	0.50	0.1	5.9
Bog #2	7/7	4.0	6.94	0.5	0.90	0.1	5.7
Bog #3	7/12	30.5	18.32	6.5	0.90	16.4	6.7
Bog #4	7/12	3.0	4.09	trace	0.21	0.2	6.1
Bog #5	7/12	2.5	1.87	trace	0.40	0.2	5.5
Bog #6	7/14	1.0	0.48	trace	0.18	trace	6.1
Seepage Lakes							
Witches	7/7	1.8	1.35	0.2	0.25	0.2	6.5
Roach	7/7	4.2	3.87	0.2	0.48	0.1	6.3
Vandercook	7/12	1.2	2.47	trace	0.35	0.2	6.1
Scaffold	7/12	5.5	3.29	0.5	1.20	4.6	6.6
Hurrah	7/24	2.5	1.6	0.8	0.10	trace	6.2
Benedict	7/24	0.9	0.8	trace	0.40	0.2	5.8
Drainage Lakes							
Arbor Vitae	7/12	24.5	14.27	5.0	0.27	14.1	8.3
Little Arbor Vitae	7/12	24.5	14.22	5.5	0.20	5.6	8.4
Erickson	7/12	12.0	6.02	2.5	0.13	1.6	6.9

The waters of Bog #3 are very much higher in dissolved material than the other bog waters. This is due to the fact that it is really a part of the drainage of Arbor Vitae Lake.

Ground Water Analyses

Some information concerning the chemistry of the ground water was obtained by analyses of well water samples. These are shown in Table 3.

TABLE 3. Chemical analyses of well waters given in parts per million.

Well	Depth	Bound CO_2	Ca	Mg	Fe	SiO_2	pH
0.3 mile west of Arbor Vitae	20'	10.5	4.9	1.8	0.7	12.9	6.4
Taxidermist's, Arbor Vitae	21'	34.5	15.2	8.7	3.5	16.2	6.5
West Side of Erickson Lake	30'	7.6	3.5	1.5	1.5	12.6	6.1
Brehm Camp, Arbor Vitae	30'	25.5	13.2	5.2	0.5	6.0	6.8
Norgal's Camp, Arbor Vitae	30'	29.0	14.8	5.6	2.7	5.6	6.8
Post Office, Arbor Vitae	30'	12.5	10.2	3.0	0.5	11.5	6.1
Pete's Tavern, Arbor Vitae	38'	31.5	13.6	6.2	0.4	8.4	6.4

Numerous test pits were dug around the shores of some of the lakes and analyses were made of the ground water at these places. The test pits are numbered and their positions are shown on the map, Figure 1. In order to eliminate contamination and in order to get a true sample of the ground water at these places, a well point, with only the bottom six inches of holes left open, was driven about two feet below the bottoms of the test pits. The water samples were drawn up through this pipe. Chemical analyses of these ground water samples are shown in Table 4.

The mineral content of the test pit waters varies greatly from that of the corresponding lake waters and there is very little similarity between the compositions of waters from pits surrounding the same lake. This may show a lack of free mixing of ground water and lake water.

Table 4. Chemical analyses of ground water from test pits. Results given in parts per million.

Pit	Lake	Bound CO$_2$	Ca	Mg	SiO$_2$	Fe
1	Witches	1.80	1.35	0.2	0.2	0.25
2	Witches	2.75	1.13	trace	5.1	0.34
4	Roach	1.80	1.40	trace	4.2	
5	Witches	3.75	1.20	trace	2.9	0.20
6	Witches	3.00	1.13	trace	2.6	0.50
7	Witches	4.10	1.90	0.1		
8	Witches	3.50	1.80	0.1		
9	Witches	2.70	1.30	trace		
10	Scaffold	5.60	5.10	0.2		
11	Scaffold	16.00	8.50	4.5	25.8	1.50
12	Scaffold	18.50	13.40	2.2	6.1	1.40
13	Scaffold	5.50	4.20	0.8	13.1	6.00
14	Bog #5	2.00	1.80	trace		trace
15	Bog #5	3.20	1.70	0.25		0.25
16	Bog #5	2.80	2.60	0.40		19.00
17	Bog #5	5.20	2.80	0.70		0.70
18	Roach	3.00	1.60	0.50		0.50
19	Bog #1	3.70	1.80	0.90		0.50
20	Bog #1	2.40	1.20	0.60		0.50
21	Bog #1	2.50	1.10	0.70		0.50
22	Bog #1	1.60	1.00	0.30		0.80
23	Hurrah	5.80	3.00	1.30		1.20
24	Hurrah	2.00	1.90	trace		9.00
25	Hurrah	5.30	2.80	1.30		0.10
26	Erickson	12.00	6.00	2.70		0.15
27	Erickson	12.00	6.40	2.10		0.15
28	Erickson	9.00	4.40	1.70		0.10
29	Erickson	9.10	4.90	1.00		0.50
30	Vandercook	6.00	4.10	trace		3.20
31	Vandercook	4.90	2.20	trace		1.00
32	Vandercook	5.10	3.50	0.30		3.80
33	Vandercook	1.70	0.70	trace		0.20
34	Vandercook	2.40	1.20	trace		2.50
35	Vandercook	3.50	1.80	trace		4.00

LAKE BASIN SEAL

The question has been raised as to why some of the lake waters are so much harder than others and whether or not there is a possibility of a lake basin seal that would effectively seal off the lake waters from the surrounding ground waters. An attempt was made to throw some light on the question and despite the difficulties involved in obtaining direct proof one way or another, some interesting information was obtained.

An explanation for the hardness of the drainage lake waters has already been given, but this will not explain the difference

in hardness of the seepage lakes. Although it has not been definitely proven, the writer would like to suggest a possible explanation for this difference. As has been shown by well samples, the surface of the old calcareous drift is quite irregular. The lakes of this region lie in kettles surrounded by fairly high hills. It is possible that in certain places, the calcareous drift, in the surrounding hills, is higher than the lake levels. Although the water-sheds are small, some of the meteoric water falling on these hills would percolate through the old drift and dissolve some of the carbonates. Some of this water will eventually find its way to the lakes and would not have to enter the lakes below lake level, but could seep in just above that level. In this way, lakes in an area where the calcareous drift is high would be enriched in $CaCO_3$, whereas lakes in areas where the calcareous drift is deeply buried would not be so enriched. This would give a difference in the carbonate content of the lakes regardless of whether there is a basin seal or not.

Probably some of the carbonate content of the lake waters may come from weathering of the feldspars and other minerals composing the drift, but this is very slight as shown by slight degree of weathering of the feldspars.

The bog lakes may be considered as practically sealed off from the ground water by the thick deposits of organic material that line the bottoms and sides of the basins. Test pits showed some clay and clayey silt along the sides of the kettles that may act as a seal.

At the time the field work was done, the lake levels were

TABLE 5. *Data showing the character of the strata in test pits dug on the shores of the various lakes.*

Witches Lake	
#1—2″ white sand	#6—3″ sand and soil
6″ dark sand	2′ red sand
4′ brown sand	1′ layered, brown and white sand
#2—4″ black soil	
3″ white sand	2′ yellow sand
6″ brown, sandy soil	#7—5″ white sand
2′ reddish, sandy soil	2″ dark sand
2′ sand and gravel	3″ white sand
#5—6″ white sand	8″ brown sand
4″ white sand and organic material	3′ yellow sand
	#8—3″ dark sand
2″ white sand	5′ brown sand and coarse gravel.
6″ dark brown sand	
14″ red sand and fine gravel	#9—10″ white sand
3″ gray clay	14″ brown sand
	2″ gray clay
	1′ white sand and fine gravel

Scaffold Lake

#10—10" red sand and gravel
    2" dark sand
    8" silty, gray clay
    6" red sand and fine gravel
    3' red sand and coarse
       gravel
#11— 6" soil
    18" blue and red clay
    8" blue clay
    8" red sand and fine gravel

#12— 3" dark soil
    2' brown sand and pebbles
       with layers of yellow and
       blue clay
    2' red, sand and gravel
#13— 4" dark soil
    2' layered, silty, red and blue
       clay
    2' sandy gravel

Bog Lake #5

#14— 4" soil
    6" gray clay
    3' brown sand and pebbles
#15— 6" soil
    7" dark sandy soil
    3' brown sand

#16— 2' soil
    8" silty, gray clay
    15' gray clay
    1' red, pebbly clay
    1½' red sand and fine gravel
#17— 3" soil
    9" silty, gray clay
    15" brown clay
    4" gray clay
    1½' sand

Roach Lake

#4—6" soil
    2' gravelly gray clay

#18—5" white sand and gravel
    1' dark sand
    2' brown sand

Bog Lake #1

#19— 4" red, sandy soil
    2" black soil
    6" white sand
    4" brown sand and organic
       material
    1" white sand
    15" sand and gravel
#20— 1' sandy soil and gravel
    8" peat
    16" sandy gravel
#21— 4" soil
    3" red sand
    3" soil
    1' sand and coarse gravel

#22— 2" soil
    5" red sand
    4" soil
    3" brown sand
    2" soil
    4" white sand
    7" peat
    1' sand
    1" gray clay
    1' sand

Hurrah Lake

#23— 8" sand and gravel
    10" sandy gravel
       red clay
    7" fine sand
    2" gray clay
    1½' sand and gravel

#24— 2" soil
    1" silty clay
    10" gray clay
    3½' gray and red clay
#25— 3" soil
    1' sand
    2' sand and gravel

Erickson Lake

#26—10″ white sand
    2′ red sand
    1½′ sand
#27— 7″ white sand
    2″ soil
    11″ sand
    2″ peat
    15″ brown, clayey sand
    20″ sand and clay

#28— 5′ sand and gravel
#29— 8″ sandy soil
    1½′ sand
    2″ peat
    1′ sand

Vandercook Lake

#30— 1′ sand and gravel
    4″ brown sand and gravel
    6″ layered peat and yellow clay
    2½′ peat
    1′ coarse sand
#31— 2″ sand
    3″ soil
    2½′ brown, gravelly, clayey sand
#32— 7″ sand
    8″ brown, clayey sand
    18″ gray, silty clay
    2′ sand and gravel

#33—10″ white sand
    1′ red sand
    1½′ sand and gravel
#34— 5″ white sand
    10″ brown sand
    6″ brown sand and gravel
    2′ gray, silty clay
    1′ gravel
#35— 1′ brown sand and gravel
    8″ silty, gray clay
    1′ blue clay
    6″ sand and gravel

lower than they had been during past years and in some cases extensive beaches were left above the present water levels. Test pits were dug in these old deposits on the assumption that they would show early deposits of the lakes. From the type and structure of the material, it is quite evident that these are made up of lake deposited materials. The locations of the test pits are shown on the map (Fig. 1).

Many of the test pits showed the presence of one to several beds of red and blue clay which vary from 2 inches to 5 feet in thickness. This material is a very tenacious, silty clay, some beds of which are almost entirely free from silt and would very effectively act as a lake basin seal. All of the pits did not show this clay, but that does not mean that it is not present at those places. In these areas the clay may have been buried too deep to be shown in the pits.

Vandercook Lake, which lies in Section 1 of T. 40 N, R. 6 E. and in Section 36 of T. 41 N., R. 6 E. on the northwest corner of the area included in this report, was also studied by test pits. The lake lies at the south edge of the Muskellunge Moraine.

Test Pit #32, at the north end of the lake, showed 18 inches of impervious clay and when this layer was penetrated by the shovel, water bubbled up into the pit, overflowed it, ran down into the lake. This indicates that the clay layer is impervious enough to shut off ground water from lake water and that a hydraulic head is formed in the ground water in the adjacent moraine.

It appears probable that the thick organic deposits on the bottoms and sides of the lakes and the above clay deposits form a very effective, partial, if not total, seal to the lake basins.

A brief recapitulation of the history of these lakes may make the above statement clearer, but it must be remembered that this is merely speculation. As the glacier receded, ice blocks became isolated along its front and were surrounded and in some cases covered up by outwash sands and gravels. When these ice blocks melted, large depressions were left and these became filled with water from the still receding glacier to the level of the ground water table at that time. This water contained large amounts of rock flour and colloidal particles in suspension. The suspended material slowly settled out and was deposited on the sides and bottoms of the basins and may show today as some of the silty, clayey material. Because of the low relief, only the finest of the materials in the hills surrounding the depressions were washed into the lakes. These deposits of very fine material probably acted as a partial seal to the basins and the effect of this seal was increased by the deposits of fine organic muds that followed.

The deposits in the bottoms of some of the small kettles were studied by means of samples collected with a soil auger. It was assumed that if the lakes occupy large kettles, then their initial bottom deposits should resemble the bottom deposits in the smaller kettles. The kettles that were sampled in this way contained a little water or showed signs of having contained water. In all cases it was found that there is a layer, or several layers, of heavy, thick, yellow and blue, silty clay on the bottoms. This clayey material could very well seal the basins so as to make them practically impervious.

Summary and Conclusions

No surface outcrops of bed rock are exposed within the area studied and the surface is entirely underlain by glacial debris. The glacial deposits are of outwash except where the Muskellunge Moraine touches the northern edge of Section 5 and extends southward between Sections 1 and 2. The surface drift is non-calcareous and has a known thickness of 35 feet to 200 feet. An older calcareous drift underlies the surface deposits. For the most part, the outwash is extremely pitted with the largest kettles occupied by the lakes.

Three types of lakes are recognized, namely: bog lakes, seepage lakes, and drainage lakes. The bog lakes contain the softest waters, the drainage lakes contain the hardest waters and the seepage lake waters are intermediate in hardness. The major source of the carbonates in the waters is the buried calcareous drift. Surface streams, by accumulating ground water from the surrounding hills, act as collecting and carrying agents for the carbonates and eventually add them to the waters of the drainage lakes. This is probably the main reason that the drainage lakes have a higher carbonate content than the seepage and bog lakes. There is no similarity between the carbonate content of the lake waters and the surrounding ground water.

The lakes appear to have quite effectively sealed off their basins from the influence of the surrounding ground waters. This sealing was probably accomplished by the lakes themselves by depositing clays, silty clays and organic muds over the sides and bottoms of the basins.

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HYDROGRAPHY AND MORPHOMETRY OF SOME NORTHEASTERN WISCONSIN LAKES

C. JUDAY AND E. A. BIRGE

INTRODUCTION

In connection with the other investigations that have been carried on at the Trout Lake Limnological Laboratory since its establishment in 1925, 34 lakes and lakelets have been surveyed and sounded. From the data obtained in these surveys, hydrographic maps of the various bodies of water have been made and these maps, in turn, have been used to determine the areas and volumes.

With the exception of Trout Lake, these surveys were made between 1930 and 1934. Through the cooperation of the State Board of Forestry, most of Trout Lake was sounded through the ice during the winters 1913-14 and 1914-15; to complete the work on this lake, several hundred soundings were made during the summers of 1930-34 at the time the other lakes were being surveyed. Thanks are due the Armour Institute of Chicago for hydrographic data on the north part of Trout Lake; the Institute has operated a summer surveying camp on the north part for a number of years and the data obtained in various surveys were kindly placed at our disposal by the Director of the camp.

The surveys were confined chiefly to the larger and deeper lakes but several of the smaller and shallower bodies of water were included as shown by the maps and tables. One of the important considerations in this phase of work was to select bodies of water that offered good opportunities for future physical, chemical and biological studies. In order to obtain a complete picture of the biological productivity of a lake, it is necessary to know its area, depth and volume since they are important factors in the productivity problem.

These lakes represent different types of water as shown in Table I. They belong to two general groups, namely seepage and drainage lakes. Those that are landlocked and have no outlet

are classed as seepage lakes because the exchanges of water in them take place by seepage through the ground. Those that have outlets, either temporary or permanent, are designated as drainage lakes.

METHODS

About half the soundings on Trout Lake were made through the ice in winter. The remainder of those on Trout Lake and all of those on the other lakes were made from a row boat in summer. The outlines of the various lakes were surveyed by means of an alidade and stadia rod; likewise the locations of the various soundings were determined with these two instruments. A surveying crew consisted of three men; one was stationed on shore to make the alidade readings and two were in the boat, one to row and the other to make the soundings and record the readings. The lengths of the lines of soundings were also determined by means of the surveying instruments.

GEOLOGY OF REGION

The geological character of the region in which most of these lakes are situated was described by Thwaites in 1929. Previous to that time, data regarding location, area and maximum depth were published by Juday in 1914; also information regarding the entire northeastern lake district, including a general map, was published by Juday and Birge in 1930. The results of chemical investigations on a few of these lakes were included by Birge and Juday in Bulletin No. 22 of the Wisconsin Survey published in 1911.

These bodies of water lie in a glaciated area which is covered with second growth pine and deciduous forests. The thickness of the glacial material varies from 35 to 70 meters and the underlying rock consists of schist and gneiss in the northern part of this lake district and granite in the southern part.

The southern members of the group of 34 lakes lie in a pitted outwash plain which is characterized by relatively small differences in elevation. The northern group, consisting of the Adelaide-Yolanda chain (Fig. 1), is situated within the Winegar moraine where the topography is more rugged; some of the hills in this area rise to heights of 25 meters or more above the lakes.

The surfaces of the surveyed lakes lie between 480 and 515 meters above sea level, the elevation of Trout Lake, for example, is 492 meters, or 1614.4 feet as determined by an Armour Institute survey.

In general the shores of most of the lakes do not rise more than a few meters above the surface of the water, and they are made up, for the most part, of the usual glacial material, such as sand, gravel, boulders, and some clay, in various proportions. Some of them, such as Cardinal and Forestry bogs and Helmet Lake are typical bog lakelets in which the open water is surrounded by a wide margin of bog deposit. The waters of these lakelets contain varying amounts of vegetable extractives derived from the surrounding bogs so that they have a fairly high color as indicated in Table I. Some of the other lakes also have rather highly colored waters, especially those that receive drainage water from marshes.

Fries (1938) made a more detailed study of the geology and ground water of part of the region in which the surveyed lakes are situated, particularly in the vicinity of Crystal and Weber lakes. He found three types of drift overlying the crystalline bedrock of the region. (1). A deep drift which was found only in deep wells and which is gray in color and has a high percentage of dark-colored minerals; pebbles of gray dolomite and deposits of gray calcareous clay are found in it. (2) The second type is brown-red in color, contains very little clay, with little or no dark-colored minerals; the fine material in this deposit is low in carbonates and the thickness of the stratum is extremely variable. (3). The third type of drift contains a large percentage of clay and is bright red in color, with low calcareous content; it is found chiefly in the Winegar moraine. A good exposure of such a deposit is found on the shore of Helmet Lake.

Physics and Chemistry of the Water

Table I gives a general idea of some of the physical and chemical characteristics of the waters of the 34 lakes. It will be noted that 20 of them are seepage lakes and 14 belong to the drainage group. The disc readings show that there is a wide range in the transparency of the water; the readings vary from a little more than half a meter up to more than 9 meters in two

TABLE I. *This table shows some of the physical and chemical characteristics of the waters of the various lakes included in these surveys. Drainage lakes (those with an outlet) are indicated by D and seepage lakes (those without an outlet) by S. The disc readings represent the transparency of the water and the values are expressed in meters. The color of the water is based on the platinum-cobalt standard and the conductance or specific conductance is expressed in reciprocal megohms. The hydrogen ion concentration is indicated as pH. The remaining chemical results are stated in milligrams per liter of water. Tr. equals trace.*

Lake	Drainage or Seepage	Disc	Color	Conductivity	pH	Bound CO_2	SiO_2	Ca	Mg	Nitrate	Total Residue	Organic Matter
Adelaide	D	2.4	37	23	6.5	3.2	0.4	1.2	0.6	0.018	32.0	15.3
Big Carr	S	5.0	2	12	5.9	1.3	0.2	0.8	0.6	0.010	17.3	6.6
Black Oak	D	4.0	8	43	7.3	9.6	Tr	6.6	2.2	0.013	35.1	8.1
Bragonier	S	2.5	29	13	6.2	2.1	0.5	1.2	1.3	0.023	21.4	12.1
Cardinal Bog	S	2.2	37	7	5.4	1.7	0.5	0.5	0.1	0.019	19.7	13.6
Clear	S	6.4	2	17	6.6	2.5	0.4	2.2	1.0	0.011	18.2	6.2
Crystal	S	9.4	2	10	6.1	1.5	Tr	0.7	Tr	0.016	12.3	3.2
Diamond	S	9.0	0	12	5.7	1.2	Tr	1.4	1.0	0.010	12.0	2.6
Finley	S	3.9	5	13	6.7	2.4	Tr	1.3	1.3	0.014	21.3	9.1
Forestry Bog	S	1.8	56	9	5.2	1.7	0.8	0.5	0.0	0.011	32.8	24.2
Helen	D	1.3	95	20	6.1	3.1	1.0	1.7	0.7	0.024	39.5	24.3
Helmet	S	0.6	316	20	5.4	2.2	2.5	3.1	0.0	0.030	79.0	50.4
Hillis	S	6.5	0	14	5.6	0.6	Tr	1.2	0.6	0.013	17.3	5.3
Little Bass	S	7.3	3	12	5.8	1.3	Tr	0.6	0.2	0.019	12.8	3.3
Little John	D	2.6	17	71	7.5	17.8	2.3	14.0	4.0	0.014	56.7	9.7
Little John Jr.	S	3.4	14	9	5.8	1.3	0.1	0.6	0.2	0.016	15.8	7.8
Little Long	D	1.5	100	29	6.9	6.0	2.4	3.9	2.2	....	52.7	28.6
Lost Canoe	D	4.1	14	43	7.4	9.9	0.3	6.8	3.0	0.015	37.3	9.3
Mary	D	1.6	110	21	6.0	2.8	1.8	1.8	Tr	0.024	53.1	34.4
Midge	S	2.8	36	12	5.7	2.3	Tr	0.2	Tr	0.021	24.7	12.9
Muskellunge	D	4.0	5	41	7.3	10.0	0.2	5.8	2.0	0.015	36.4	9.4
Nebish	S	6.0	8	19	6.8	4.0	0.2	2.3	1.7	0.012	22.0	7.3
Nelson	S	3.6	8	12	6.2	2.9	0.2	0.7	:	0.020	18.0	7.6
Pallette	S	4.5	4	19	6.7	3.8	0.2	2.0	1.5	0.014	28.6	12.6
Pauto	S	9.4	4	10	5.7	1.7	2.1	0.2	:	0.011	12.2	4.1
Rahr (Mud)	S	2.5	35	16	6.3	3.0	0.3	1.4	1.0	0.025	28.0	17.3
Rose	D	1.1	128	25	6.7	2.7	1.2	1.8	Tr	0.022	53.9	33.1
Ruth	S	4.7	20	9	5.6	1.0	0.2	0.3	0.2	0.012	13.6	5.1
Silver	D	5.6	4	64	7.5	15.5	3.1	8.7	2.7	0.015	48.4	6.7
Sweeney	D	0.6	52	60	8.2	18.3	4.2	16.2	3.5	0.012	66.7	22.3
Trout	D	4.6	10	76	7.5	18.8	3.2	11.4	3.5	0.012	57.5	8.1
Weber	S	7.4	Tr	9	6.1	1.2	Tr	0.7	0.6	0.012	13.2	4.1
White Sand	D	3.6	15	62	6.8	15.1	3.8	9.6	3.5	0.015	52.4	8.5
Yolanda	D	1.0	146	16	5.8	2.2	1.0	:	:	0.018	43.0	30.6

lakes. A maximum of approximately 14 meters is recorded for one reading in Crystal Lake. The color column also shows that there is a marked variation in the color of the water in the various lakes; the readings range from zero up to 316 on the platinum-cobalt scale. A maximum reading of 364 was obtained in one surface sample of Helmet Lake. As indicated above, these stains represent vegetable material extracted from bog and marsh deposits.

The specific conductance or conductivity of the various waters ranges from a minimum of 7 to a maximum of 76 reciprocal megohms. Low conductivity means small amounts of electrolytes and the waters with the lowest readings approach ordinary distilled water in their mineral content. The hydrogen ion concentration of the various waters also shows a wide variation, ranging from pH 5.4 to pH 8.2; these are average results and represent the mean of several readings on the surface water.

Similar variations in the quantity of bound carbon dioxide, nitrate nitrogen, calcium, magnesium, silica, total residue and dry organic matter are shown in Table I. In general the landlocked or seepage lakes have much softer waters than the drainage lakes. The mean calcium content of the 20 seepage lakes is 1.07 mg/l and that of the 13 drainage lakes on which such determinations were made is 6.4 mg/l. The waters of some of the drainage lakes however, have a smaller calcium content than those of certain seepage lakes; this is due to the fact that these drainage lakes are the sources of small intermittent streams which function only when the water is unusually high, but their other characteristics are much like those of the seepage lakes. None of these lakes has enough mineral material in solution to give it the rating of a hard water lake; this is true also of all of the other lakes in the northeastern district.

Table I shows that the highly colored waters contained the largest amounts of organic matter, while those with lowest colors yielded the smallest amounts. This is shown by Helmet Lake which has both maximum color and maximum organic matter, as well as by Mary and Rose which rank second and third in both color and organic matter. Diamond Lake with a color of zero yielded the smallest amount of organic matter.

The two other tables give the locations, the areas, the depths and the volumes of the various lakes, while the hydrographic maps show their shapes and depth contours.

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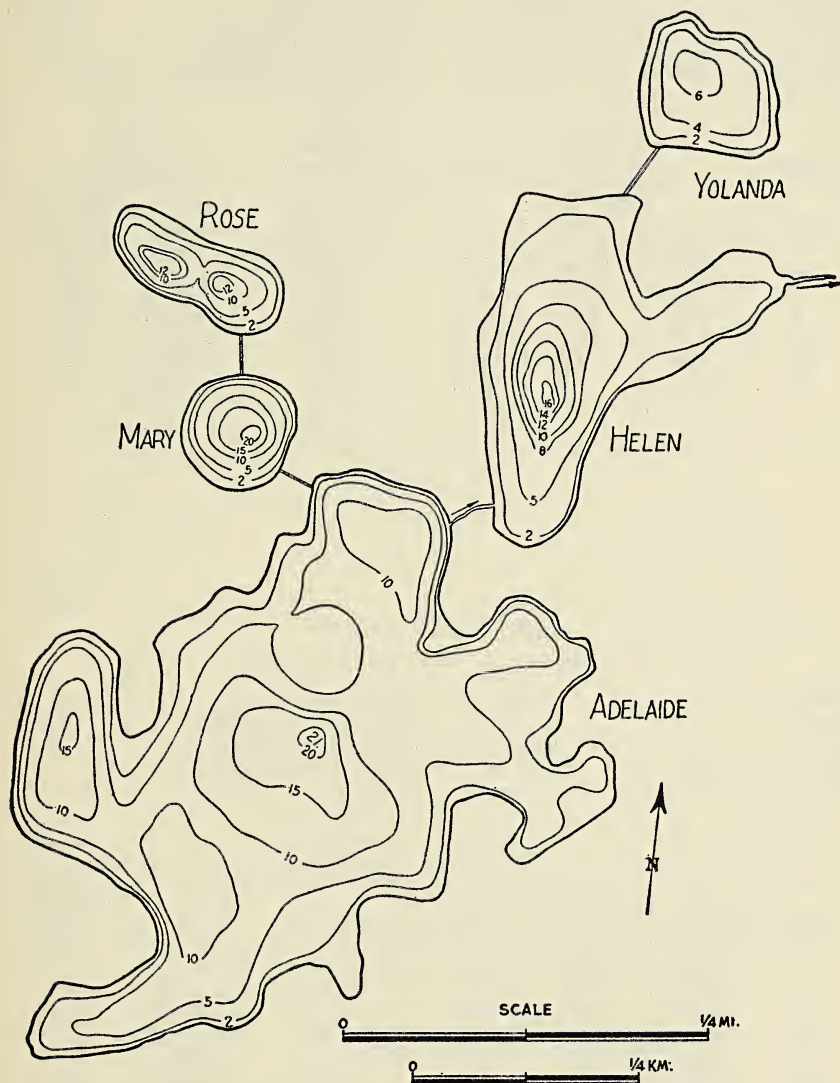
FIG. 1. Hydrographic map of Adelaide-Yolanda group of lakes. Depths are given in meters.

ADELAIDE LAKE
T. 44 N., R. 5 E., Sec. 32.

Length .... 750 m.   Mean depth .... 6.78 m.
Breadth .... 500 m.   Length of shoreline ..... 3.2 km.
Area .... 22.16 ha.   Shore development 1.91
Maximum depth .... 21.0 m.   Number of soundings 103

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	22.16	100.0	0-2	3.15	411,300	27.4
2	19.01	85.7	2-5	5.55	484,700	32.3
5	13.46	60.7	5-10	8.11	455,100	30.3
10	5.35	24.1	10-15	4.39	129,400	8.6
15	0.96	4.3	15-20	0.90	21,000	1.4
20	0.06	0.3	20-21	0.06	200	0.0
			Total		1,501,700	

BIG CARR LAKE
T. 38 N., R. 7 E., Sec. 9, 16, 17

Length .... 1.40 km.   Mean depth .... 9.40 m.
Breadth .... 1.02 km.   Length of shoreline .. 6.5 km.
Area ....94.5 ha.   Shore development ... 1.68
Maximum depth ....22.0 m.   Number of soundings . 143

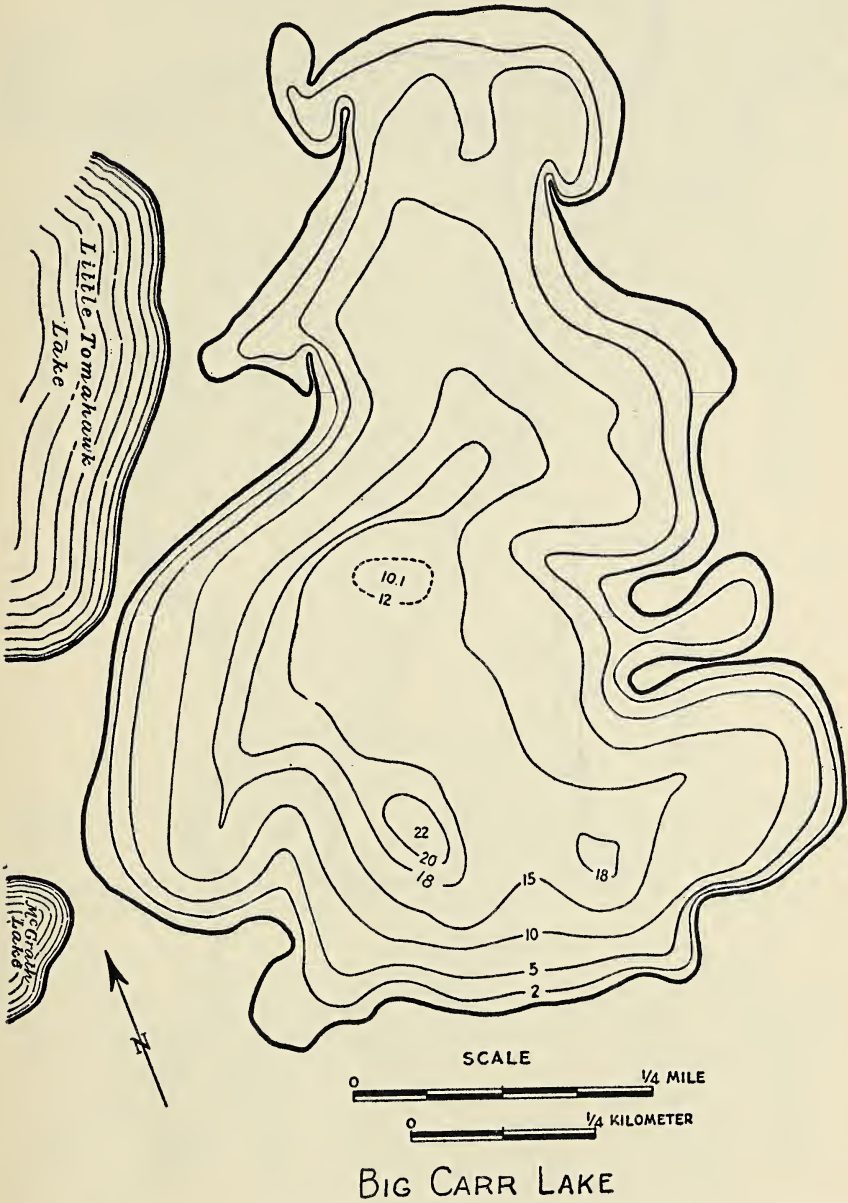| Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	94.50	100.0	0-2	14.11	1,747,000	19.7
2	80.39	85.0	2-5	13.74	2,202,400	24.8
5	66.65	70.5	5-10	19.32	2,835,800	31.9
10	47.33	50.1	10-15	24.85	1,680,300	18.9
15	22.48	23.8	15-18	18.01	369,600	4.2
18	4.47	4.7	18-20	3.95	41,500	0.5
20	0.52	0.5	20-22	0.52	3,400	0.0
			Total		8,880,000	

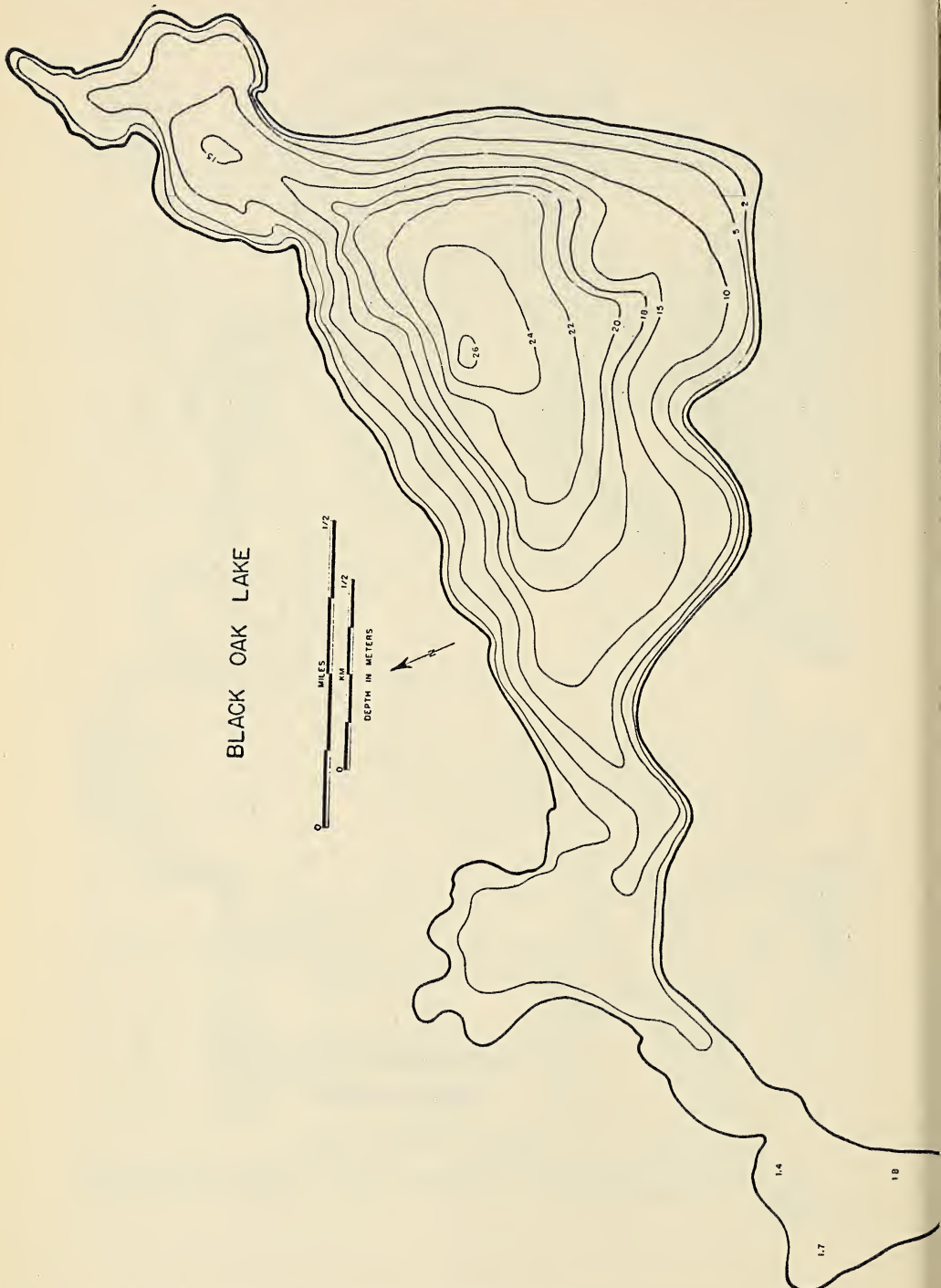FIG. 2. Hydrographic map of Big Carr Lake. Depths are indicated in meters.

FIG. 3. Hydrographic map of Black Oak Lake. Depths are indicated in meters.

BLACK OAK LAKE

T. 43 N., R. 9 & 10 E., Sec. 31, 35, 36

Length .... 3.76 km.   Mean depth .... 10.34 m.
Breadth .... 1.23 km.   Length of shoreline .... 11.50 km.
Area .... 230.15 ha.   Shore development 2.13
Maximum depth ...... 26.0 m.   Number of soundings ..158

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	230.15	100.0	0-2	47.95	4,114,200	17.2
2	182.20	79.1	2-5	29.90	4,855,200	20.4
5	142.30	61.3	5-10	33.40	6,262,800	26.3
10	108.90	47.3	10-15	36.57	4,512,700	18.9
15	72.33	31.4	15-18	9.59	2,024,400	8.6
18	62.74	27.3	18-20	24.06	1,004,600	4.2
20	36.68	16.8	20-22	13.28	636,200	2.7
22	25.40	11.0	22-24	17.06	322,300	1.4
24	8.34	3.6	24-26	8.34	68,800	0.3
				Total	23,801,200	

BRAGONIER LAKE

T. 40 N., R. 9 E., Sec. 31, 32

Length .... 730 m   Mean depth .... 3.46 m.
Breadth .... 430 m.   Length of shoreline ...... 2.3 km.
Area .... 19.24 ha.   Shore development 1.20
Maximum depth ...... 8.7 m.   Number of soundings 52

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	19.24	100.0	0-2	4.43	339,600	51.1
2	14.81	76.9	2-4	7.20	220,300	33.2
4	7.61	39.5	4-6	5.86	87,900	13.2
6	1.75	9.1	6-8	1.36	16,100	2.4
8	0.39	2.0	8-8.7	0.39	900	0.1
				Total	664,800	
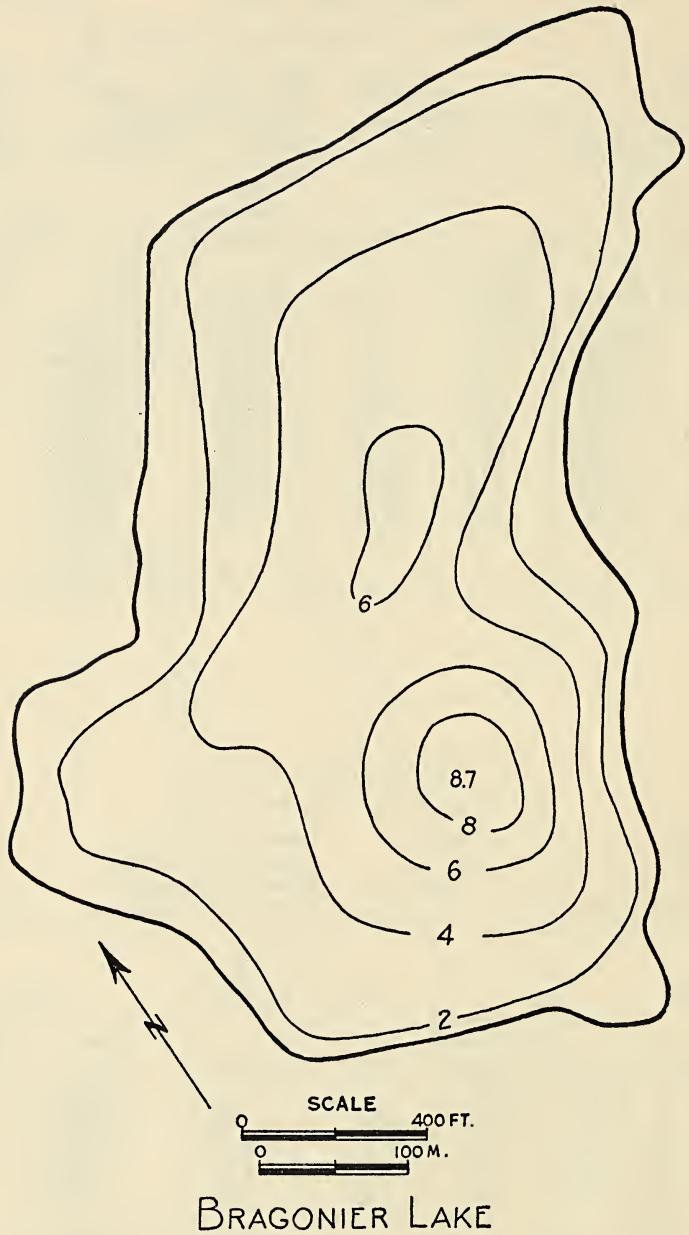
FIG. 4. Hydrographic map of Bragonier Lake. Depths are indicated in meters.

CARDINAL BOG
T. 41 N., R. 6 E., Sec. 14

Length .... 29 m.   Mean depth .... 2.40 m.
Breadth .... 20 m.   Length of shoreline ......84 m.
Area ....397 sq. m.   Shore development 1.19
Maximum depth .... 5.5 m.   Number of soundings 10

Depth	Area		Stratum	Area between contours	Volume		
Meters	Square Meters	Per Cent of total	Meters	Square Meters	Cubic meters	Per Cent of total
0	397	100.0	0-1	56	372	39.3
1	341	85.9	1-5	325	575	60.5
5	16	4.0	5-5.5	16	3	0.2
			Total		950	

CARDINAL BOG

0   20   40 FEET

0   5   10 METERS

FIG. 5. Hydrographic map of Cardinal Bog. Depths are indicated in meters.

CLEAR LAKE

T. 39 N., R. 7 E., Sec. 9, 10, 15, 16, 17, 21

Length .... 3.36 km.	Mean depth .... 8.75 m.
Breadth .... 2.04 km.	Length of shoreline ..... 22.2 km.
Area ....417.77 ha.	Shore development 3.06
Maximum depth .... 29.3 m.	Number of soundings 1121

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	417.77	100.0	0-3	89.73	11,609,700	31.8
3	328.04	78.5	3-5	60.44	5,951,800	16.3
5	267.60	64.0	5-10	115.24	9,897,100	27.1
10	152.36	36.4	10-15	72.70	5,351,400	14.6
15	79.66	18.9	15-20	46.48	2,629,500	7.1
20	33.18	7.9	20-25	23.06	1,026,700	2.8
25	10.12	2.4		10.12	118,700	0.3
				Total	36,584,900	

CRYSTAL LAKE

T. 41 N., R. 7 E., Sec. 27, 28

Length ....710 m.	Mean depth .... 9.68 m.
Breadth ....510 m.	Length of shoreline .... 2.30 km.
Area .... 30.20 ha.	Shore development 1.11
Maximum depth .... 21.0 m.	Number of soundings ..226

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	30.20	100.0	0-2	7.03	531,800	18.2
2	23.17	76.7	2-5	3.31	645,300	22.1
5	19.86	65.7	5-10	4.12	889,000	30.4
10	15.74	52.1	10-15	6.75	611,500	20.9
15	8.99	2.3	15-18	5.05	189,800	6.5
18	3.94	1.3	18-20	1.58	51,200	1.8
20	1.36	0.4	20-21	1.36	4,500	0.1
				Total	2,923,100	

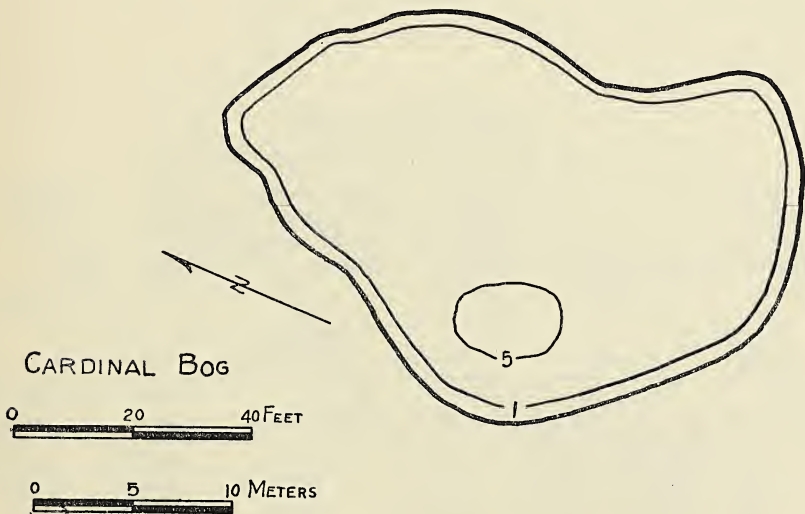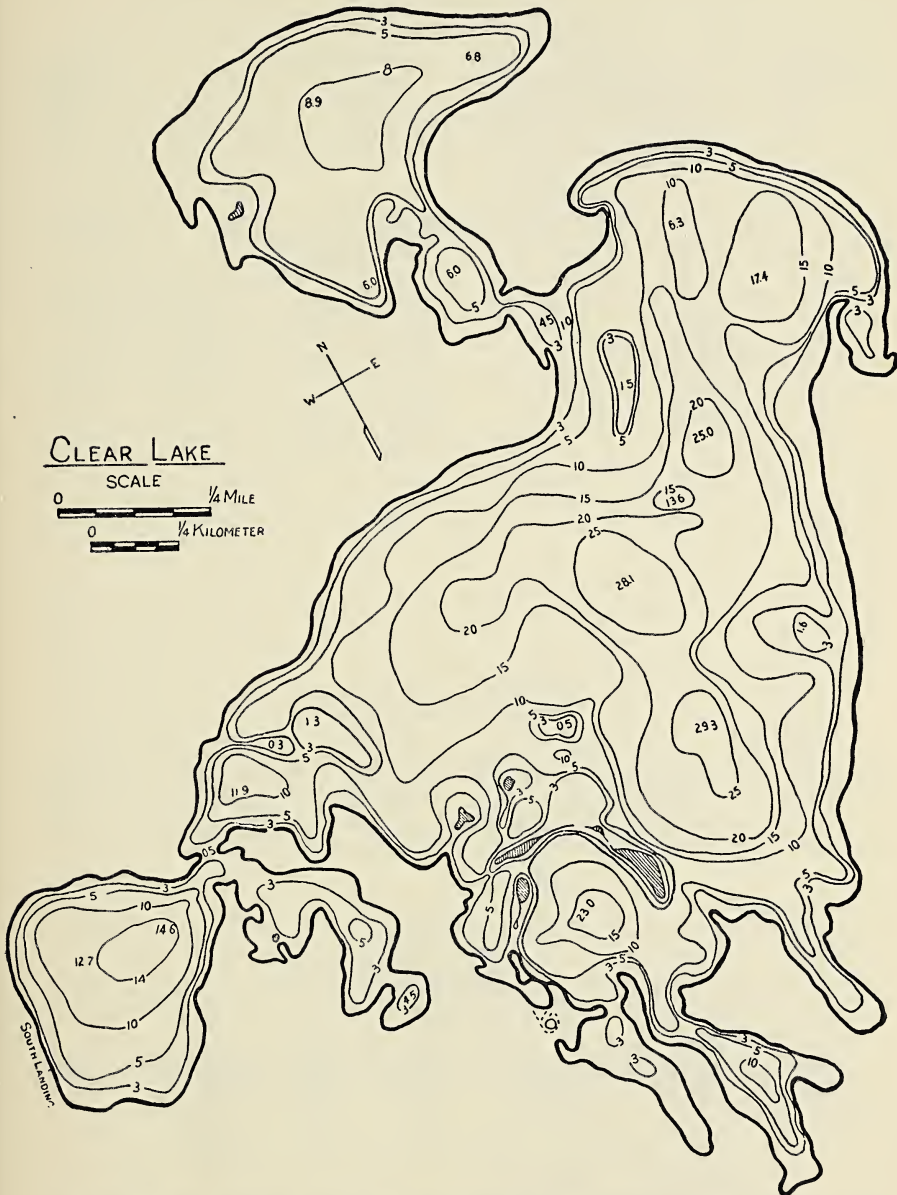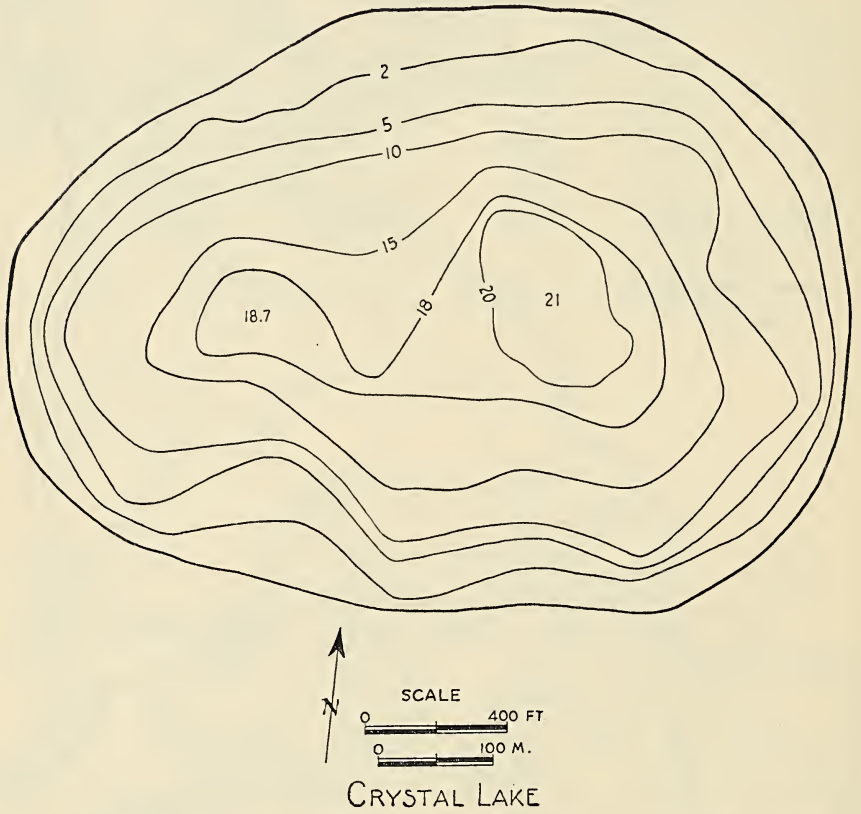Fig. 6. Hydrographic map of Clear Lake, Oneida County. Depths are indicated in meters.

Fig. 7. Hydrographic map of Crystal Lake. Depths are indicated in meters.

DIAMOND LAKE
T. 41 N., R. 6 E., Sec. 11

Length .... 1000 m.
Breadth .... 750 m.
Area .... 48.43 ha.
Maximum depth ...... 12.2 m.

Mean depth .... 7.0 m.
Length of shoreline ..... 3.25 km.
Shore development 1.31
Number of soundings ...93

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	48.43	100.0	0-2	5.36	915,000	27.0
2	43.07	88.5	2-4	4.99	811,000	24.0
4	38.08	78.5	4-6	6.46	696,000	20.6
6	31.62	65.3	6-8	9.16	538,000	15.9
8	22.46	46.4	8-10	11.16	331,000	9.8
10	11.30	23.3	10-12.2	11.30	94,000	2.7
				Total	3,385,000	

FINLEY LAKE
T. 40 N., R. 9 E., Sec. 30, 31

Length .... 1.2 km.
Breadth .... 0.8 km.
Area .... 62.78 ha.
Maximum depth .... 8.5 m.

Mean depth .... 5.43 m.
Length of shoreline .... 3.57 km.
Shore development 1.27
Number of soundings ..181

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	62.78	100.0	0-2	9.03	1,164,000	34.2
2	53.57	58.6	2-4	7.36	1,000,000	29.4
4	46.39	73.8	4-6	8.19	838,000	24.6
6	38.20	60.8	6-7	12.80	287,500	8.4
7	25.40	40.4	7-8	21.81	112,500	3.3
8	3.59	5.7	8-8.5	3.59	6,000	0.1
				Total	3,408,000	
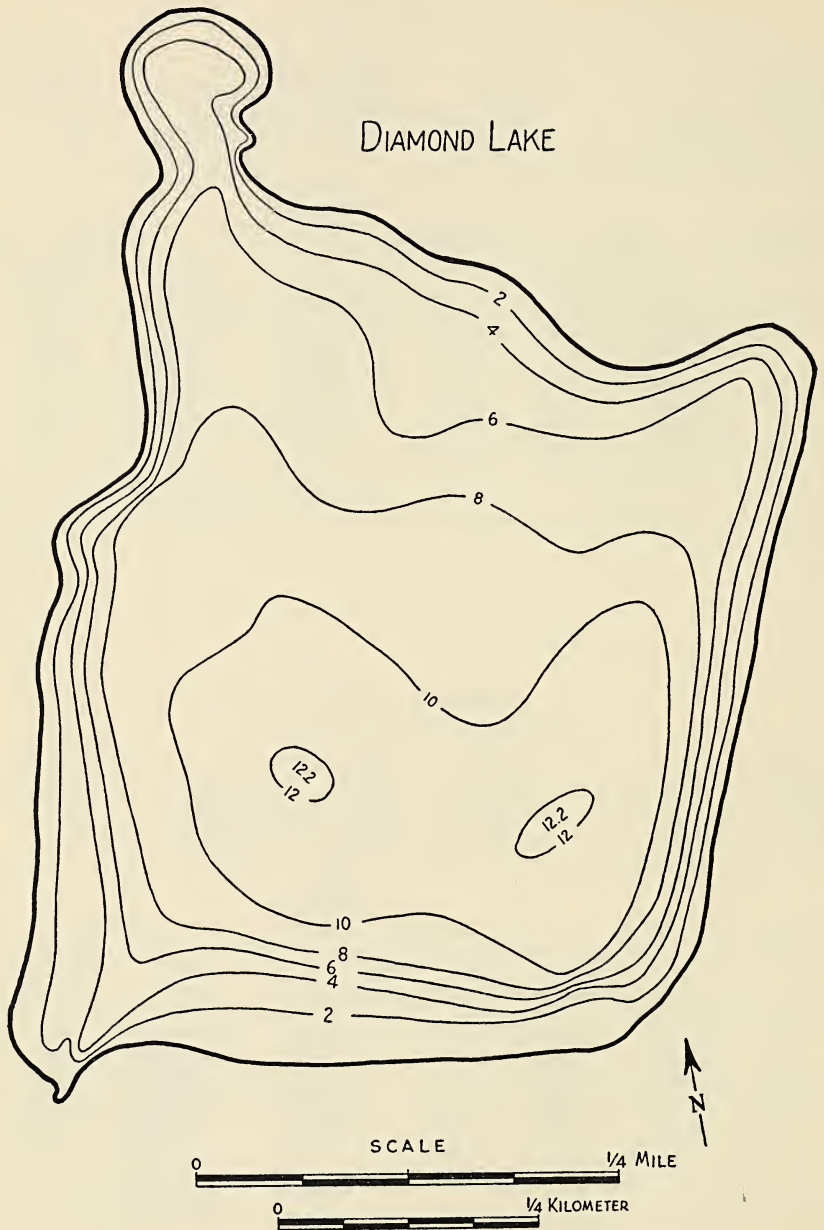
FIG. 8. Hydrographic map of Diamond Lake. Depths are indicated in meters.
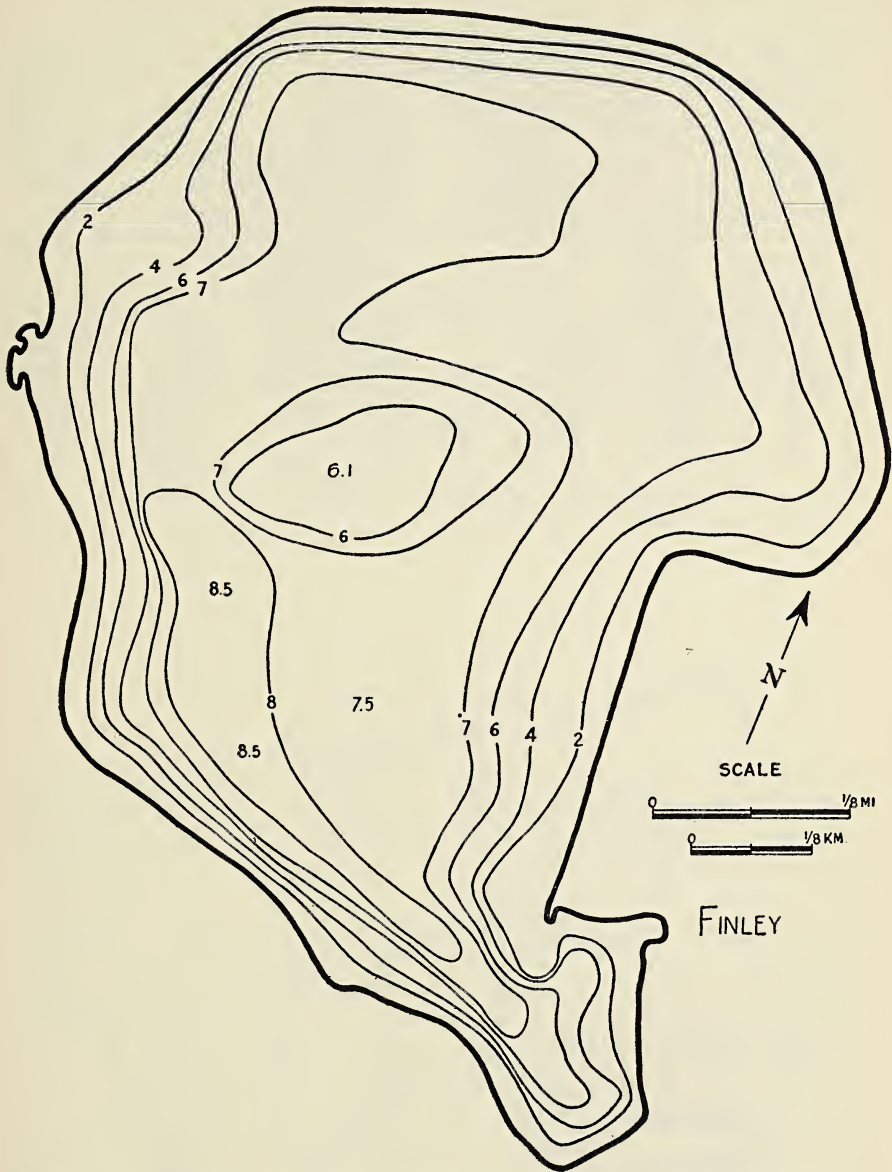
Fig. 9. Hydrographic map of Finley Lake. Depths are indicated in meters.

FORESTRY BOG

T. 41 N., R. 7 E., Sec. 8

Length .... 52 m.   Mean depth .... 1.06 m.
Breadth .... 30 m.   Length of shoreline ...... 200 m.
Area ....1011 sq. m.   Shore development 1.75
Maximum depth ...... 2.25 m.   Number of soundings 12

Depth	Area		Stratum	Area between contours	Volume	
Meters	Square Meters	Per Cent of total	Meters	Square Meters	Cubic meters	Per Cent of total
0	1011	100.0	0-2	840	1,065	98.9
2	170	16.9	2-2.25	170	14	1.1
				Total	1,079	

FORESTRY BOG

0   30 FEET

0   10 METERS

FIG. 10. Hydrographic map of Forestry Bog. Depths are indicated in meters.

LAKE HELEN

T. 44 N., R. 5 E., Sec. 32

Length .... 385 m.   Mean depth .... 4.37 m.
Breadth .... 325 m.   Length of shoreline ..... 1.40 km.
Area .... 5.97 ha. Shore development 1.61
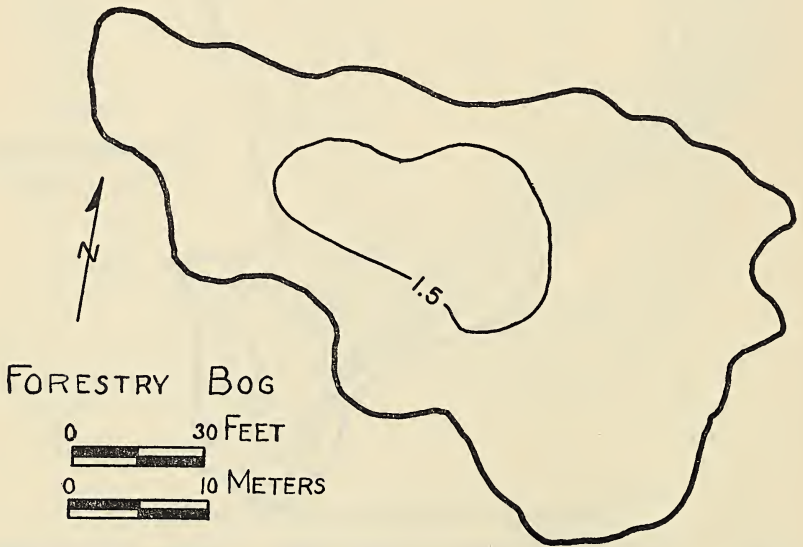Maximum depth .... 16.0 m.   Number of soundings ...45

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	5.97	100.0	0-2	1.65	102,450	39.2
2	4.32	72.3	2-5	2.39	91,330	35.00
5	1.93	32.3	5-8	1.04	41,280	15.80
8	0.89	14.9	8-10	0.37	13,900	5.32
10	0.52	8.7	10-12	0.27	7,550	2.9
12	0.25	4.1	12-14	0.14	3,590	1.4
14	0.11	1.8	14-16	0.11	1,000	0.4
				Total	261,000	

HELMET LAKE

T. 43 N., R. 7 E., Sec. 20

Length .... 310 m.   Mean depth .... 4.11 m.
Breadth .... 210 m.   Length of shoreline .....985 m.
Area .... 3.00 ha. Shore development 1.6
Maximum depth .... 10.4 m.   Number of soundings ... 53

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	3.00	100.0	0-2	0.90	50,660	41.2
2	2.10	70.0	2-4	0.63	35,520	28.8
4	1.47	49.0	4-6	0.53	23,930	19.4
6	0.94	31.3	6-8	0.71	10,860	8.8
8	0.23	7.6	8-10	0.20	2,230	1.8
10	0.03	1.0	10-10.4	0.03	30	0.0
				Total	123,230	
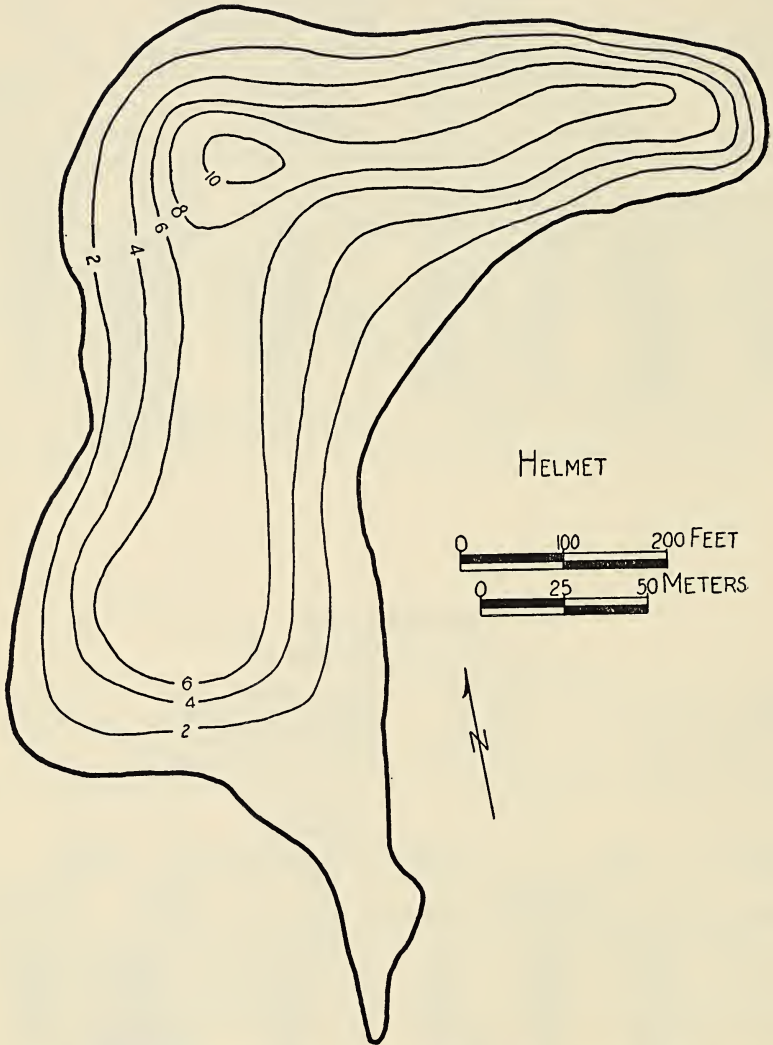
FIG. 11. Hydrographic map of Helmet Lake. Depths are indicated in meters.

SCALE

0 ——————— 400 FT.

0 ——————— 100 M.
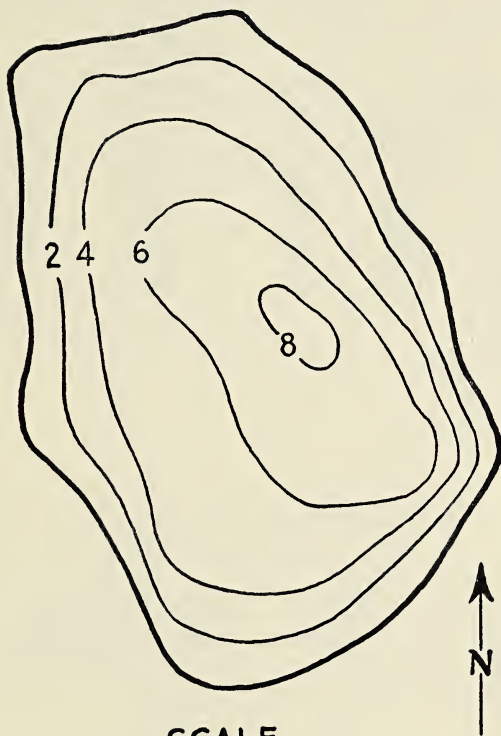
HILLIS LAKE

FIG. 12. Hydrographic map of Hillis Lake. Depths are indicated in meters.

HILLIS LAKE

T. 40 N., R. 6 E., Sec. 35

Length .... 325 m.   Mean depth ....   3.93 m.
Breadth .... 225 m.   Length of shoreline ..... 910 m.
Area ....   5.21 ha.   Shore development 1.13
Maximum depth ....   9.0 m.   Number of soundings ... 28

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	5.21	100.0	0-2	1.29	91,000	44.4
2	3.92	75.2	2-4	1.20	66,000	32.2
4	2.72	52.2	4-6	1.58	37,500	18.3
6	1.14	21.8	6-8	0.39	10,100	5.0
8	0.75	14.3	8-9	0.75	300	0.1
――――				Total	204,900	

LITTLE BASS LAKE

T. 40 N., R. 6 E., Sec. 26, 35

Length .... 385 m.   Mean depth .... 5.41 m.
Breadth .... 280 m.   Length of shoreline ..... 1.09 km.
Area ....   6.63 ha.   Shore development 1.20
Maximum depth .... 14 m.   Number of soundings ...38

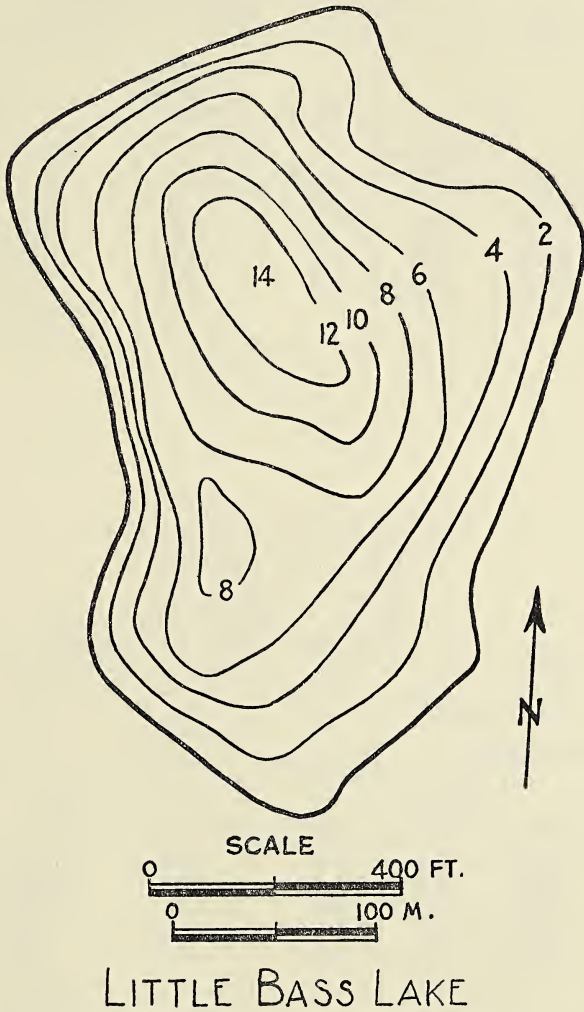| Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	6.63	100.0	0-2	1.46	117,600	32.9
2	5.17	78.0	2-4	1.20	91,200	25.5
4	3.97	59.9	4-6	1.11	68,100	18.9
6	2.86	43.1	6-8	1.20	44,700	12.5
8	1.66	25.0	8-10	0.84	23,400	6.5
10	0.82	16.3	10-12	0.48	11,200	3.1
12	0.34	5.1	12-14	0.34	2,200	0.6
				Total	358,400	

SCALE

0 _____ 400 FT.

0 _____ 100 M.

LITTLE BASS LAKE

FIG. 13. Hydrographic map of Little Bass Lake. Depths are indicated in meters.

LITTLE JOHN LAKE

T. 41 N., R. 7 E., Sec. 20, 29

Length .... 1.04 km.
Breadth .... 0.60 km.
Area ....67.20 ha.
Maximum depth .... 6.0 m.

Mean depth .... 3.77 m.
Length of shoreline ..... 4.8 km.
Shore development 1.65
Number of soundings 145

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	67.20	100.0	0-2	14.53	1,196,200	47.1
2	52.67	78.4	2-4	13.64	919,500	36.2
4	39.03	58.6	4-5	12.97	323,300	12.8
5	26.06	38.8	5-6	26.06	98,200	3.9
			Total		2,537,200	

LITTLE JOHN JUNIOR LAKE

T 41 N., R. 7 E., Sec. 28, 29

Length .... 413 m.
Breadth .... 382 m.
Area .... 8.62 ha.
Maximum depth .... 9.4 m.

Mean depth .... 3.46 m.
Length of shoreline .... 1.30 km.
Shore development 1.25
Number of soundings ...109

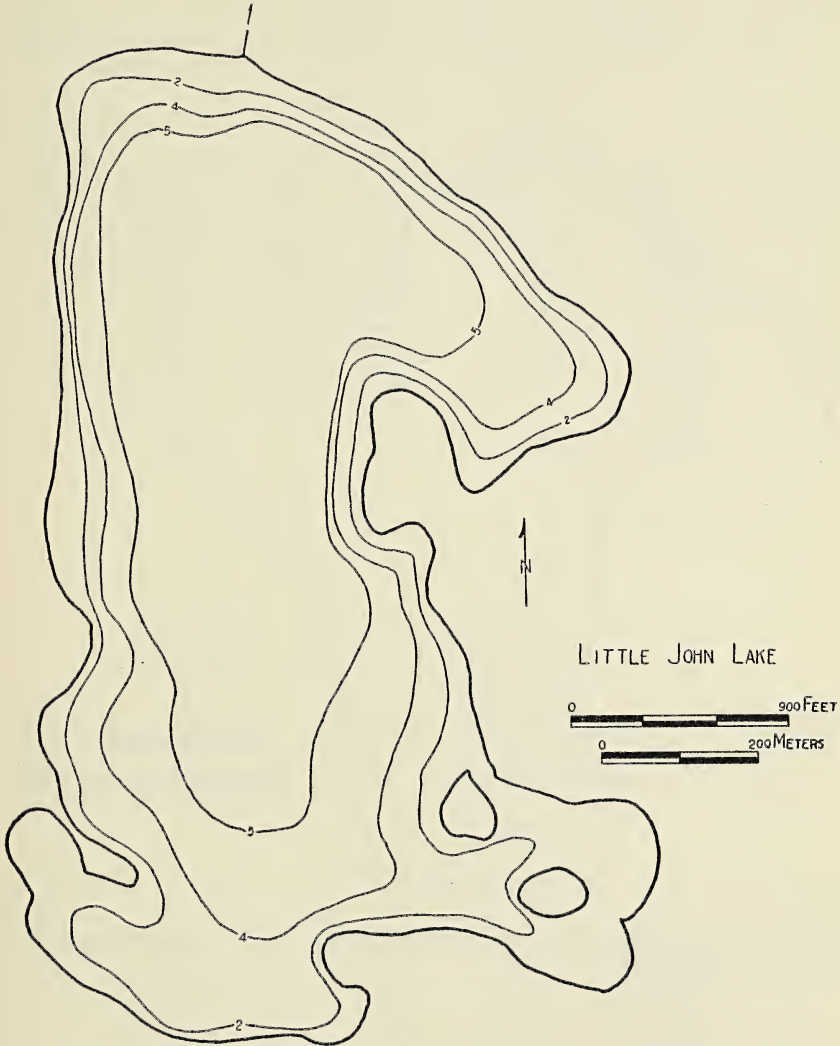| Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	8.62	100.0	0-2	2.00	151,880	50.9
2	6.62	76.8	2-4	2.72	103,950	34.9
4	3.90	45.2	4-6	3.45	37,770	12.6
6	0.45	5.2	6-8	0.40	4,380	1.5
8	0.05	0.6	8-9.4	0.05	250	0.1
			Total		298,230	

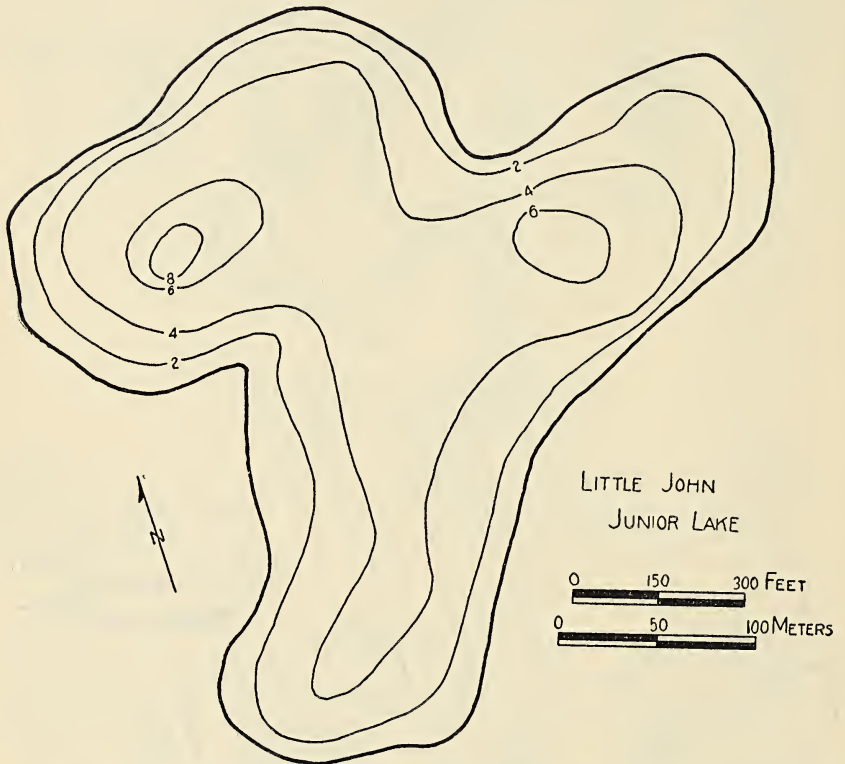Fɪɢ. 14. Hydrographic map of Little John Lake. Depths are indicated in meters.

Fig. 15. Hydrographic map of Little John Junior Lake. Depths are indicated in meters.

LITTLE LONG LAKE

T. 43 N., R. 5 E., Sec. 23

Length .... 790 m. Mean depth .... 8.43 m.
Breadth .... 260 m. Length of shoreline ..... 1.97 km.
Area .... 14.59 ha. Shore development 1.45
Maximum depth .... 18.0 m. Number of soundings ...80

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	14.59	100.0	0-2	1.94	272,200	22.2
2	12.65	86.7	2-5	2.43	342,400	27.9
5	10.22	70.0	5-8	2.61	266,400	21.7
8	7.61	52.1	8-10	1.56	136,200	11.0
10	6.05	41.4	10-12	1.91	101,300	8.2
12	4.14	28.3	12-14	1.68	65,300	5.3
14	2.46	16.7	14-16	1.22	36,300	2.9
16	1.24	8.5	16-18	1.24	9,700	0.8
			Total		1,229,800	

LOST CANOE LAKE

T. 42 N., R. 7 E., Sec. 34, 35

Length .... 1.8 km. Mean depth .... 6.58 m.
Breadth .... 0.7 km. Length of shoreline .... 6.45 km.
Area .... 96.47 ha. Shore development 1.85
Maximum depth .... 12.5 m. Number of soundings ...342

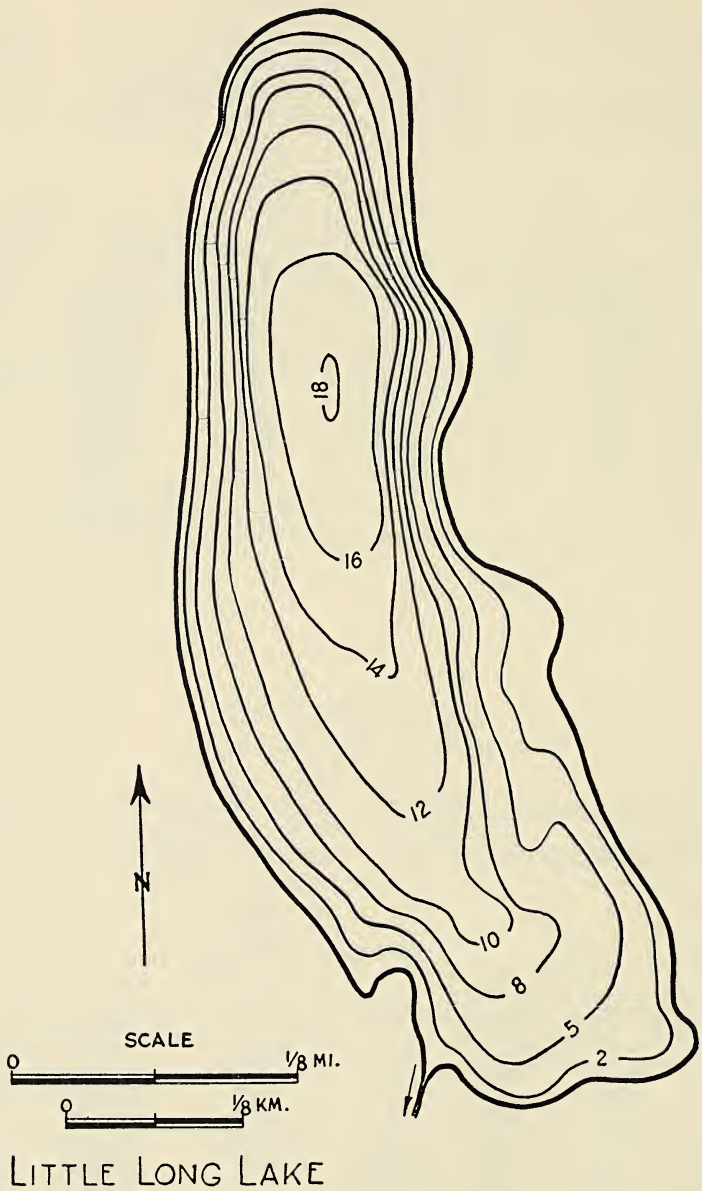| Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	96.47	100.0	0-2	16.49	1,762,800	27.9
2	79.98	82.9	2-4	13.40	1,463,500	23.1
4	66.58	68.8	4-6	10.21	1,228,100	19.4
6	56.37	58.4	6-8	14.59	977,900	15.4
8	41.78	43.3	8-10	17.15	652,600	10.3
10	24.63	25.6	10-12	21.37	245,200	3.9
12	3.26	3.4	12-12.5	3.26	16,300	0.0
			Total		6,346,400	

FIG. 16. Hydrographic map of Little Long Lake. Depths are indicated in meters.
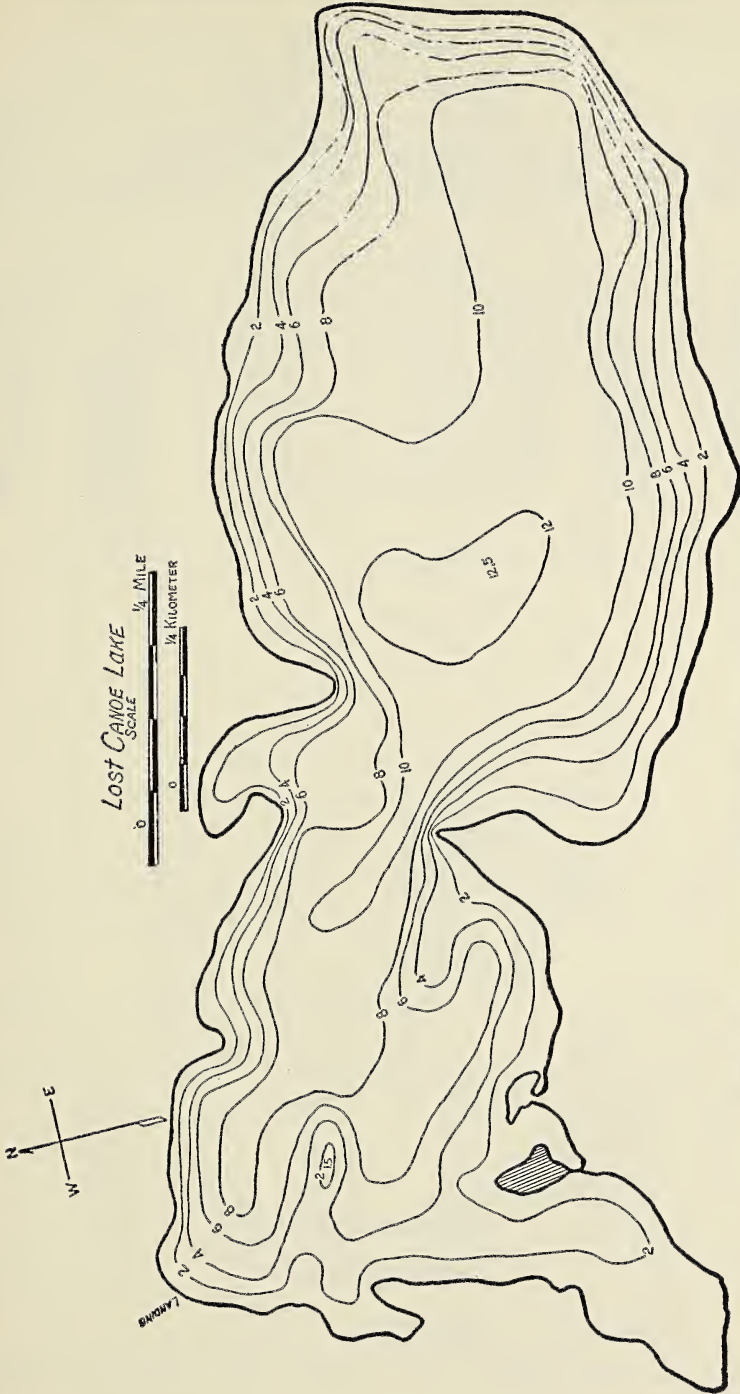
Fig. 17. Hydrographic map of Lost Canoe Lake. Depths are indicated in meters.

MIDGE LAKE

T. 41 N., R. 6 E., Sec. 25

Length .... 275 m.   Mean depth ....   4.45 m.
Breadth .... 205 m.   Length of shoreline ..... 727 m.
Area ....   3.41 ha.   Shore development 1.11
Maximum depth .... 11.6 m.   Number of soundings ... 43

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	3.41	100.0	0-2	1.18	56,000	36.5
2	2.23	65.3	2-4	0.55	38,900	25.5
4	1.68	49.2	4-6	0.48	28,700	18.8
6	1.20	35.1	6-8	0.47	19,000	12.5
8	0.73	22.2	8-10	0.50	9,200	6.0
10	0.23	6.7	10-11.6	0.23	1,200	0.7
			Total		153,000	
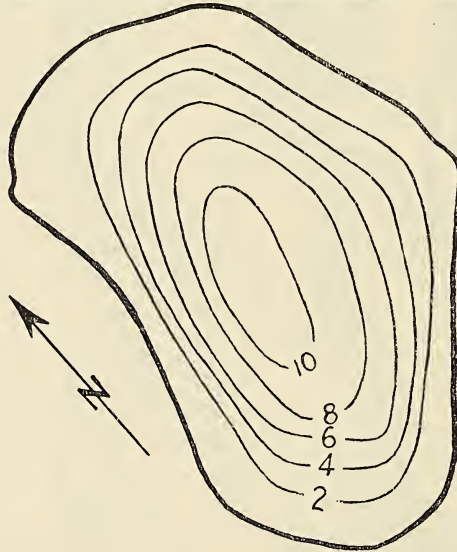
FIG. 18. Hydrographic map of Midge Lake. Depths are indicated in meters.

LAKE MARY

T. 44 N., R. 5 E., Sec. 32

Length .... 125 m.　　Mean depth .... 7.76 m.
Breadth .... 120 m.　　Length of shoreline ..... 415 m.
Area .... 1.2 ha.　　Shore development 1.07
Maximum depth .... 21.5 m.　　Number of soundings 24

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	1.20	100.0	0-2	0.25	21,430	23.2
2	0.95	79.1	2-5	0.23	25,000	27.0
5	0.72	60.0	5-10	0.33	27,270	29.4
10	0.39	32.5	10-15	0.20	14,340	15.5
15	0.19	15.8	15-20	0.17	4,450	4.8
20	0.02	1.6	20-21.5	0.02	110	0.1
			Total		92,600	

MUSKELLUNGE LAKE

T. 41 N., R. 7 E., Sec. 15, 16, 21, 22, 27, 28

Length .... 3.1 km.　　Mean depth .... 7.02 m.
Breadth .... 2.0 km.　　Length of shoreline ..... 14.5 km.
Area ....372.34 ha.　　Shore development 2.12
Maximum depth .... 20.7 m.　　Number of soundings 315

| Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	372.34	100.0	0-2	102.29	6,396,500	24.5
2	270.05	72.5	2-5	54.68	7,266,800	27.8
5	215.37	57.8	5-8	56.71	5,588,800	21.3
8	158.66	42.6	8-10	51.64	2,639,900	10.1
10	107.02	28.7	10-14	52.30	3,110,300	11.8
14	54.72	14.6	14-16	26.56	813,200	3.1
16	28.16	7.5	16-18	22.64	307,700	1.2
18	5.52	1.4	18-20	5.19	48,000	0.2
20	0.33	0.1	20-20.7	0.33	800	0.0
			Total		26,172,000	
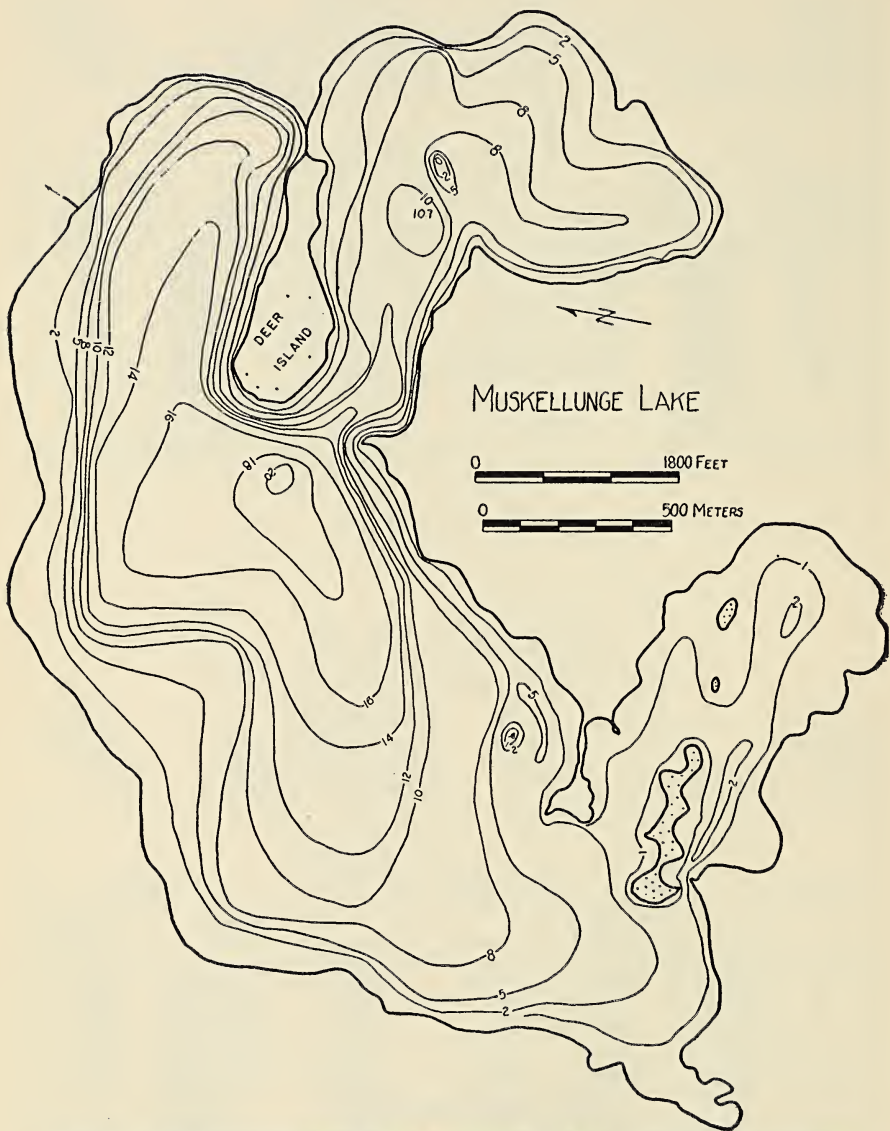
FIG. 19. Hydrographic map of Muskellunge Lake. Depths are indicated in meters.
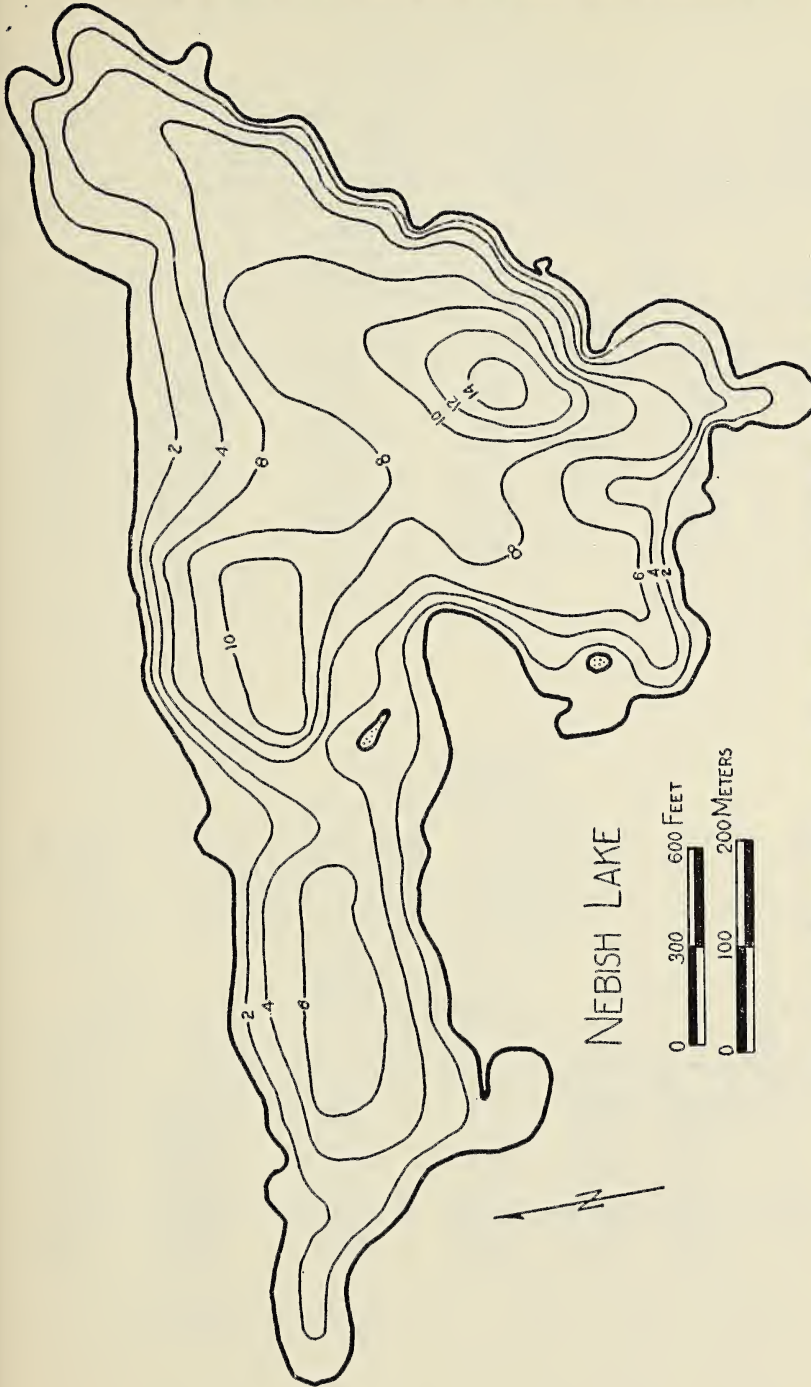
FIG. 20. Hydrographic map of Nebish Lake. Depths are indicated in meters.

NEBISH LAKE

T 41 N., R. 7 E., Sec. 10, 11

Length .... 1.32 km.   Mean depth .... 5.24 m.
Breadth .... 0.66 km.   Length of shoreline ..... 4.2 km.
Area ....38.47 ha.   Shore development 1.90
Maximum depth ....15.8 m.   Number of soundings 156

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	38.47	100.0	0-2	7.61	691,200	34.4
2	30.86	80.2	2-4	7.12	545,600	27.2
4	23.74	61.2	4-6	7.35	400,000	19.8
6	16.39	42.6	6-8	8.41	238,500	11.8
8	7.98	24.8	8-10	5.36	96,500	4.8
10	2.62	6.8	10-12	1.78	33,000	1.6
12	0.84	2.1	12-14	0.65	9,400	0.4
14	0.19	0.4	14-15.8	0.19	1,100	0.0
				Total	2,015,300	

NELSON LAKE

T. 42 N., R. 6 E., Sec. 31

Length .... 485 m.   Mean depth .... 6.80 m.
Breadth .... 350 m.   Length of shoreline ..... 1.45 km.
Area .... 11.80 ha.   Shore development 1.19
Maximum depth .... 14.8 m.   Number of soundings 81

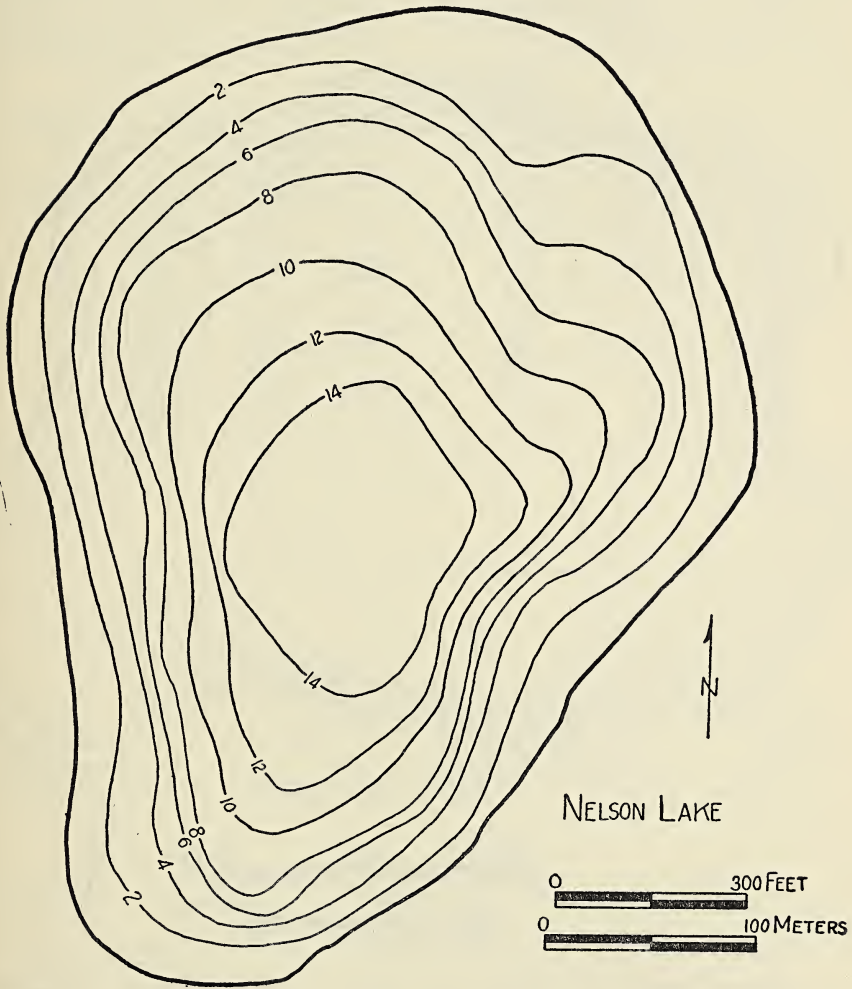| Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	11.80	100.0	0-2	2.48	210,750	26.3
2	9.32	79.0	2-4	1.85	167,560	20.9
4	7.47	63.3	4-6	1.29	136,290	17.0
6	6.18	52.3	6-8	1.22	111,140	13.9
8	4.96	42.0	8-10	1.58	82,810	10.3
10	3.38	28.6	10-12	1.17	55,440	6.9
12	2.21	18.7	12-14	0.99	33,790	4.2
14	1.22	10.3	14-14.8	1.22	4,220	0.5
				Total	802,000	

FIG. 21. Hydrographic map of Nelson Lake. Depths are indicated in meters.
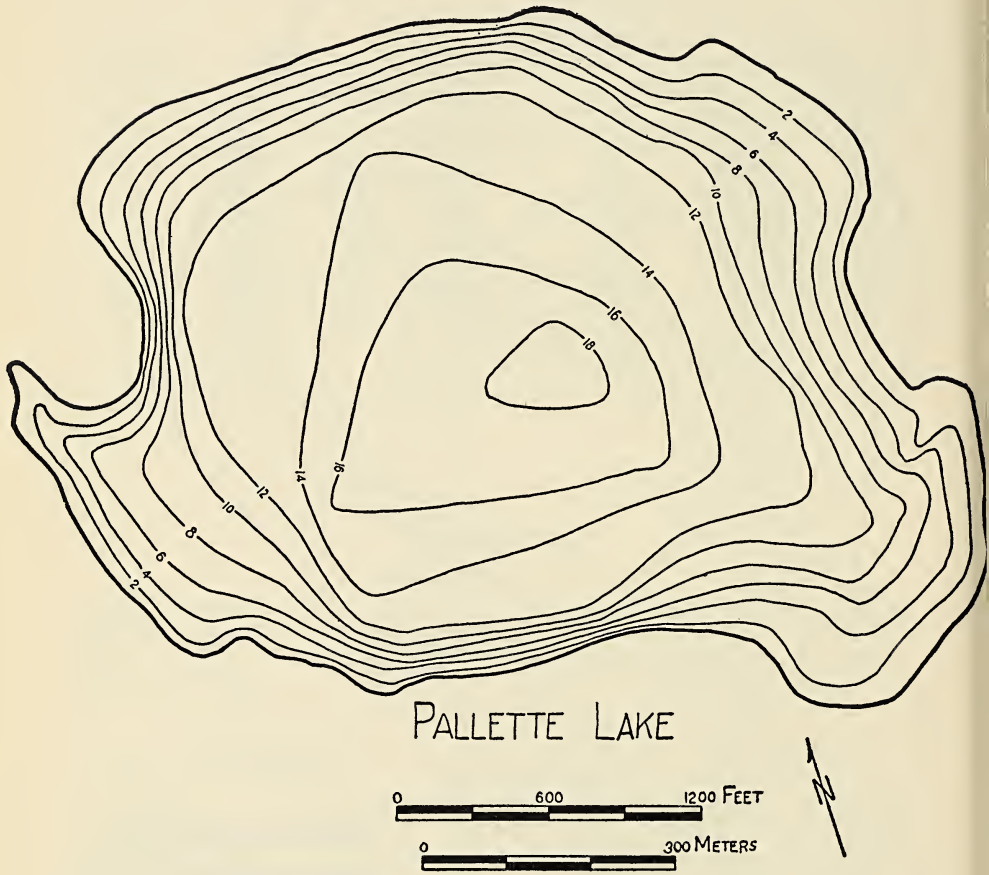
FIG. 22. Hydrographic map of Pallette Lake. Depths are indicated in meters.

PALLETTE LAKE

T. 41 & 42 N., R. 7 E., Sec. 3, 34

Length .... 1.14 km.	Mean depth .... 9.73 m.
Breadth .... 0.78 km.	Length of shoreline ..... 3.56 km.
Area ....68.58 ha.	Shore development 1.21
Maximum depth ....18.0 m.	Number of soundings ...144

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	68.56	100.0	0-2	6.56	1,305,000	19.5
2	62.00	90.4	2-4	6.39	1,175,700	17.5
4	55.61	81.1	4-6	5.61	1,055,300	15.1
6	50.00	72.9	6-8	5.46	895,300	13.3
8	44.54	64.9	8-10	5.61	834,000	12.4
10	38.93	57.9	10-12	6.37	713,900	10.6
12	32.56	47.5	12-14	14.51	499,000	7.4
14	18.05	26.3	14-16	9.33	131,000	1.9
16	8.72	12.7	16-18	8.72	85,800	1.3
18	1.08	1.5				
			Total		6,695,000	

PAUTO LAKE

T. 41 N., R. 6 E., Sec. 35

Length .... 480 m.	Mean depth .... 6.85 m.
Breadth .... 280 m.	Length of shoreline ...... 1.52 km.
Area .... 10.48 ha.	Shore development 1.32
Maximum depth .... 17.2 m.	Number of soundings ...82

| Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	10.48	100.0	0-2	1.70	192,300	27.0
2	8.78	83.7	2-4	1.54	160,000	22.5
4	7.24	68.9	4-6	1.87	125,600	17.5
6	5.37	50.8	6-8	1.35	93,600	12.6
8	4.02	38.3	8-10	1.46	65,200	9.1
10	2.56	24.4	10-12	0.96	41,000	5.7
12	1.60	15.2	12-14	0.66	25,000	3.5
14	0.94	8.9	14-16	0.50	13,500	1.9
16	0.44	4.1	16-17.2	0.44	1,800	0.2
			Total		718,000	
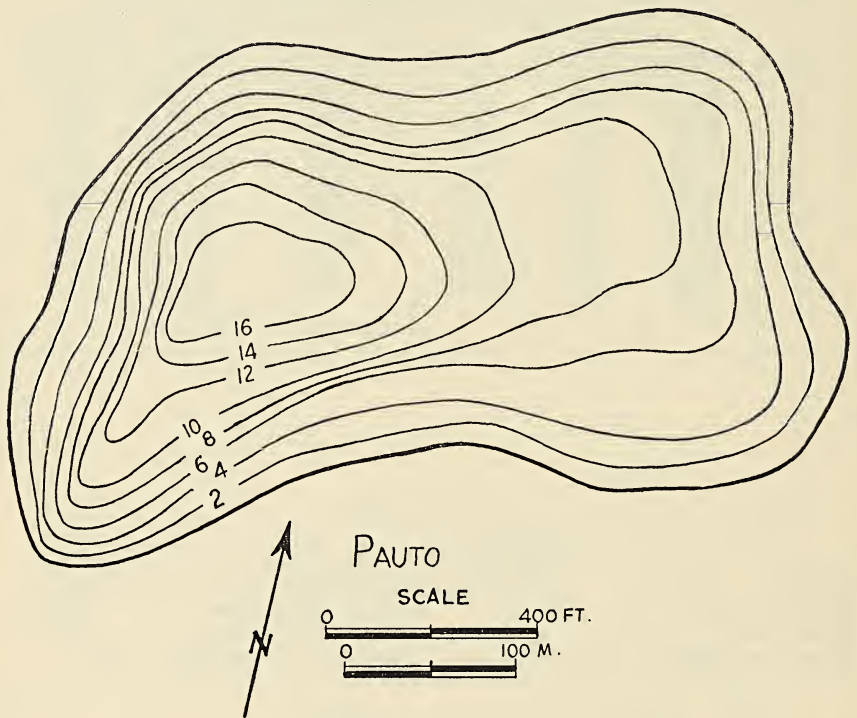
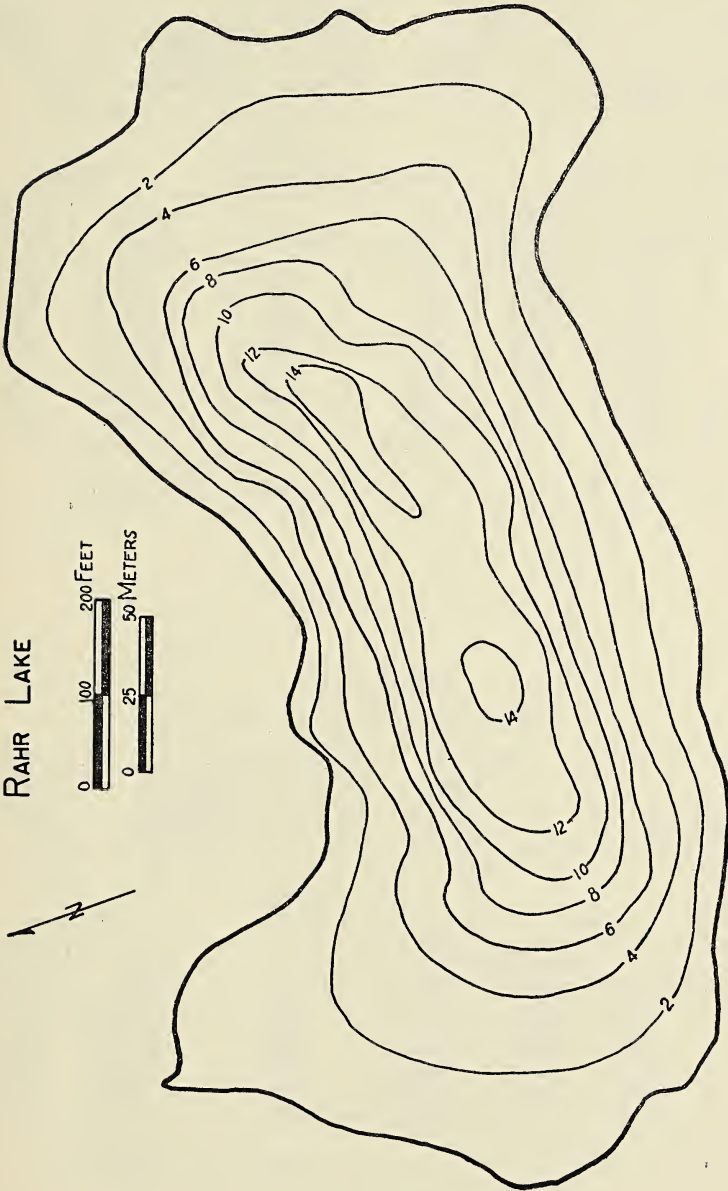FIG. 23 Hydrographic map of Pauto Lake. Depths are indicated in meters.

FIG. 24. Hydrographic map of Rahr (Mud) Lake. Depths are indicated in meters.

RAHR LAKE (MUD)

T. 43 N., R. 7 E., Sec. 27

Length .... 390 m.	Mean depth .... 4.93 m.
Breadth .... 170 m.	Length of shoreline ..... 1.17 km.
Area .... 5.48 ha.	Shore development 1.41
Maximum depth .... 15.7 m.	Number of soundings .. 137

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	5.48	100.0	0-2	1.72	88,570	32.8
2	3.76	68.6	2-4	1.23	65,530	24.3
4	2.53	46.1	4-6	0.74	42,780	15.8
6	1.79	32.6	6-8	0.49	30,750	11.3
8	1.30	23.7	8-10	0.38	22,100	8.2
10	0.92	16.7	10-12	0.38	14,440	5.3
12	0.54	9.8	12-14	0.44	5,800	2.1
14	0.10	1.8	14-15.7	0.10	470	0.2
			Total		270,440	

ROSE LAKE

T. 44 N., R. 5 E., Sec. 32

Length .... 210 m.	Mean depth .... 5.17 m.
Breadth .... 92 m.	Length of shoreline ..... 523 m.
Area .... 1.43 ha.	Shore development 1.24
Maximum depth .... 13.0 m.	Number of soundings 27

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	1.43	100.0	0-2	0.38	24,700	33.4
2	1.05	73.4	2-5	0.39	25,440	34.4
5	0.66	46.1	5-10	0.45	20,690	28.0
10	0.21	14.6	10-12	0.13	2,850	3.9
12	0.08	5.5	12-13	0.08	210	0.3
			Total		73,890	
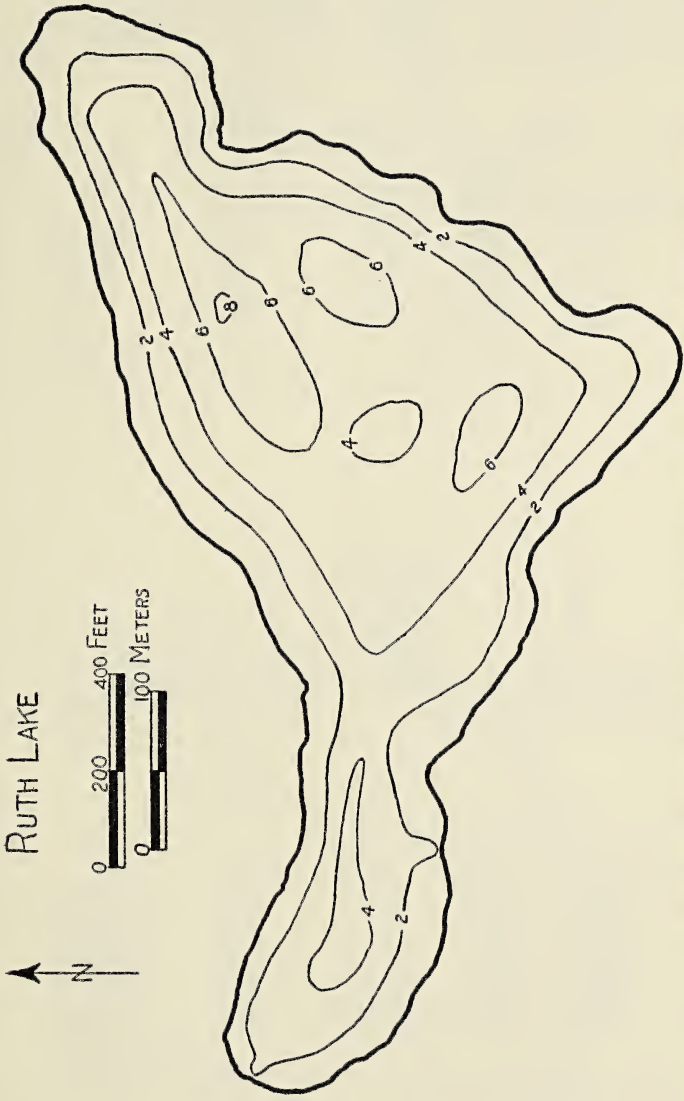
Fig. 25. Hydrographic map of Ruth Lake. Depths are shown in meters.

RUTH LAKE

T. 41 N., 7 E., Sec. 32, 33

Length .... 610 m.	Mean depth .... 3.40 m.
Breadth .... 360 m.	Length of shoreline ..... 1.95 km.
Area .... 11.72 ha.	Shore development 1.59
Maximum depth .... 8.5 m.	Number of soundings ... 65

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	11.72	100.0	0-2	3.20	201,600	50.6
2	8.50	72.6	2-4	3.40	135,070	34.0
4	5.10	43.6	4-6	4.00	55,140	13.9
6	1.10	9.4	6-8	1.10	5,860	1.5
8	0.02	0.0	8-8.5	0.02	30	0.0
			Total		397,700	

SILVER LAKE

T. 41 N., R. 6 E., Sec. 23, 24, 25, 26

Length .... 1.75 km.	Mean depth .... 11.32 m.
Breadth .... 0.66 km.	Length of shoreline .... 4.34 km.
Area .... 87.30 ha.	Shore development 1.31
Maximum depth 19.5	Number of Soundings .. 144

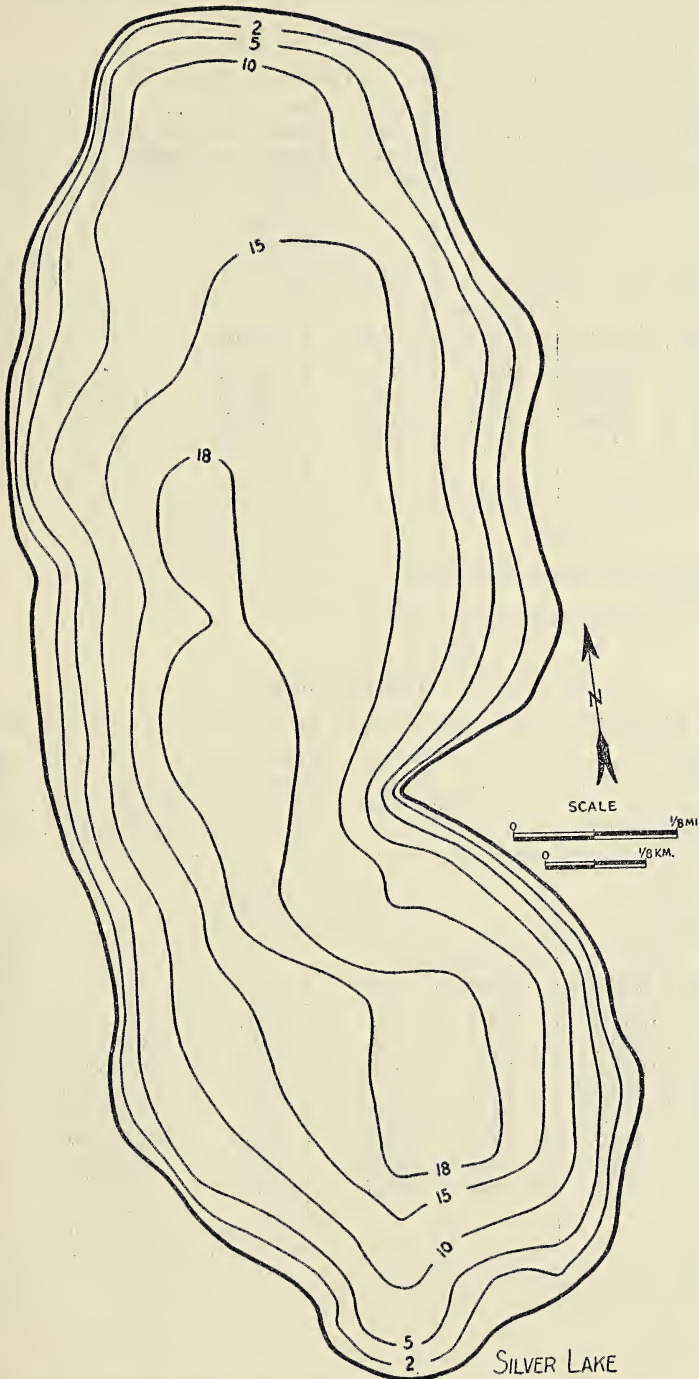| Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	87.30	100.0	0-2	7.99	1,665,700	16.9
2	79.31	90.8	2-5	9.18	2,240,000	22.7
5	70.13	80.3	5-10	14.66	3,132,900	31.7
10	55.47	62.4	10-15	22.42	2,188,900	22.1
15	22.05	37.8	15-18	23.30	607,500	6.1
18	9.75	11.2	18-19.5	9.75	48,700	0.5
			Total		9,883,700	

FIG. 26. Hydrographic map of Silver Lake. Depths are indicated in meters.

SWEENEY LAKE

T. 39 N., R. 7 E., Sec. 14, 15, 22, 23

Length .... 1.6 km.   Mean depth .... 3.08 m.
Breadth .... 0.76 km.   Length of shoreline .... 4.42 km.
Area .... 73.46 ha. Shore development 1.45
Maximum depth .... 5.7 m.   Number of soundings ... 332

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	73.46	100.0	0-1	9.44	686,800	30.3
1	64.02	87.1	1-3	23.16	1,040,200	46.0
3	40.86	55.6	3-5	28.98	498,600	22.1
5	11.88	16.1	5-5.7	11.88	35.800	1.6
			Total		2,261,400	

TROUT LAKE

T. 41, 42 N., R. 6, 7 E., Sec. 5, 6, 7, 8, 12, 13, 14, 17, 18, 19, 20, 31, 32

Length .... 7.0 km.   Mean depth .... 13.77 m.
Breadth .... 4.0 km.   Length of shoreline ..... 25.9 km.
Area .... 1583.4 ha. Shore development 1.83
Maximum depth .... 35 m.   Number of soundings ... 1250

| Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	1583.4	100.0	0-3	232.5	43,917,000	20.2
3	1350.9	85.3	3-5	141.9	26,921,000	12.4
5	1209.0	76.3	5-10	272.0	53,495,000	24.6
10	937.0	59.1	10-15	276.0	39,745,000	18.1
15	661.0	41.7	15-20	226.8	27,165,000	12.5
20	434.2	27.2	20-25	175.7	17,108,000	7.8
25	258.5	16.3	25-30	172.9	8,141,000	3.7
30	85.6	5.4	30-35	85.6	1,545,000	0.7
			Total		218,037,000	
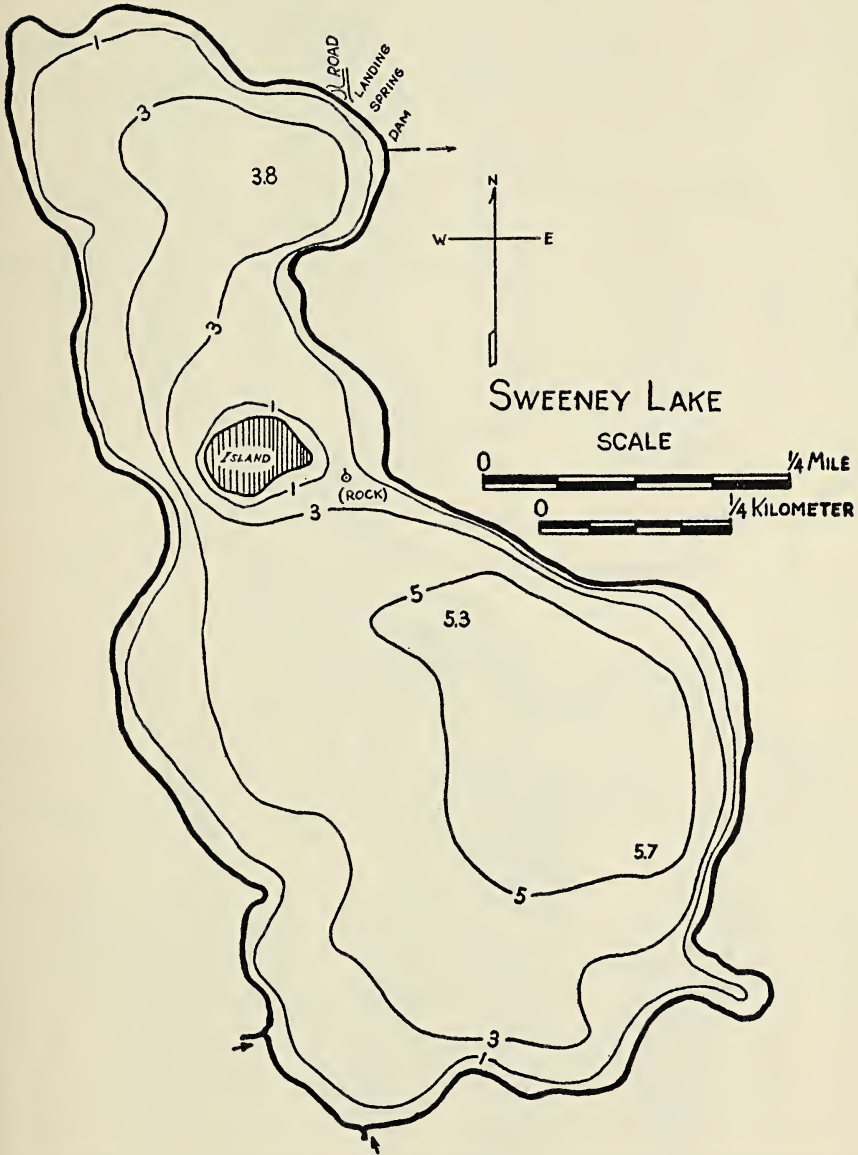
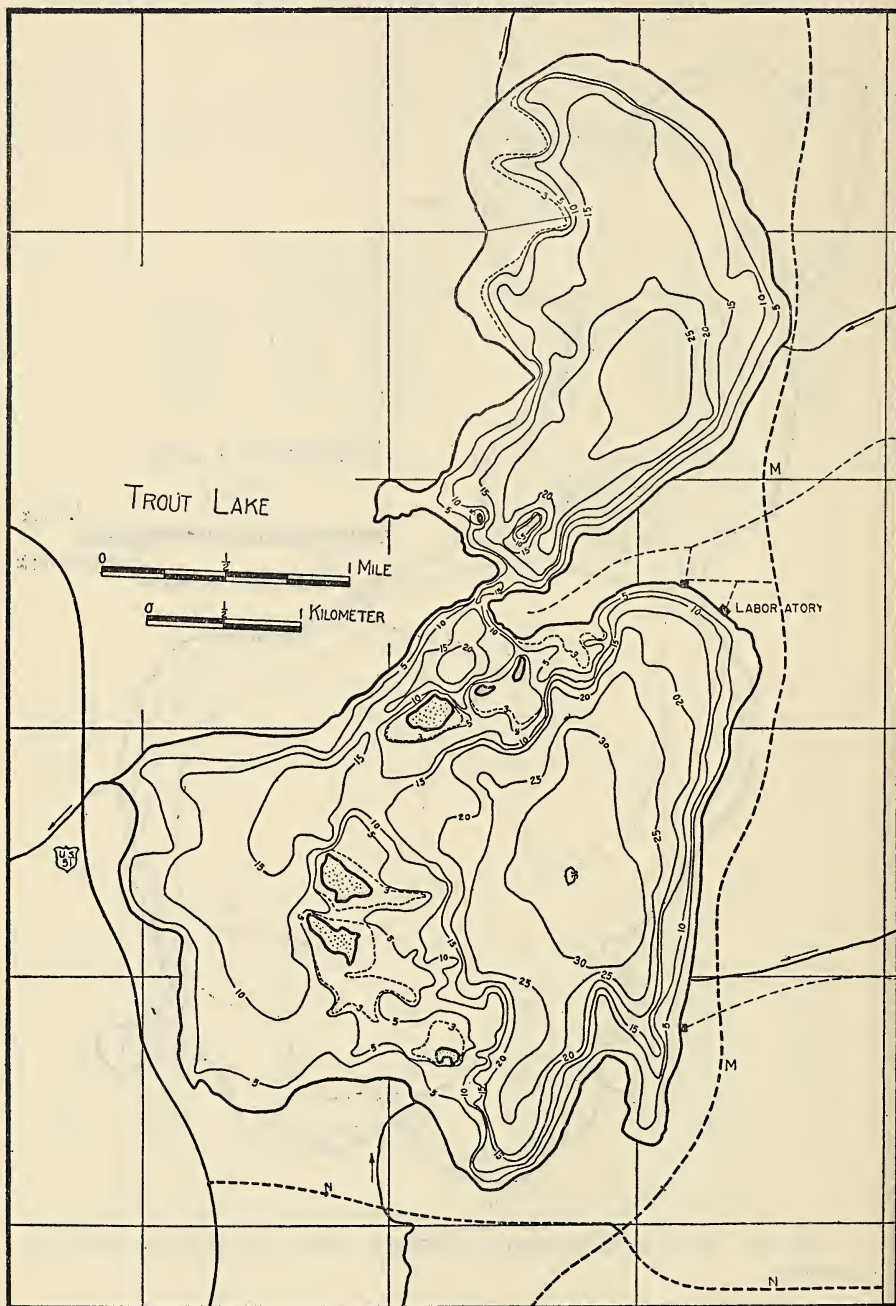FIG. 27. Hydrographic map of Sweeney Lake. Depths are indicated in meters.

FIG. 28. Hydrographic map of Trout Lake. Depths are indicated in meters.

WEBER LAKE

T. 41 N., R. 7 E., Sec. 28, 33

Length .... 554 m.   Mean depth .... 7.24 m.
Breadth .... 360 m.   Length of shoreline .... 1.60 km.
Area .... 15.61 ha.   Shore development 1.14
Maximum depth .... 13.5 m.   Number of soundings ... 121

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	15.61	100.0	0-2	3.22	279,400	24.7
2	12.39	79.3	2-4	1.44	233,300	20.5
4	10.95	70.1	4-6	1.30	205,900	18.2
6	9.65	61.8	6-8	1.73	175,500	15.5
8	7.92	50.7	8-10	1.91	138,900	12.3
10	6.01	38.5	10-12	3.22	86,000	7.6
12	2.79	17.8	12-13.5	2.79	13,900	1.2
				Total	1,132,900	

WHITE SAND LAKE

T. 42 N., R. 7 E., Sec. 26, 27, 35

Length .... 2.3 km.   Mean depth .... 8.91 m.
Breadth .... 1.2 km.   Length of shoreline ..... 7.8 km.
Area .... 216.16 ha.   Shore development 1.50
Maximum depth .... 21.0 m.   Number of soundings ... 165

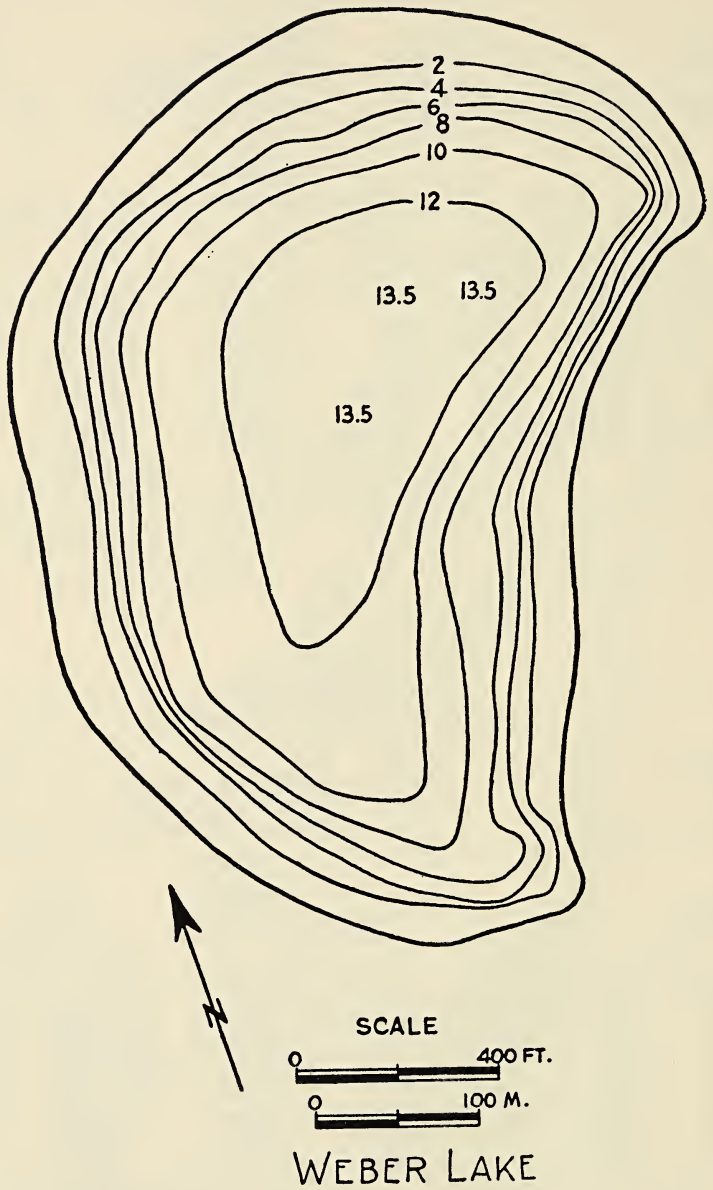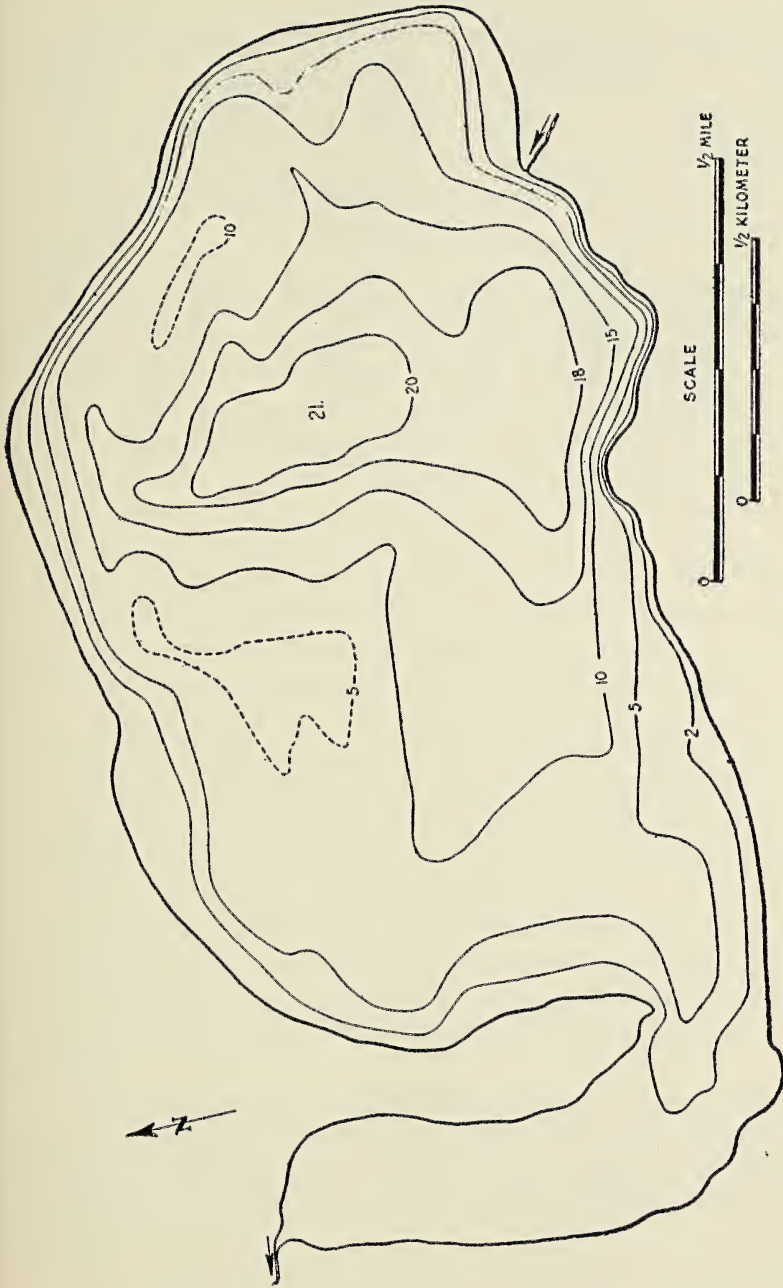| Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	216.16	100.0	0-2	40.44	3,911,900	20.3
2	175.72	81.3	2-5	29.35	4,878,000	25.4
5	146.37	67.7	5-10	56.16	5,879,800	30.5
10	90.21	41.7	10-15	45.36	3,311,200	17.2
15	44.85	20.7	15-18	22.42	990,000	5.1
18	22.43	10.3	18-20	15.37	280,600	1.4
20	7.06	3.2	20-21	7.06	23,500	0.1
				Total	19,274,800	

FIG. 29. Hydrographic map of Weber Lake. Depths are indicated in meters.

WHITE SAND LAKE

FIG. 30. Hydrographic map of White Sand Lake. Depths are indicated in meters.

YOLANDA LAKE

T. 44 N., R. 5 E., Sec. 32

Length .... 150 m.	Mean depth .... 3.60 m.
Breadth .... 140 m.	Length of shoreline ..... 540 m.
Area .... 1.85 ha.	Shore development 1.12
Maximum depth .... 7.5 m.	Number of soundings 16

Depth	Area		Stratum	Area between contours	Volume	
Meters	Hectares	Per Cent of total	Meters	Hectares	Cubic meters	Per Cent of total
0	1.85	100.0	0-2	0.44	32,560	48.9
2	1.41	76.2	2-4	0.49	23,190	34.7
4	0.92	49.7	4-6	0.74	10,130	15.0
6	0.18	9.7	6-7.5	0.18	920	1.4
			Total		66,800	

BEER'S LAW AND THE PROPERTIES OF ORGANIC MATTER IN LAKE WATERS

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From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. Notes and reports No. 97.

Introduction

Organic colloids, as well as organic matter in solution, play an important part in determining the transmission of light in the waters of inland lakes. These colloids exist in a great variety of forms, but most of them seem to be lyophylic in character. This is to be expected since they are derived largely from aquatic plants. A general property of colloids is that any change in concentration, or in the physical or chemical state of the suspending medium, may bring about considerable changes in the state of aggregation of the colloidal particles. For example, a dilution of a lyophyllic colloid will probably cause the colloidal groups to disperse to finer particles while an increase in the pH of the solution may cause coagulation. With some colloids, however, such changes in conditions as mentioned above have the opposite effect, depending upon the particular colloid concerned.

Conditions within a lake are by no means constant. There are seasonal variations due to varying quantities of plant material from different phases of plant activity, and changes caused by rain or drought. Heavy rainfall brings in extracts from bogs, marshes and the soil; this increases the organic content of some lakes, while in others, where the drainage area has little boggy or marshy land and consists of wooded areas or cultivated land, a heavy rainfall serves to dilute the water and the color of the lake.

Since the amount of light transmitted into a water determines directly the quantity of plant life and indirectly the amount of animal life which the lake can support, the following questions arise in connection with the colloidal material in the water:

(1) Will normal variations in weather alter lacustrine conditions enough to cause any considerable change in the transmission of light into a lake?

(2) How much dilution is needed to make any great change in the nature of the organic matter in the lake so that the effect can be noticed in the changed transmission of light?

(3) Does the form, or nature, of the organic matter in a lake change much with dilution; that is, is there likely to be coagulation, or dispersion when the concentration is changed?

In connection with the above questions a study was made of certain highly colored lake waters to determine the sensitivity of the organic materials to changes in their physical surroundings, such as would come by dilution with rain; another purpose was to determine what limits of change are possible and yet have the materials retain the characteristic action on light which they had originally in the lake. The method adopted was to use a series of dilutions and measure the absorption of light for different wave-lengths in each of the dilutions. These data were then studied from the standpoint of their agreement with Beer's law which furnishes a means of telling whether the organic particles in the water retain the same physical character in all dilutions.

All of the data for the following discussion are taken from the report by James and Birge (Trans. Wis. Acad. Sci., and Let. 31: 1-154, 1938) though similar tests have been run occasionally since that time with results in good agreement with those presented in this report.

BEER'S LAW

If the medium is a solution, Beer's law states that the intensity of the light transmitted through a layer of thickness x of the liquid is given by the equation $I = I_0 \, e^{-ax}$ where a is the "coefficient of attenuation", or the "coefficient of absorption" of the medium; I_0 is the intensity of the incident radiation and I the intensity of the transmitted radiation. The assumption is made that the solvent absorbs light in exactly the same degree as though the solute were absent; likewise the solute has its own individual effect on light independent of the solvent. Therefore, the effect of one is merely added to the other. This fact is expressed in the equation $a = a_0 + (A)C$ where $a_0 =$ coefficient of

absorption of the pure solvent, a the absorption coefficient of
the solution being studied, (A) = molecular absorption coeffi-
cient and C = concentration of solute in gram-molecules per
liter.

Beer's law is generally accepted, but it can not be correctly
applied to solutions in which chemical or physical changes take
place in the solution when diluted. Such changes are fairly
common; for example where there is a change in ionization or
in the size of the colloidal particles. Validity of the law may be
expected for lake water containing coloring matter in true solu-
tion, but there is some doubt about lake water which contains
coloring matter in the colloidal state. In applying the law to
these waters the fact that much of the organic matter is not in
true solution is recognized, but all of the larger particles were
either removed by filtration or, in one sample, by allowing the
water to stand in cold storage for several months so that the
larger particles could settle out. In any case, it is expected that
the action on light by any material, colloidal or dissolved, is
unchanged so long as it maintains its form in all concentrations.

Results

In this study the concentration is expressed in terms of **per
cent** of lake water by volume added to the distilled water, rather
than in terms of some average value of molecular concentration.
From the equation of Beer's law, the value of (A) is as follows:

$$(A) = \frac{a - a_0}{c}.$$ Accordingly the values of (A) were calcu-

lated for several wave-lengths in the most complete sets of dilu-
tions and the results were platted as shown in the accompanying
diagrams.

In all samples the dilutions of less than 5 per cent concentra-
tion showed great variations in the values of (A). This is an
indication that conditions within the dilutions were such that
the organic matter was very unstable in these highly diluted
specimens. Above 5 per cent concentration, the curves at all
wave-lengths indicate approximately stable conditions by the
relatively small variations in (A). However, the usual effect is
a slight decrease in (A) as the concentration is increased to 100
per cent. This behavior indicates that the colloids coagulate

slightly with increased concentration, thus having the effect of reducing the number of particles present.

The lakes chosen for this study were three high-colored ones that had representative waters of somewhat different types. Helmet Lake (two samples) furnished high-colored water which appeared, from filtration, to have most of the color in solution. The colors were 180 in sample No. 1 and 264 in sample No. 2, and they were not changed by filtration through the medium filter. This filter removes all particles greater than one micron in diameter and many particles of smaller size when the filter pores become clogged by the larger particles as filtration progresses. Turtle Lake, color 43, showed some change due to filtration, thus indicating the presence of some colloidal coloring matter too large to go through the filter. The water of Lake Mary, color 109, was used without filtering, but a filtration test showed that the color was reduced to 74, which indicated that much of its color was colloidal in form.

The two samples of Helmet Lake were taken at different seasons of the year and were tested to see what differences might accompany such marked changes in color. In all samples, the dilutions were run with increasing percentages of lake water in distilled water, ranging from 0.1 per cent up to 100 per cent.

The different wave-lengths represented are, 4078 A where the effect of the organic color is greatest, 5040 A which is near the minimum point of absorption of distilled water, 5970 A where the absorption of water begins to increase rapidly and the color effect shows a sharp decrease; wave-lengths 6300 and 7000 A represent the spectral region where water alone has fairly high absorption; thus enough points have been used to gain a fair idea of the general effect of these organic coloring materials in absorbing light in the different parts of the visible spectrum.

Figure 1 shows the results of the readings on the two samples of water from Helmet Lake where the color was in true solution or in particles so fine that they passed through the medium filter. The outstanding peculiarity of the curves is the erratic behavior shown by the variations in the coefficients in concentrations below 5 per cent, from which point the values increase rapidly with increasing concentrations. The curves for

dilutions below 5 per cent are drawn to a different scale (inset Fig. 1) in order to show these facts more clearly. In concentrations above 5 per cent, the values of the coefficients remain substantially constant, except for the slight reduction with higher concentrations. The minor variations are probably not significant; for example the rapid change which appears between 5 per cent and 15 per cent on the curve for wave-length 7000 A. is due to the fact that there were small changes in absorption at that point in the 5 per cent and 10 per cent concentrations, so that small experimental variations are of considerable importance. However, the gradual decrease in (A) with increased concentrations signifies a tendency of the organic matter to coagulate.

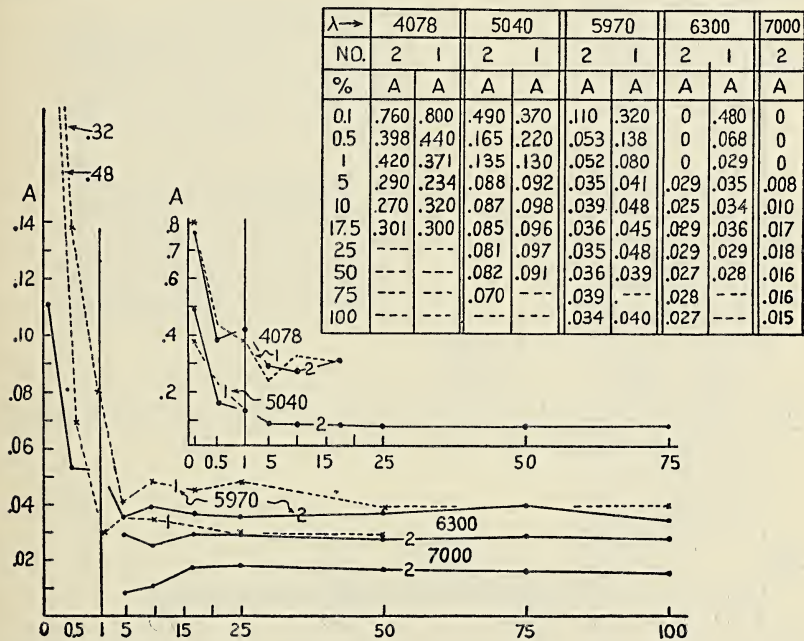| λ→	4078		5040		5970		6300		7000
NO.	2	1	2	1	2	1	2	1	2
%	A	A	A	A	A	A	A	A	A
0.1	.760	.800	.490	.370	.110	.320	0	.480	0
0.5	.398	440	.165	.220	.053	.138	0	.068	0
1	.420	.371	.135	.130	.052	.080	0	.029	0
5	.290	.234	.088	.092	.035	.041	.029	.035	.008
10	.270	.320	.087	.098	.039	.048	.025	.034	.010
17.5	.301	.300	.085	.096	.036	.045	.029	.036	.017
25	---	---	.081	.097	.035	.048	.029	.029	.018
50	---	---	.082	.091	.036	.039	.027	.028	.016
75	---	---	.070	---	.039	---	.028	---	.016
100	---	---	---	---	.034	.040	.027	---	.015

Fig. 1. Values of molecular absorption coefficients, (A), for two samples of Helmet Lake, computed for four wave-lengths. The horizontal scale is enlarged in the upper diagram below 1 per cent to show more clearly the variations for these low concentrations. Note the rapid fall in (A) as the concentration increases to about 5 per cent; only small variations are shown above this concentration. The organic matter appears to be more highly dispersed in the 0.1 per cent dilution than in the succeeding dilutions up to 5 per cent; apparently it coagulates rapidly until the latter concentration is reached and then remains fairly constant. Both dilutions were made with filtered water and the color seemed to be in true solution.

The curve for 4078 A shows variation of a similar sort. The solid line curves represent the results obtained on sample No. 2, color 180, and the dotted curves show results for No. 1, color 264. At 5040 A in the upper diagram of Figure 1, there is a gradual decrease in the (A) values of both samples in dilutions below 5 per cent, but above this concentration they are nearly constant; values for sample No. 1 run slightly higher than those for No. 2. Readings were not taken at 7000 A on sample No. 1.

The table of absorption coefficients included in Figure 1 shows that the (A) values increase rapidly with shorter wavelengths. At 4078 A, for example, the coefficient for No. 2 sample at 17.5 per cent dilution is 0.301, at 5040 A 0.085, at 5970 A

VALUE OF A

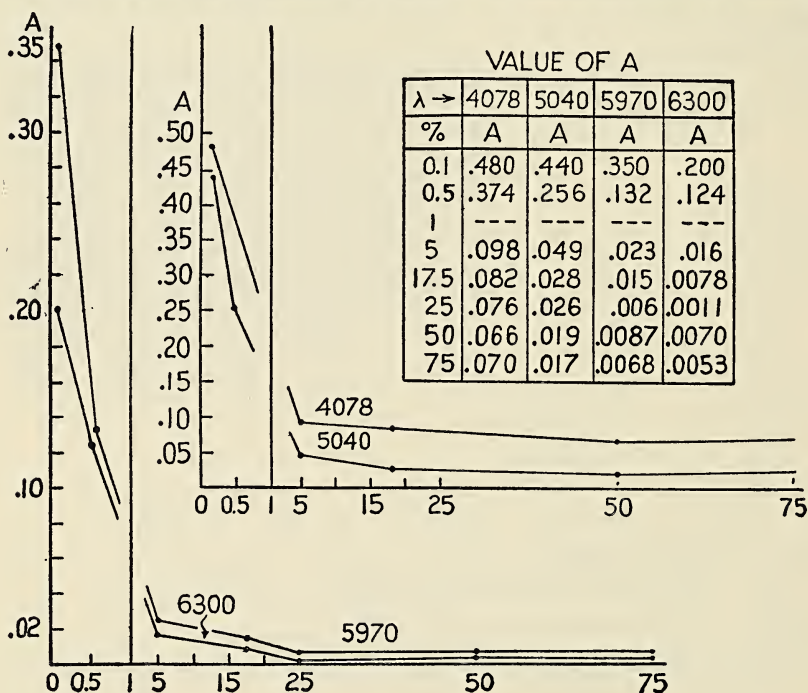| $\lambda \rightarrow$	4078	5040	5970	6300
%	A	A	A	A
0.1	.480	.440	.350	.200
0.5	.374	.256	.132	.124
1	- - -	- - -	- - -	- - -
5	.098	.049	.023	.016
17.5	.082	.028	.015	.0078
25	.076	.026	.006	.0011
50	.066	.019	.0087	.0070
75	.070	.017	.0068	.0053

Fig. 2. Values of (A) at four wave-lengths in filtered water of Turtle Lake; there is a rapid decrease in the absorption coefficient between 0.1 per cent and 5 per cent, with more stable conditions at higher concentrations. At 4078 A and 5040 A the coefficients continue to decrease slightly as concentration increases; at 5970 A and 6300 A, the decrease is more gradual between 5 per cent and 25 per cent and is much reduced above the latter. This behavior was not found in Helmet Lake (Fig. 1). The organic matter in Turtle Lake seemed to be in larger colloid particles than in Helmet Lake because the filter reduced the color somewhat in the latter but not in the former.

0.036, at 6300 A 0.029 and at 7000 A 0.017. It may be remarked here that, since this coloring matter seems to be in true solution, the agreement with Beer's law should be more satisfactory than it would be if applied to coloring materials of a colloidal type. Hence different types of water were used for the readings.

Figure 2 shows the coefficients for the dilutions of Turtle Lake water as computed for four wave-lengths. All of the curves show the rapid increase in values of the coefficients in concentrations below 5 per cent as indicated for Helmet Lake (Fig. 1). At 4078 A and 5040 A the values are reasonably constant at 5 per cent and above, while the values at 5970 A and 6300 A do
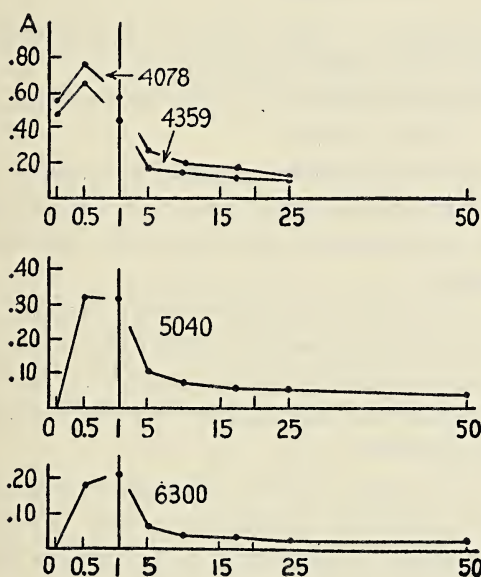
λ→	4078	4359
%	A	A
0.1	.460	.420
0.5	.750	.660
1	.570	.470
5	.250	.180
10	.200	.140
17.5	.170	.110
25	.140	.106
50	---	.073

λ→	5040	6300
%	A	A
0.1	0	0
0.5	.320	.180
1	.314	.213
5	.100	.062
10	.077	.032
17.5	.060	.028
25	.051	.015
50	.040	.015

Fig. 3. Molecular absorption coefficients for unfiltered water of Lake Mary. Some of the color materials in this water were colloidal. Low values of (A) were found for 0.1 per cent dilution for all four wave-lengths, with higher values for 0.5 and 1 per cent. At 5 per cent dilutions, the coefficients decline to values which show much less change in the higher concentrations. There is a gradual decrease in (A) with concentration, however, which is much greater than in either Helmet or Turtle lakes, particularly at the shorter wave-lengths. Apparently the colloidal material dispersed greatly in the lower concentrations and then continued to reaggreate with increased concentrations. This represents a marked difference in the behavior of dissolved and colloidal color in low concentrations, thus showing that the colloidal matter is sensative to physical changes in its surroundings.

not become constant until the concentration is 25 per cent lake water, beyond which they are nearly constant.

Figure 3 shows the Beer's law coefficients for the Lake Mary series of dilutions computed at four wave-lengths. The great irregularity below 5 per cent concentration is again evident and the values decrease with increasing concentrations in all curves. The curves for 4078 A and 4359 A are identical in form, but the values are higher at the shorter wave-length. The usual erratic variations below 5 per cent are present, but the coefficients decrease steadily up to 25 per cent in this case. At 5040 A the action is similar, while at 6300 A there is a similar but less rapid decline than at the shorter wave-lengths.

Discussion

A satisfactory explanation of the behavior represented in these curves must include the following points:

1. The explanation of the erratic values of (A) found in dilutions below 5 per cent of lake water.

2. Why the values of (A) become gradually smaller with increase in concentration in Lake Mary while in the waters from Helmet (both samples) and from Turtle Lake the values are much more nearly constant.

3. Why the 0.1 per cent dilution of Lake Mary shows lower values of (A) than the 0.5 dilution while beyond the latter they decline to the approximately constant values found at the 5 per cent concentration. The other two lakes show the highest values of A in the lowest concentration.

The explanations of the above points probably depend upon a full knowledge of the changes produced in the conditions within the waters which make for stability or instability of the colloids and other materials present in the waters. It is known that the stability of colloids is greatly affected by the concentration of electrolytes and the mere dilutions of the lake water with distilled water may produce a change in the degree of dispersion of the colloidal material and this, in turn, may cause a difference in the absorbing action on light.

Another factor involving the stability and size of the lyophyllic colloids, such as albumin and gelatin, is the change in the hydrogen ion concentration. It is possible that many of the col-

loids found in lake waters are albuminous materials and a change in pH accompanying the dilution with distilled water may produce considerable changes in them.

The molecules of many organic substances are so large that they come within the range of very fine colloidal sizes and this may be the situation in many of the materials found in lake waters, so that even the material in solution may behave in a manner similar to colloids. In Figure 1 for instance, the color material is nearly all molecular in size, yet the action in dilute solutions indicates a reduction in the molecular absorption coefficients as the concentration increased such as would accompany a decrease in concentration. This effect could be due to slight coagulation of these particles to larger units. At 5 per cent concentration the units attain a maximum or normal size and remain that way in all higher concentrations. The same sort of effect is evident in Turtle Lake in Figure 2 since the water was filtered and the organic matter was probably in much the same state.

In Figure 3 where the results of the dilutions of the unfiltered waters of Lake Mary are shown, the values of (A) are smaller in the 0.1 per cent concentration than at 0.5 per cent; then the values fall rapidly to those at 5 per cent. This shows that there is a small difference between materials that are known to be colloidal and those in solution, and these differences become evident in the very dilute solutions. Whether the observed effects are due to changes in pH attendant upon these dilutions or to more mechanicals effects of varying concentration is not shown by these data.

In conclusion it may be emphasized that Beer's law is followed in nearly all cases up to a dilution of at least 20 to 1, and that it may be applied with confidence in calculating the absorption of light in the lake waters included in this investigation when they are diluted with distilled water to any concentration that would be found under natural conditions due to rain and snow falling on the lakes. At still greater dilutions the absorption becomes greater than that calculated according to Beer's formula; it is likely that at these dilutions the colloidal material is rendered unstable. In support of this explanation, it may be pointed out that the deviation from Beer's law is greatest in

lake water which is known to contain the greatest amount of colloidal material.

Summary

1. Four complete sets of dilutions were studied with respect to agreement with Beer's law, which expresses the relation of absorption of light in solutions to the absorptions by the pure solvent and the solute independently as affected by the concentration of the solute. The effect of the solute is calculated in terms of "molecular absorption coefficient" (A). A fairly close agreement with the law was found for dilutions with concentrations of 5 per cent of lake water or more, but much irregularity in absorption was found in dilutions with less than 5 per cent of the original lake water. This shows that in higher dilutions the physical state of the colloids is altered by changes in pH or other physical conditions with resulting irregularities in selective absorption. In dilutions of 5 per cent or more the state of the colloids is more stable. These results confirm the conclusion that changes in colloid particles as such, and probably other particles as well, produce minor irregularities in absorption except in waters with very low color, while the color of the water is the primary factor in modifying radiation.

2. Attention is called to the fact that, though the color in Helmet and Turtle lake waters was treated as being in true solution as indicated by the Berkefeld filter, the molecules may be of such size as to come within the range of colloidal particles and, as such, may show some of the characteristics of colloids. That this is true is shown by the similar behavior of these waters below concentrations of 5 per cent to that of the colloidal water of Lake Mary.

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SURFACE LOSS OF SOLAR AND SKY RADIATION BY INLAND LAKES*

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From the Physics Department and the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. Notes and reports No. 98.

Introduction

In recent years "surface loss" of solar and sky radiation at the surface of bodies of water has become an important subject of investigation since it is a factor in the problem of light penetration. Powell and Clarke (1936) divided the incident light intensity, I, into three components: A, that which penetrates the surface and is absorbed; R, that which is reflected at the surface; and U, that which penetrates the surface but is scattered back into the air again by particles in suspension. Thus $I = A + R + U$. The present paper deals particularly with R and U in reference to lake water; continuous records of these two factors were obtained by means of a self-registering instrument.

Apparatus

The apparatus consisted of three Weston photocells mounted on a buoy about 1000 feet (300 m.) off the shore of Trout Lake, Wisconsin. These cells were connected by water-proof electric cables to a Cambridge Double Recorder installed on shore. The Weston cells were clamped to galvanized iron pipes which formed an upright "T". This T was fastened to the south end of a buoy by a flexible connection using a clevis. The lower (submerged) end of the T was weighted so that the pipe remained perpendicular when the buoy was disturbed by waves. Two cells were mounted on the crossbar of the T so as to balance each other, one face up to measure I, the other face down to measure R + U. A third cell was mounted face down just beneath the surface of the water to measure U. The Cambridge

automatic recorder, with Ayrton shunts for variable sensitivity, gave continuous records of the measurements throughout the day. This recorder is described more fully in a paper by Whitney (1938a). The Weston cells were mounted in cases similar to those recommended by the International Council for the Exploration of the Sea (Atkins et al. 1938).

CALIBRATIONS AND CORRECTIONS

In order to calibrate the cells, all three were mounted on the crossbar face up and allowed to record on a clear day. From this record the relative sensitivities of the cells were determined. The same procedure was followed when the red filters were used.

Polished opal glass diffusing windows were used on the three photometers. The total loss of light in passing from air to glass is larger than from water to glass. Light also is scattered back from the diffuse layer of the glass and internally reflected from the upper air-glass surface and thus contributes to the reading; this effect is much reduced when the instrument is submerged in the water. These effects are discussed in a paper by Atkins and others (1938) who suggest a correction factor of 1.09 for the readings of submerged cells.

Since knowledge concerning the amount of light scattered back out of the water is desired, another correction must be applied. The submerged cell readings indicate the intensity of light scattered up beneath the surface of the water; some of this light, however, is internally reflected at the water-air surface of the lake so that the light scattered out of the water is less than the submerged cell indicates. The correction due to this cause was calculated theoretically and it results in the nullification of the previous 1.09 correction. Another correction is that due to the absorption of the water above the submerged cell. Data for this correction were obtained on a day when the surface of the water was smooth. A final correction for the submerged cell must be made for its shadow. A theoretical computation of this error resulted in applying a correction which varied for different angles of the sun, ranging from a maximum of 18 per cent to a minimum of 12 per cent for the cell mounting used.

Observations and Results

In one series of observations covering different types of days, the Weston cells were used only with flashed opal glass over them; in a second series both opal glass and Schott red filters (RG1) were used. The spectral sensitivity of the cells with and without the red filters is shown in Figure 1. These curves were taken from "Technical data on Weston photoelectric cells" published by the Weston Electrical Instrument Corporation and from curves of the Schott filters obtained from the Fish-Schurmann Corporation.
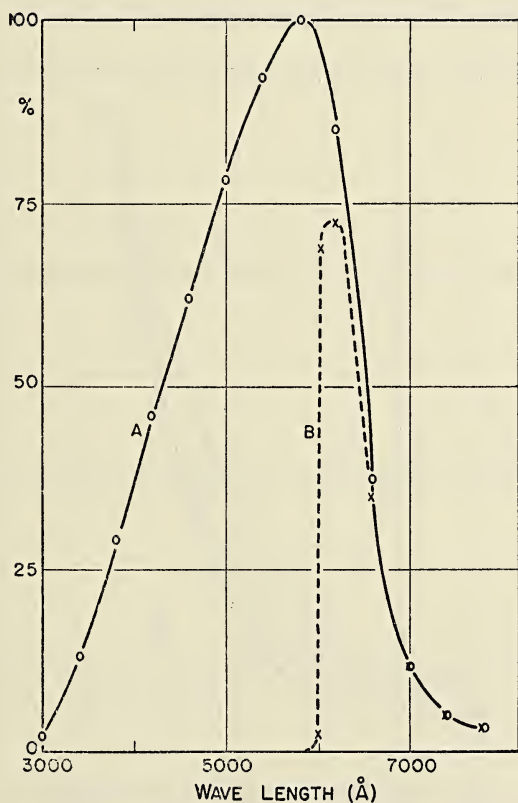

Fig. 1. Curve A shows the spectral sensitivity of the Weston photocells; taken from "Technical data on Weston Photronic cells" published by the Weston Electrical Corporation. Curve B shows the spectral region covered by the Photronic cell when used with the Schott red filter RG1.

The Cambridge recorder gave the variations in light intensity with time; hence it was necessary to compute the angle of the sun for different times of the day. These angular distances have been used in plotting three of the figures.

Figures 2 and 3 show results of measurements of R + U as per cent of total incident light plotted against the angle of the sun from the zenith. Curve A in Figure 2 represents the theoretical per cent of total incident light lost at the surface by reflection and upward scattering (R + U) on a clear day with a smooth surface. It was computed by using (1) Fresnel's formula for reflection, (2) an average distribution of sun and sky energy given by Kimball (1919), (3) a value of 6.8 per cent reflection for diffuse sky suggested by Whitney (1938a), and finally (4) adding U values from Figure 4. As thus computed

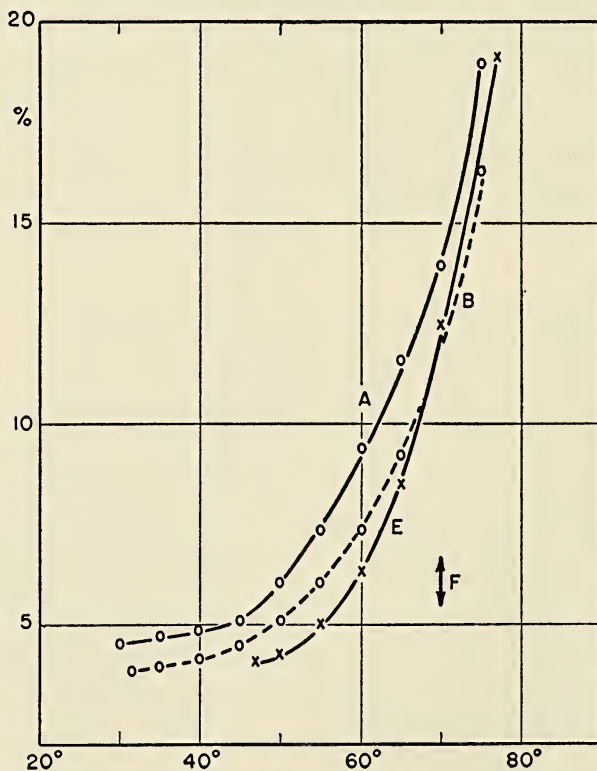FIG. 2. R + U losses on a clear day with smooth surface and for different zenith angles of the sun. Curve A represents the theoretical loss; B is the observed loss; E is the loss with red filters. F shows the range of loss with a diffuse sky (fog).

curve A is notably higher than the others. A closer agreement would be obtained by using a value of 6 per cent reflection for diffuse sky as shown in curve F, but it would still be higher than the experimental results obtained with the recorder (curve B).

Curves A and B are roughly parallel; the percentage of surface loss in general is greater for low altitudes or large zenith angles of the sun, particularly when the angle is greater than 50°. Curve E in Figure 2 shows the percentage of surface loss (R + U) when the red filters were used on a clear calm day. It will be noted that E and B meet at 70°; at larger zenith angles, curve E closely approaches the theoretical curve A.

The double headed arrow (F) in Figure 2 shows the range of variation of the R + U loss over a period of an hour or more on a foggy morning when the disc of the sun was not visible.
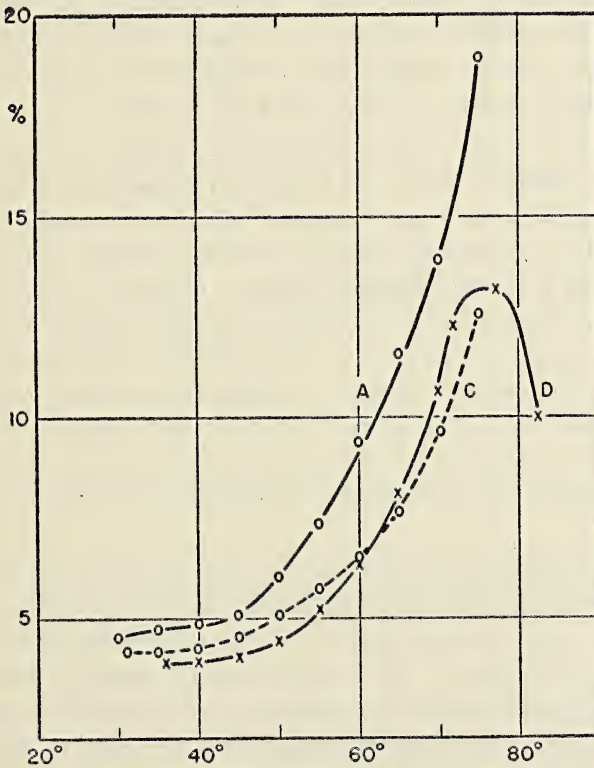

FIG. 3. R + U losses on a clear day with waves 10-30 cm. high for different zenith angles of the sun. A is the theoretical loss; C observed loss with 20 cm. waves; D loss with red filters and 10 cm. waves. Note the decrease in percentage loss shown in D at greater angles than 76°.

The mean loss was about 6 per cent. The arrow is placed at 70°
because that was the average zenith angle of the sun during the
observations; however, the angle of the sun has no great signi-
ficance with a diffuse sky.

Curves C and D in Figure 3 show the results obtained on a
clear day when the surface of the water was disturbed by waves
10 to 20 cm. high, measured from trough to crest. The theo-
retical curve A is included in the diagram for purposes of com-
parison. From the zenith down to 50°, the percentage of surface
loss with opal glass alone was somewhat larger for a rough than
for a smooth surface (curve B Fig. 2 and curve C Fig. 3), but
at larger zenith angles the loss from a smooth surface was
greater than that from a rough surface; that is, at 75° the loss
from a smooth surface was about 16 per cent and that from a
rough surface was 13 per cent. This result is to be expected
since a rough surface makes the average incident angle of the
light with the surface larger for a small zenith angle of the sun
and conversely smaller for a large zenith angle.

Curve E in Figure 2 and curve D in Figure 3, representing
the results obtained with red filters on smooth and rough sur-
faces respectively, are very similar down to a zenith angle of
about 55°, but the smooth surface shows a greater loss at larger
zenith angles than the rough surface. Curve D shows a maxi-
mum surface loss of 13.2 per cent at zenith angle 76° which is
followed by a decline to 10 per cent at 82.5°. Maximum surface
loss is to be expected, however, at some large zenith angle in all
cases because the contribution of the sky becomes relatively
larger at low altitudes of the sun and this lowers the effective
angles of incidence and therefore decreases the per cent of re-
flection.

In general the precentage of R + U loss for red light was
less than that for total light, especially down to zenith angles of
60° to 70°; most of this difference was due to the U component
as shown in Figure 4. For larger zenith angles however, the
red light showed a larger percentage of loss than the total light.
This is probably due to the fact that the per cent of sky energy
is much less for red light at large angles than for total light;
hence the average incident angle of the red light would be effec-
tively greater, thus giving a larger reflection.

Figure 4 shows the results of measurements of U as per cent of incident light (I). These curves represent data for either smooth or rough surface. The differences due to the condition of the lake surface were found to be smaller than the experimental errors involved. The percentage of total light scattered up varied between two and three per cent. It is interesting to compare this result with recent measurements by Atkins and Poole (1940) on sea water. They found the percentage of light scattered up varied from 5.5 to 2.1 per cent for waters with vertical transmissions of 82 to 93 per cent per meter, respectively. The corresponding vertical transmission of Trout Lake water was about 73 per cent per meter.
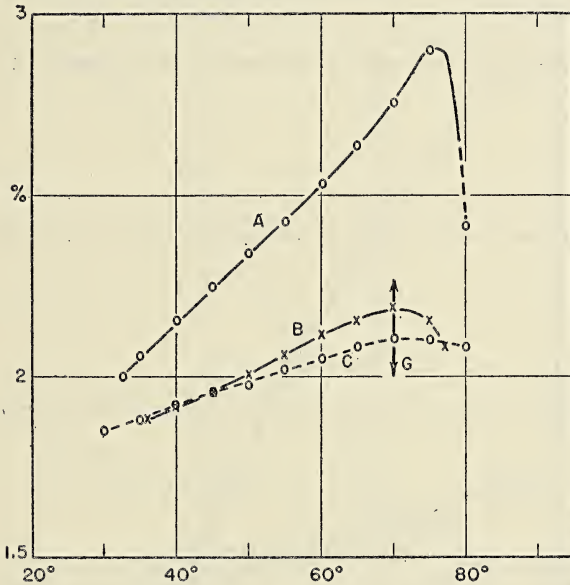
Fig. 4. Total scattering up on a clear day with either smooth or rough surface. Curve A shows observed upward loss by scattering; C theoretical loss by upward scattering fit to curve B at zenith angle of 45°; B loss by upward scattering with red filters; G variation in loss by upward scattering with diffuse sky (fog).

The curves in Figure 4 for both red and total light rise with greater zenith angles of the sun since I declines much more rapidly than does U; I approximates the cosine law. Both curves show a marked decline at greater zenith angles than 75°, especially curve A for total light. At a large zenith angle sky radiation becomes more prominent and decreases the mean path

length, thus giving a downward slope on all three curves at large zenith angles. Intensity of U, assuming to first approximation uniform spherical distribution of light intensity from scattering particles, depends somewhat on the mean path length and the latter depends on the angle of the sun. Mean path length is defined by Whitney (1938a) as the average length of path which the light must travel to reach a depth of one meter. The curve for red light (B) is much lower than A which is due in part to higher absorption of red light by water and in part to less scattering of red light by small particles in suspension.

The theoretical curve (C) as derived by Whitney (1938b) is

$$\frac{U}{I} = \frac{s}{k} \frac{1}{F(b)} \text{ where } F(b) = \frac{2b}{b - \log_e (1 + b)} \text{ ; } s \text{ and } k \text{ are}$$

FIG. 5. Total illumination and R + U loss on a clear day, July 13, 1939. Curve A shows total illumination at different times in the afternoon, taking noon as 100. Curve C shows R + U loss with smooth surface and B with 20 cm. waves. Note that the scale for the R + U loss on right side of diagram is ten times as large as that for total illumination on left side.

scattering and extinction coefficients, b is the mean path length and is a function of zenith angle. The ratio s/k was taken so that curves B and C fit at an angle of 45°. This theoretical curve was derived on the assumption that the scattering particles were spheres, thus giving uniform sphercial distribution of intensity of scattered light, and also that k was a constant which is not true near the surface of the water because it is not monochromatic light. It does have the same general shape, especially for small angles, as the curve for red light (B) since the red light approximates monochromatic light.

The double headed arrow in Figure 4 (G) represents the variation in the total scattering during a foggy day with diffuse sky. The mean is a little more than 2.1 per cent.
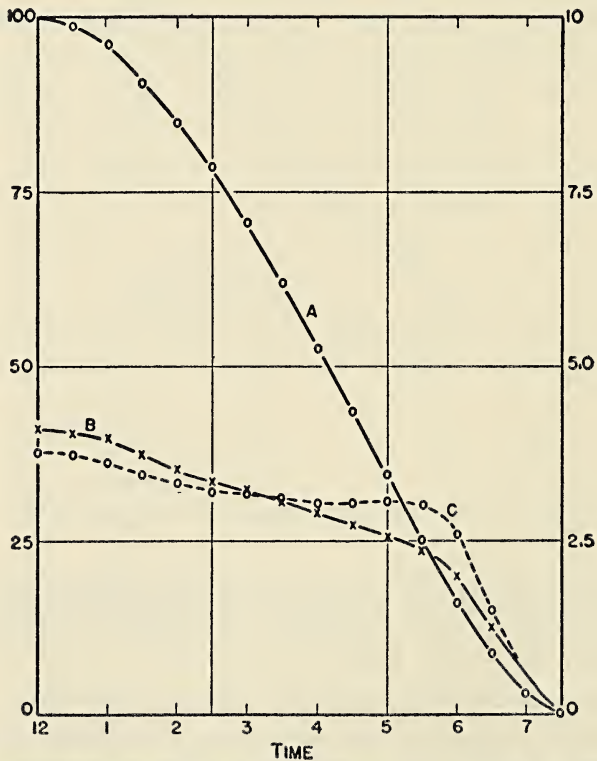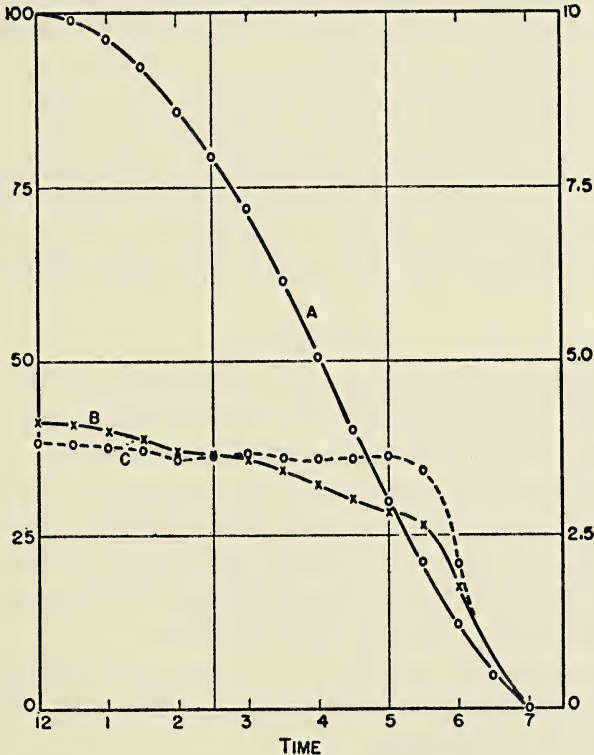

FIG. 6. Total illumination and R + U loss on a clear day, August 15, 1939. Curve A shows total illumination at different times of the afternoon, taking noon as 100. Curve B shows R + U loss for a rough surface and C for a smooth surface; note that the scale for R + U loss on right side of diagram is ten times as large as that for total illumination on left side. Compare with Figure 5.

Records of the intensity of the solar radiation in the Trout Lake region, latitude 46° N., were taken daily with a self-registering solarimeter during the months of July and August, 1939. July 13 and August 15 were exceptionally clear days and the relative intensity of the sun and sky radiation during the afternoons (12 noon to 7:30 p.m.) of these two days is plotted in Figures 5 and 6; the noon intensity is taken as 100 (curve A in both figures). Using data from Figures 2 and 3, the intensity of R + U for both smooth and rough surfaces was calculated and plotted against time in Figures 5 and 6 (curves B and C). The scale for R + U, shown in the right hand margin of both figures, is ten times as large as that for total solar radiation in the left hand margin.

It is interesting to note, especially for a smooth surface on August 15, that the percentage of light coming up from the lake was almost constant from 6:30 a.m. to 5:30 p.m., after which it declined with decreasing light intensity (curve C in Figure 6). The ratio of the areas in these two figures gives the percentage of total incident light that is lost at the surface during the day. On July 13, the surface loss amounted to 5.21 and 5.05 per cent for smooth and rough surfaces respectively, and on August 15, to 5.66 and 5.35 per cent for smooth and rough surfaces.

Summary

1. Surface loss of solar and sky radiation in lakes is made up of two parts, namely that which is reflected (R), and that which is scattered upward out of the water by suspensoids (U).

2. The surface loss varies with the elevation of the sun, the condition of the sky and of the surface of the water. It was substantially the same for smooth and rough surface down to a zenith angle of 50°, but at larger angles the loss was greater from a smooth than from a rough surface.

3. The percentage of the R + U loss for a diffuse sky was about 6 per cent; for a clear sky it was 5.2 per cent in July and 5.5 per cent in mid-August.

4. The percentage of the R + U loss for red light was less than that for total light down to zenith angles of 60° to 70°; at greater angles red light showed a greater percentage surface loss than total light.

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A MULTIPLE ELECTROMAGNETIC WATER SAMPLER

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From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. Notes and reports No. 99.

Introduction

In many inland lakes the water is sharply stratified into layers, some layers being but a few centimeters thick. Great care must be exercised to avoid mixing the layers when apparatus is lowered or raised through them. In the microstratifica-
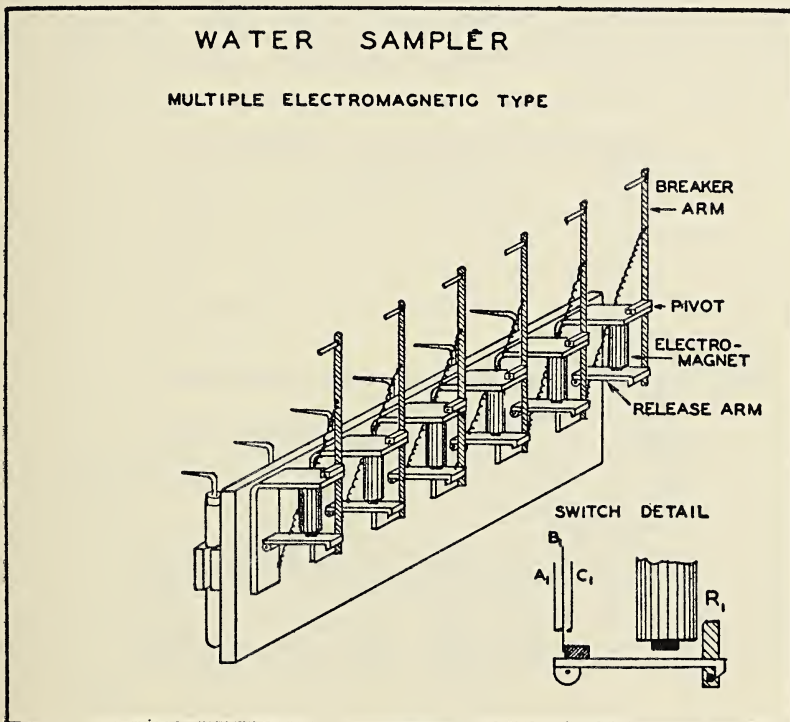
FIG. 1. General view of electromagnetic water sampler.

tion work done by the author, samples were first obtained by pumping water to the surface through a rubber tube attached to a long horizontal pipe which was part of the transparency meter. This method required but a single lowering and raising of the apparatus for a complete set of water samples, and reliable results were obtained. However, it was necessary to flush 10-15 liters of water through the tubing from each layer before taking water samples, and the withdrawal of this amount of water from a narrow layer undoubtedly disturbed conditions to some extent.

SAMPLER

An electrically operated water sampler was devised which avoided this difficulty and which made it possible to obtain six water samples for bacterial counts in one operation. Six relays, each consisting of an electromagnet, release bar, switch, and breaker arm, were mounted on a board. Six test tubes were clamped to the opposite side of the board. Only two wires were
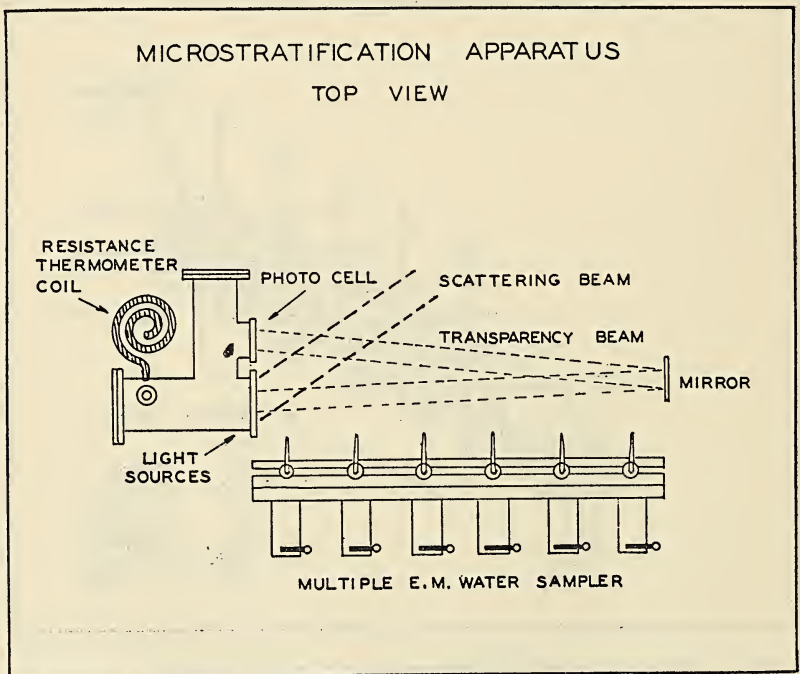
FIG. 2. Top view showing microstratification apparatus, resistance thermometer, and water sampler.

necessary between the boat and the water sampler. One wire was connected to all six electromagnets in parallel, the other to B_1 the middle terminal of the first relay switch. Fig. 1. A_1 was connected to the first electromagnet, E_1. The release bar was drawn upward when voltage was applied to the lead wires, and the catch attached to the first breaker arm was disengaged. The breaker arm was then pulled down by a strong spring and the tip of the evacuated test tube broken off. When the voltage was removed the release bar dropped and B_1 was connected to C_1. C_1 was connected permanently to B_2, which is not shown in the drawing but which was the middle terminal of the second relay. All connections for the second relay and the second electromagnet were similar to those shown for the first, and the second pulse of current consequently released the second breaker arm, and so on.

The contact switches were immersed in water, but they operated perfectly. When the relays were constructed, the electromagnets were made sufficiently sensitive to operate on about 3 volts and less than 2 watts of power. In practice, a $22\frac{1}{2}$ volt small sized radio "C" battery was used to insure positive operation. The current drain on this battery was negligible since the breaker arms could be released by flipping a switch on and off as quickly as possible. The current remained on only about $\frac{1}{10}$ of a second each time. When the last relay was actuated, the electric current had to pass through all six switches in series, but no trouble was experienced.

The multiple water sampler was fastened to the microstratification apparatus as shown in Figure 2. The break-off tips on the test tubes were on the same horizontal level as the light beam. A series of transparency readings were taken with the apparatus descending; experimental points were immediately plotted on graph paper. The graph showed the exact position of stratified layers and indicated the best places to obtain water samples. The apparatus was then elevated while the transparency meter was kept in operation as a guide, and samples were taken at the desired levels.

CHEMICAL ANALYSES OF THE BOTTOM DEPOSITS OF WISCONSIN LAKES. II. SECOND REPORT

C. Juday, E. A. Birge and V. W. Meloche

From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. Notes and reports No. 100.

Introduction

Investigations have been in progress on Wisconsin lakes for a considerable number of years and during the progress of these studies, especially in recent years, some attention has been given to the bottom deposits that are found in the different types of lakes. Samples of bottom material have been obtained from time to time for the purpose of making physical and chemical analyses of them; up to the present time some 200 samples have been collected. Most of these samples were taken in lakes situated in the northeastern lake district of Wisconsin and they were collected chiefly during the period from 1925 to 1932 when a general survey of the lakes in this district was being made. Eighteen of the 21 lakes included in the present report are located in the northeastern district; they are Adelaide to Wildcat, inclusive, in Table I, while the other three, Green, Nagawicka and Oconomowoc, are situated in the southeastern lake district.

Through the cooperation of the Works Progress Administration and the National Youth Administration, chemical analyses of 21 samples in this collection have been completed recently and the results form the basis of the present report. Black (1929) made analyses of samples obtained from three southeastern and 12 northeastern lakes, as well as three from Alaska, and published a report on his results; the present report, therefore, is the second one dealing with this collection of bottom samples.

Material and Methods

The bottom samples were taken with a small Ekman dredge which is 15 X 15 cm. in area and 15 cm. deep; thus the material

obtained in these hauls represents only the upper 15 cm. of the deposits. They were taken in the deeper waters of the various lakes and no attempt has yet been made to explore the entire bottom of any of the lakes. Black, however, analyzed material that was obtained at two different stations in Lake Monona, of which one sample was taken at 8 m. and the other at 22 m.

Most of the lakes represented in this report have sandy and gravelly margins and this type of material usually extends out to a depth of 3 m. to 6 m., beyond which the bottom changes more or less rapidly to the type of material represented in these analyses. In the typical bog lakes, of course, the entire bottom consists of a mucky deposit containing a large percentage of organic material which seems to be largely ligneous in character (Steiner and Meloche 1935).

The fresh samples of mud were spread out on drying trays and air dried as promptly as possible after they were obtained; when dry the material was placed in sealed containers and kept for the analyses. In some instances, small portions of the mud were preserved with formaldehyde for microscopic examination.

For the chemical analyses, the air dried material was ground and representative samples of it were then dried in a vacuum desiccator for several days at a temperature of 60° C. The weight of the vacuum dried samples was used in computing the results given in Table II. The loss of moisture from the air dried samples ranged from 2 per cent to a little more than 7 per cent. Standard methods were used both for the inorganic and the organic analyses.

THE LAKES

The 21 lakes included in this report differ widely in their physical, chemical and biological characteristics and the analyses show that the same is true of their bottom deposits. The results given in Tables I and II indicate that there is a definite correlation between the chemical character of the water and that of the bottom deposit. Likewise the chemical character of the water has a geological background.

All of these lakes are glacial in origin but the underlying geological formations in the two districts are very different. The three southeastern lakes (Green, Nagawicka and Oconomo-woc) are located in a region where the glacial drift is not very

thick and where the underlying rock consists of Niagara limestone. In the northeastern lake district, the glacial deposits range from 39 to 71 m. (129-234 ft.) in depth and the underlying rocks consist of schist and gneiss in the northern part of the district and granite in the southern part. Furthermore the glacial deposits themselves contain a much smaller amount of carbonates in the northeastern than in the southeastern district. These differences in the geological characteristics of the two lake districts help to account for the marked differences in their waters, especially with respect to the amount of calcium and magnesium in them.

These 21 lakes may be separated roughly into two groups; (1) those that are landlocked and do not have outlets (seepage lakes) and (2) those that have permanent or intermittent outlets (drainage lakes). In Table I the former are indicated by the letter S and the latter by D. The 9 seepage or landlocked lakes are situated in the northeastern lake district where bodies of water of this type are fairly abundant. The northeastern lake district occupies the highest plain in Wisconsin and streams flow out of it toward the four cardinal points of the compass. The youthfulness of the district is shown by the fact that so many of the lakes and lakelets have not yet been connected by streams with the three principal drainage systems represented in this region.

In the seepage group of northeastern lakes, Helmet is a typical bog lakelet and practically all of the shore consists of sphagnum bog material. The water is highly colored by the material extracted from the bog; the color ranges from 166 to 528 on the platinum-cobalt standard of the U. S. Geological Survey. The high color of the water reduces the transparency so that the Secchi disc readings are very low (0.5-1.5 m.).

Rahr Lake has bog deposits along about half of its shore line, so that it represents an intermediate condition between a regular bog lake and one that is free of bog material. The color of its water ranges from 26 to 45 on the platinum-cobalt scale and the disc readings fall between 2.0 and 3.0 m.

The shores of the other lakes represented in Table I, both seepage and drainage, consist of sand and gravel with some boulders in a few cases; some of them have rather marshy areas

along parts of their shores, but none of them has regular bog deposits. In general the color of their waters is low, rarely exceeding 8, and the transparency is rather high, the disc readings ranging from 4 m. to 14 m. Crystal Lake has the most transparent water in the group. Hydrographic maps of ten of the northeastern lakes are included in another paper (Juday and Birge, Trans. Wis. Acad. 33:21-72, 1941).

The Lake Waters

Table I shows some of the chemical characteristics of the various lake waters. Regular observations on the pH, the conductivity, the bound CO_2 and the SiO_2 have been made on the northeastern lakes for two or more years and the results given for these lakes in the table are the means of the different determinations. The data given for Green, Nagawicka and Oconomowoc lakes, however, represent only one set of observations on each lake.

The waters of the seepage lakes of northeastern Wisconsin are usually much softer than those of the drainage lakes. This is especially true of Big Carr, Crystal and Weber lakes, for example, in comparison with such drainage lakes as Big, Oxbow and Wildcat. The seepage lakes usually have very small drainage basins so that their chief water supply is the rain and snow precipitated on their surfaces. The water derived from their limited drainage basins has only small amounts of inorganic substances in solution because the soil is sandy and contains very small quantities of carbonates. Thus the limited amounts of water received from their small drainage basins contribute very little to the inorganic content of the water. In some of the seepage lakes, however, such as Anderson and Blue lakes, the surrounding glacial material contains larger amounts of carbonates and as a consequence their waters hold larger amounts of these substances in solution. These seepage lakes with higher carbonate content are usually, but not always, found near the edges or within the boundaries of moraines rather than in the outwash plain areas.

The hydrogen ion concentration of the various lake waters ranged from pH 5.6 in Helmet Lake to pH 8.4 in Oconomowoc Lake, thus covering a range of almost three whole units; one

TABLE I. *Chemical analyses of the waters of 21 Wisconsin lakes from which samples of the bottom deposits were obtained. Seepage lakes, those without an outlet, are indicated by an S and drainage lakes, those with outlets, by a D. Hydrogen ion concentration is indicated in terms of pH and conductivity or specific conductance in reciprocal megohms. The other results of the analyses are stated in milligrams per liter of water.*

Lake	Seepage or drainage	Area		Max. depth		pH	Conductivity	Residue	Bound CO_2	SiO_2	Ca	Mg
		Hectares	Acres	Meters	Feet							
Anderson	S	21.0	53	19.5	64	7.2	42	39.4	10.5	3.3	4.8	2.2
Big	D	382.0	945	18.5	61	8.0	94	76.3	23.0	2.4	16.3	3.8
Big Carr	S	94.5	233	22.0	72	6.0	12	17.3	1.3	0.2	0.8	0.6
Blue	S	168.7	417	13.5	44	7.2	42	33.0	9.8	0.2	5.0	1.5
Boulder	D	239.6	592	6.0	20	7.5	54	57.0	13.3	4.0	8.6	2.5
Clear	S	417.8	1032	29.5	97	6.7	17	18.2	2.3	0.5	2.1	1.0
Crystal	S	30.2	75	21.0	69	6.1	10	12.3	1.5	0.1	1.0	0.6
Finley	S	62.8	155	8.5	28	6.7	13	21.3	2.4	Trace	1.2	0.5
Helmet	S	3.0	7	10.4	34	5.6	20	79.6	2.0	2.5	3.1	0.0
Lit. Tomahawk	D	54.0	133	13.7	45	7.8	82	59.5	19.7	3.9	8.5	4.0
Muskellunge	D	372.3	919	20.7	68	7.3	41	36.4	10.0	0.6	6.3	2.0
Nebish	S	38.5	95	15.8	52	6.8	19	22.0	4.0	0.4	2.3	1.7
Oxbow	D	242.4	599	15.0	49	7.3	33	56.3	6.9	1.2	13.5	3.3
Rahr (Mud)	S	5.5	13	15.7	51	6.4	16	28.0	4.0	0.3	1.4	1.0
Tomahawk	D	1476.0	3648	22.5	74	7.6	69	48.4	16.7	1.4	9.0	3.0
Weber	S	15.6	38	13.5	44	6.1	9	13.2	1.2	0.1	0.7	0.5
White Sand	D	216.2	534	21.0	69	7.6	62	52.4	15.1	3.8	9.6	3.5
Wildcat	D	130.0	321	12.4	40	7.9	120	91.7	30.5	2.9	19.8	10.5
Green	D	2972.0	7342	68.0	223	8.4	275	195.0	73.2	8.0	28.7	25.9
Nagawicka	D	371.0	917	28.8	94	8.2	343	265.0	88.0	4.0	46.4	28.8
Oconomowoc	D	328.2	811	19.0	62	8.4	307	210.6	75.0	4.0	31.4	24.9

reading on Helmet Lake was pH 5.3 which gives a range of more than three units. The conductivity or specific conductances also showed a wide range, varying from a minimum of 9 reciprocal megohms in Weber Lake to a maximum of 120 in Wildcat Lake, both in the northeastern group; in the three southeastern lakes, Nagawicka had a maximum of 343 reciprocal megohms.

In the northeastern lakes, the total residue upon evaporation varied from a minimum of 12.3 mg/l in Crystal Lake to a maximum of 91.7 mg/l in Wildcat Lake; the maximum for the southeastern lakes was 265.0 mg/l in Nagawicka Lake. The bound CO_2 was smallest in Weber Lake (1.2 mg/l), but it was only a little larger in Big Carr and Crystal lakes; the maximum amount in the northeastern lakes was 30.5 mg/l in Wildcat Lake, but it was 88.0 mg/l in Nagawicka Lake. The SiO_2 ranged from a trace in Finley Lake to a maximum of 8.0 mg/l in Green Lake. In the northeastern group the quantity of Ca varied from a minimum of 0.7 mg/l in Weber Lake to a maximum of 19.8 mg/l in Wildcat Lake; the amount of Mg in their waters ranged from zero in Helmet Lake to 10.5 mg/l in Wildcat Lake. Larger amounts of these two substances were found in the southeastern lakes. The Ca ranged from 28.7 mg/l in Green Lake to a maximum of 46.4 mg/l in Nagawicka Lake. The Mg varied from 24.9 mg/l in Oconomowoc Lake to 28.8 mg/l in Nagawicka Lake. In the northeastern group, the waters of Big, Oxbow and Wildcat lakes contain the largest amounts of Ca; Big and Oxbow lie within the Winegar Moraine and Wildcat is situated at the edge of it.

The analyses of both the water and bottom deposits of Weber Lake represent the period between 1925 and 1931; from 1932 to 1936, inclusive, fertilizers, including lime, phosphorus and nitrogen compounds, were added to the water of this lake. In 1937 the Ca content of the water was 1.2 mg/l.

ANALYSES OF THE DEPOSITS

The results of the chemical analyses of the bottom deposits are given in Table II. The soft water lakes of the Northeastern district, especially Big Carr, Crystal and Weber, represent one extreme and the southeastern hardwater lakes (Green, Nagawicka and Oconomowoc) represent the other extreme.

Loss on ignition. The loss on ignition ranged from a minimum of a little more than 29 per cent of the dry weight in Nagawicka Lake to a maximum of 74 per cent in Rahr Lake. In 15 of the 18 northeastern lakes it amounted to more than 40 per cent and in 9 it was more than 50 per cent of the dry weight. In general the loss on ignition corresponds roughly to the organic content of the mud in these lakes because there is so little Ca present. When large amounts of Ca are present in the form of $CaCO_3$, there is a corresponding loss of CO_2 from this compound during the ignition; this would be true of the deposits of the three southeastern lakes. A better estimate of the total organic matter in these deposits is obtained by doubling the amount of organic carbon. While the percentage of C in the protein, fat and carbohydrate present in the mud varies over a wide range, the mean amount in these substances constitutes approximately 50 per cent of the organic matter.

SiO_2. The quantity of silica found in these bottom deposits ranged from a minimum of 14.6 per cent in Oconomowoc Lake to a maximum of 52.7 per cent of the dry weight in Big Lake. It constituted more than 40 per cent in 11 of the 21 lakes and fell between 30 and 40 per cent in 5 others; it exceeded 50 per cent only in Big Lake. With the exception of loss on ignition, it was the largest item in the deposits of the northeastern lakes; the same was true of Green and Nagawicka lakes in the southeastern district, but in Oconomowoc Lake the percentage of CaO was larger than that of SiO_2.

Black (1929) analyzed bottom deposits from 12 northeastern and 3 southeastern lakes. In the former group he found that the SiO_2 ranged from a minimum of 9.3 per cent in the Forestry Bog to a maximum of 42.8 per cent in Star Lake. The sample from the Forestry Bog consisted of the usual bog deposit, with a high percentage of organic material and a correspondingly small percentage of mineral constituents. The next lowest percentage of SiO_2 in his results was 22.0 per cent in Ike Walton Lake and four of his samples exceeded 40 per cent. In his samples from three southeastern lakes, the SiO_2 varied from 28.1 per cent to 36.5 per cent. Bottom samples from 3 lakes situated on Kodiak Island, Alaska, yielded larger amounts of SiO_2; they ranged from 58.1 to 69.4 per cent.

TABLE II. *Chemical analyses of the bottom deposits of 21 Wisconsin lakes. The results are stated in percentages of the dry weight of the samples. The depth of the water at the stations where the samples were taken is indicated in meters. All of the lakes from Anderson to Wildcat, inclusive, are situated in northeastern Wisconsin, while Green, Nagawicka, and Oconomowoc lakes are located in the southeastern district.*

Lake	Depth, meters	Loss on ignition	SiO_2	Fe_2O_3	Al_2O_3	CaO	MgO	P_2O_5	$\dfrac{SiO_2}{Al_2O_3}$	Organic carbon	Organic nitrogen	Ether extract	$\dfrac{\text{Organ. C}}{\text{Organ. N}}$
1. Anderson	15.0	41.15	40.10	5.06	9.00	1.43	2.80	...	4.44	...	...	...	—
2. Big	17.5	34.50	52.75	4.75	5.50	1.04	1.18	...	9.60	11.64	1.30	0.98	8.9
3. Big Carr	18.5	57.35	38.79	1.12	1.56	0.56	0.02	0.07	24.86	30.30	2.50	2.38	12.1
4. Blue	13.3	45.26	43.33	2.87	7.09	0.87	0.30	...	6.11	22.95	1.99	0.73	11.5
5. Boulder	6.0	55.44	27.01	13.55	1.80	1.09	0.13	0.05	15.00	29.41	2.04	0.89	14.4
6. Clear	24.5	47.64	46.12	1.85	3.24	0.32	0.19	0.09	14.23	23.50	2.07	1.14	11.3
7. Crystal	20.0	53.37	41.21	1.88	2.64	0.33	0.02	0.31	15.61	25.60	2.66	1.36	9.6
8. Finley	8.0	41.73	49.02	1.88	4.65	1.34	1.46	...	10.54	18.00	1.58	0.92	11.4
9. Helmet	10.0	59.78	34.21	1.58	3.33	0.69	0.15	...	10.27	35.30	2.50	2.15	14.1
10. Lit. Tomahawk .	14.5	29.57	40.70	4.63	4.68	1.45	2.58	...	8.70	13.43	1.30	0.55	10.3
11. Muskellunge	19.3	58.11	37.11	1.92	1.19	0.59	0.05	0.09	31.18	29.37	2.49	1.58	11.8
12. Nebish	13.0	64.20	29.50	1.80	3.30	0.44	0.65	...	9.00	28.18	2.65	2.17	10.7
13. Oxbow (Mud) ...	13.5	54.10	28.00	5.90	9.50	1.40	0.90	...	29.47	26.09	2.30	0.62	11.3
14. Rahr (Mud)	14.0	74.00	23.20	0.86	1.22	0.29	0.09	...	19.00	40.50	2.94	3.58	13.7
15. Tomahawk	22.0	31.04	45.64	17.60	4.65	0.51	0.21	...	9.81	13.97	1.47	0.89	9.5
16. Weber	12.5	54.00	40.38	1.77	2.74	0.43	0.06	0.61	14.74	22.30	1.93	1.21	11.5
17. White Sand	20.0	30.26	34.65	20.45	12.35	1.00	0.70	...	28.05	20.58	1.80	0.37	11.4
18. Wildcat	11.5	43.15	43.89	9.71	1.73	0.64	0.08	0.21	25.37	23.77	1.88	0.57	12.6
19. Green	65.0	31.51	33.25	3.08	7.25	21.68	3.32	...	4.60	7.70	0.77	0.30	10.0
20. Nagawicka	26.5	29.57	41.42	1.50	8.17	17.70	1.50	...	5.06	6.62	0.87	0.59	7.5
21. Oconomowoc	18.5	41.00	14.62	1.02	3.18	38.00	1.60	...	4.60	6.84	0.55	0.31	12.4

Fe_2O_3. One of the most interesting features of these chemical results is the wide range in the percentage of iron in the deposits. The minimum amount was a little less than one per cent in Rahr Lake and the maximum 20.4 per cent in White Sand Lake. Iron constituted more than 9 per cent of the dry weight of the mud of 4 lakes; the quantity seems unusually large in Boulder, Tomahawk and White Sand lakes, but this mineral is fairly abundant in the glacial material of some parts of the northeastern lake district, which probably accounts for the large percentages in these three lakes.

In the 12 northeastern lakes which Black analyzed, the iron content of the bottom samples ranged from a minimum of 1.3 per cent in the Forestry Bog to a maximum of 9.5 per cent in Trout Lake; the next in rank was Plum Lake with 9.0 per cent. Thus the maximum found in the present series of samples (20.4 per cent in White Sand Lake) was more than twice as large as that in Trout Lake of the previous series. With respect to Trout Lake, rocks obtained at depths of 6 m. to 10 m. in front of the Laboratory are frequently encrusted with a rather thick deposit of iron.

Al_2O_3. Alumina did not show so wide a range in percentage as iron; a minimum of 1.2 per cent was noted in Rahr Lake and a maximum of 12.3 per cent in White Sand Lake. Only 6 of the 21 samples contained more than 7.0 per cent of alumina.

In the 16 Wisconsin samples which Black analyzed, the alumina ranged from 0.8 per cent in the Forestry Bog to a maximum of 9.6 per cent in Silver Lake.

The relation of the percentage of silica to that of alumina is given in the tenth column of Table II. A rather wide variation was found in the various samples as the percentage of silica was from four to a little more than 31 times as large as that of alumina.

CaO. Marked differences were found in the CaO content of the various bottom samples. The northeastern group of lakes, which is relatively poor in calcium, shows small percentages of CaO in their bottom deposits. It reaches one per cent of the dry material or more in only 7 of the 18 lakes in this group, with a minimum of 0.3 per cent in two of them. In the three southeastern lakes, on the other hand, there was a maximum of 38.0

per cent in the sample from Oconomowoc Lake, which is a marl lake, while the Nagawicka material yielded a minimum of 17.7 per cent.

In the samples of bottom deposits from northeastern lakes which Black analyzed, the CaO varied from 0.6 per cent in Long Lake to a maximum of 2.4 per cent in Turtle Lake; both of these percentages are higher than those obtained in the present series of samples.

Black found a minimum of 19.9 per cent and a maximum of 24.7 per cent of CaO in the 4 bottom samples of the southeastern lakes which he analyzed.

MgO. Magnesia likewise is very scarce in the mud deposits of the northeastern lakes. Scarcely more than traces were found in the samples from Big Carr, Crystal and Weber lakes. Only three of the 21 bottom samples contained more than 1.6 per cent of MgO. A maximum of 2.8 per cent was found in the sample from Anderson Lake. The bottom samples from the three southeastern lakes yielded relatively small amounts of MgO also; a maximum of 3.3 per cent was found in Green Lake. The mud from Oconomowoc Lake contained twenty times as much CaO as MgO and there was a twelvefold difference in the Nagawicka sample, with approximately a sevenfold difference in Green Lake. Magnesium carbonate is much more soluble than calcium carbonate so that the former is not so readily precipitated out of the water as the latter.

In Black's analyses the MgO in the bottom samples of the northeastern lakes varied from 0.1 per cent in Silver Lake to 1.3 per cent in Turtle Lake. The samples from the 3 southeastern lakes contained 1.4 per cent to 3.0 per cent of MgO; the maximum percentage was found in a sample taken at 8 m. in Lake Monona.

P_2O_5. Phosphorus determinations were made on 7 of the 21 lakes represented in Table II. A maximum of 0.6 per cent of P_2O_5 was found in the bottom sample from Weber Lake, while Crystal Lake was second with 0.3 per cent, and 4 of them had less than 0.1 per cent. It seems probable that the higher percentages of phosphorus in the bottom samples of Crystal and Weber Lakes are correlated with the growth of three species of bryophytes on the bottom of these two lakes; rather large beds

of these plants are found even in the deepest parts of these lakes (Juday 1934).

Black's results show a minimum of 0.2 per cent and a maximum of 1.4 per cent P_2O_5 in the samples from the northeastern lakes and a range from 0.4 per cent to 1.4 per cent for the three southeastern lakes.

Organic carbon. In general the organic carbon is a good index of the quantity of organic matter in the bottom samples. The results for organic carbon show a very striking difference between the percentages found in the northeastern and the southeastern lakes; in the former group the bottom samples contained from 11.6 per cent to 40.5 per cent of organic carbon and in the latter it ranged from 6.6 per cent in Nagawicka to 7.7 per cent in Green Lake. The mean percentage for the 17 northeastern lakes is 24.4 per cent and that of the three southeastern lakes is 7.0 per cent, or more than a threefold difference. No determination has yet been made on the deposit from Anderson Lake. Up to the present time no satisfactory explanation of this difference has been found. Large aquatic plants and phytoplankton organisms are much less abundant in the northeastern than in the southeastern lakes, so that the reverse condition of the bottom deposits might be expected from this standpoint. Steiner and Meloche (1935) found larger percentages of lignin in the muds of some of the northeastern lakes than in that of Lake Mendota; since lignin is more resistant to decomposition than other carbohydrates, it may accumulate to a certain extent in bottom deposits of the northeastern lakes and thus furnish a larger percentage of organic material in the muds of these lakes.

It is possible also that the larger percentage of organic matter in the muds of the northeastern lakes is correlated with differences in bacterial populations and in the abundance of other organisms that inhabit the bottom deposits. Bacteriological studies indicate that the bacteria are only about one-tenth to one-hundredth as abundant in the muds of the northeastern lakes as in those of the souhteastern lakes. (Henrici and McCoy 1938). Similar results have been obtained for the bottom fauna. The smaller population of bacteria in the northeastern muds would use less organic matter in their metabolic processes and

the smaller populations of animals would also consume a smaller quantity of organic matter for food. It seems probable, however, that other factors are also involved in the phenomenon.

Black's results also show a marked difference between the two groups of lakes. The mean percentage of organic carbon in his four southeastern samples is 6.4 per cent and for the 12 northeastern lakes 23.5 per cent or almost four times as large.

Organic nitrogen. Table II shows that the organic nitrogen in the muds of the northeastern lakes is considerably larger than it is in those of the southeastern lakes; the mean content of the latter is 0.7 per cent and that of the former is 2.1 per cent, or three times as large, as compared with a fourfold difference in organic carbon. In the northeastern samples the ratio of the organic carbon to organic nitrogen ranges from 8.9 in Big Lake to 14.4 in Boulder Lake. In the three southeastern lakes, the ratios range from 7.5 to 12.4.

Ether extract. The ether extract (fat) obtained from these
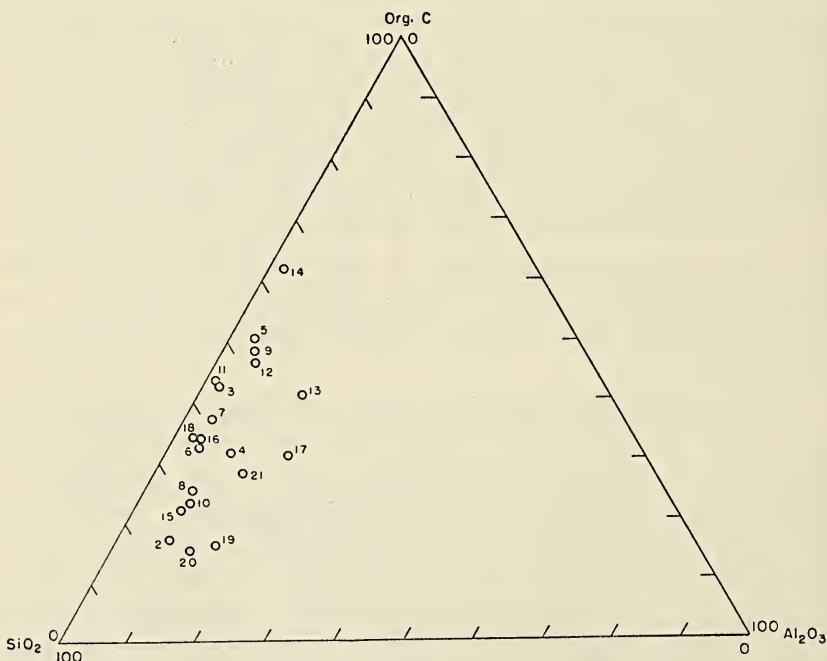
FIG. 1. This diagram shows the relation between SiO_2, Al_2O_3 and organic C. The various lakes are represented by the same numbers given them in Table II. Anderson Lake is not included.

bottom samples ranged from a minimum of 0.3 per cent in Green Lake to a maximum of approximately 3.6 per cent in Rahr Lake. More than one per cent of ether extract was found in 8 of the 17 northeastern lakes on which such determinations were made; of these, one sample yielded more than 3.0 per cent, three of them more than 2.0 per cent and the other four ranged between 1.0 and 2.0 per cent.

Figure 1 shows the correlation between the SiO_2, Al_2O_3 and organic carbon in 20 of the bottom samples; no determination of organic carbon is available for Anderson Lake so that it cannot be included. The results are platted on triangular coordinate paper frequently used by petrologists and mineralogists. Strom (1935) has recently called attention to the usefulness of this type of diagram for the purpose of classifying bottom deposits of Norwegian and Wisconsin lakes.

The diagram shows that SiO_2 is the dominant material in most of the bottom samples as compared with organic carbon and Al_2O_3; that is, it comprises more than half the material contributed by these three substances in 15 of the 20 lakes represented. The silica is mainly organic in origin since it is made up largely of diatom shells; this is especially true in Crystal and Wildcat lakes where a special microscopical study of the bottom deposits has been made. (Conger 1939).

The sample from Rahr Lake has a large amount of organic matter, which is to be expected since this body of water has many bog characteristics. Helmet Lake, on the other hand, is a typical bog lakelet, but it does not contain so large a percentage of organic matter as Rahr Lake. All of the bottom deposits show a relatively small amount of Al_2O_3, which has a mineral origin; clay is scarce in the glacial deposits of the northeastern lake district so that it is correspondingly low in the lake deposits.

The diagram does not show any distinct grouping of the various lakes. While they are widely distributed, there is no definite break in the series which would indicate a division into definite groups. Rahr Lake (14) is the only one which is well separated from the others and this is due to the large percentage of organic carbon and the relatively smaller amount of SiO_2.

When CaO is substituted for organic carbon in this type of

diagram, the great preponderance of SiO_2 is clearly shown in the case of the northeastern lakes, where CaO plays a minor rôle; in such a diagram the three southeastern lakes are widely separated from the former group and also from each other.

RESULTS ON OTHER LAKES

Strom (1935) gives chemical analyses of the bottom deposits of 15 Norwegian lakes which range in depth from 19 m. to 461 m. In his group of lakes, the SiO_2 ranged from a minimum of 43.1 per cent to a maximum of 59.4 per cent; both minimum and maximum percentages are larger in the Norwegian lakes than in the Wisconsin lakes represented in the present report as well as those in Black's report. In samples from three Alaskan lakes analyzed by Black, the SiO_2 was larger than in the Norwegian lakes, namely 58.1 per cent to 69.4 per cent.

The amount of Al_2O_3 in the Norwegian lakes varied from 4.3 per cent to 20.1 per cent, but in 33 Wisconsin lakes the range was from 0.8 to 12.3 per cent, which is considerably smaller than in the former group. The amount of Fe_2O_3 in the Norwegian lakes ranged from approximately 2.0 to 9.6 per cent, a smaller range than found in the Wisconsin lakes, namely 0.9 to 20.4 per cent. The CaO content of the Norwegian lake deposits varied from 0.9 to 3.2 per cent as compared with 0.3 to 38.0 per cent in the Wisconsin lakes. The range in MgO was 0.7 to 2.9 per cent in the Norwegian lakes and 0.02 to 3.3 in the Wisconsin lakes. The amount of organic carbon in deposits of the 15 Norwegian lakes constituted from 0.6 to 11.1 per cent of the dry weight of the deposits and in 33 Wisconsin lakes from 4.4 to 40.5 per cent.

In Upper Lunz Lake, Austria, Mulley (1914) found that the loss on ignition fell between 20.3 per cent and 54.4 per cent; in Lower Lunz Lake the percentages were 28.1 to 43.8 per cent. The maximum loss on ignition was found in the upper part of the sample and the minimum about 39 cm. below the surface of the mud. The CaO content of the samples varied from 4.3 per cent near shore to 53.5 per cent in the deeper water. The various samples yielded 0.14 per cent to 6.2 per cent of MgO. One sample from Upper Lunz Lake contained 23.0 per cent of Fe_2O_3, which is higher than the maximum found in the Wisconsin lakes.

In 5 samples of bottom deposits from different localities in

Lake Balaton, Hungary, Emszt (1911) found that SiO_2 varied from 1.5 to 54.0 per cent, Fe_2O_3 from 0.6 to 3.8 per cent, Al_2O_3 from 0.4 to 8.6, CaO from 12.3 to 52.2 and MgO from 0.7 to 4.6 per cent. In general the samples from the different parts of Lake Balaton showed a wider range of variation in these constituents than the entire group of Wisconsin lakes.

SUMMARY

1. This report is based on the chemical analyses of the bottom deposits of 21 lakes, 18 situated in northeastern and three in southeastern Wisconsin.

2. SiO_2 made up 14.6 to 52.7 per cent of the dry weight of the samples. It was the largest item in the mineral content of the northeastern lake deposits and in one of the southeastern lakes; it was exceeded by CaO in the other two southeastern lakes.

3. Fe_2O_3 varied from less than one per cent to 20.4 per cent.

4. Al_2O_3 ranged from 1.2 to 12.3 per cent.

5. The CaO content of the northeastern lake deposits was small, not exceeding 1.4 per cent; in the three southeastern lakes it ranged from 17.7 to 38.0 per cent.

6. MgO was scarce, ranging from a trace up to 3.3 per cent.

7. In the northeastern lakes, the organic carbon of the deposits varied from a minimum of 11.6 per cent to a maximum of 40.5 per cent; in the three southeastern lakes the percentages varied from 6.6 to 7.7. The organic nitrogen reached a maximum of 2.9 per cent and the ether extract 3.5 per cent.

8. On the basis of the relative content of SiO_2, Al_2O_3 and organic carbon, these deposits do not fall into distinct groups, but they form a substantially continuous series without any definite grouping.

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OXIDATION-REDUCTION POTENTIALS AND pH OF LAKE WATERS AND OF LAKE SEDIMENTS

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From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. Notes and reports No. 101.

INTRODUCTION

The potentials of lake and sea waters, including bottom muds, have been subjects of several investigations during recent years. It has been suggested that such potentials may be regarded as oxidation-reduction potentials. Similar researches have been made by a number of investigators in soil surveys and they have been adequately reviewed by Burrows and Cordon (1936).

METHODS

In previous lake studies, the potentials have been determined by hauling the samples of water to the surface from various depths and making the determinations in the boat. In some instances the methylene blue reduction test was employed (Kusnetzow 1935) ; this method is known to give comparative results, but it does not give as accurate values as the electrometric method.

Since pH determinations were made *in situ* by Freeman, Meloche and Juday (1933), it seemed best to make oxidation-reduction potential readings in a similar manner. After some experimentation an apparatus was finally developed which can be used for obtaining both oxidation-reduction and hydrogen ion readings *in situ* at any desired depth in a few minutes by simply throwing a switch.

With respect to the data on which this paper is based, it may be said that they represent the resultant values obtained by the conventional electrometric method of securing such determinations. A more detailed study of the problem will be required for

a better understanding of the various reduction processes that take place in the lower waters of lakes.

APPARATUS

Figure 1 shows the electrode part of the apparatus.   The electrodes are mounted in a rubber housing consisting of a bicycle inner tube which is closed at top and bottom by rubber stoppers.   The rubber tube is fastened over the rubber stoppers by metal expansion clamps so that the seals are water tight. The glass electrode for pH readings, the bright platinum electrode for Eh determinations and the calomel half-cell project
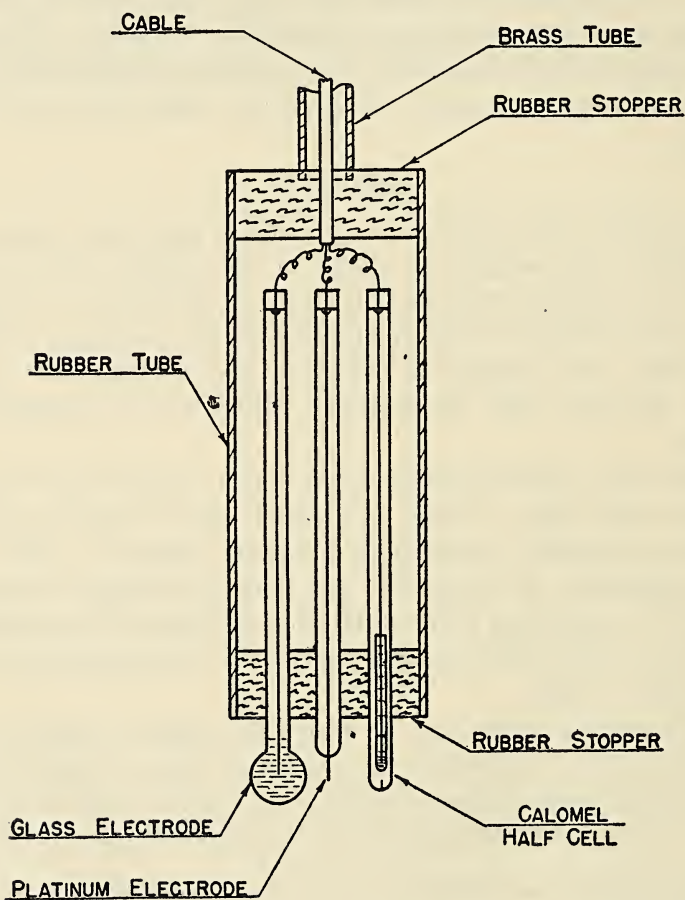
FIG. 1.   Apparatus used in getting oxidation-reduction potentials and pH.

below the lower stopper as shown in the figure. The platinum electrode and the glass electrode are connected with the calomel half-cell by means of a saturated potassium chloride solution; contact is made by sealing an asbestos thread into the bottom of the half-cell tube as described by ZoBell and Rittenberg (1937).

By means of a jack at the top, each electrode wire is fastened to one wire of the three-wire water proof cable which is 40 meters long; the cable is wound on a portable windlass which serves to raise and lower the electrodes. The three wires in the surface end of the cable are attached to jacks which are easily connected to the reading instrument, a portable Beckman pH Meter, Model G. This potentiometer is equipped with a scale which is calibrated directly in pH units; temperature corrections for these readings are made by a compensating dial on the instrument. By means of a switch, Eh readings in millivolts are made on the same scale which is used for pH readings. It was considered inadvisable to lower the electrodes into the bottom mud *in situ* so the mud samples were brought to the surface for the pH and Eh readings.

LAKES INVESTIGATED

During the summer of 1939, eleven lakes situated in northeastern Wisconsin were studied. The waters of these lakes vary widely in physical and chemical characteristics. Crystal, Trout and Weber are oligotrophic; Adelaide, Anderson, Muskellunge, Nebish, Scaffold and Silver are eutrophic; Helmet and Mary are dystrophic. Thus the three general types of lakes are represented in the investigation.

In order to see what changes might take place during the summer, most of the lakes were visited twice, once in July and again in August. At the same time the pH and Eh readings were made at the various depths, samples were taken for chemical determinations, such as dissolved oxygen, free and bound carbon dioxide, hydrogen sulphide, manganese, and ferrous, ferric and total iron.

RESULTS

The oxidation-reduction potentials of the surface waters of the various lakes ranged from Eh $+ 0.380$ to $+ 0.505$ volt. The

bottom waters varied from Eh + 0.057 to + 0.444 volt and the bottom sediments from Eh — 0.140 (Anderson) to + 0.200 volt (Silver).

Fig. 2. Oxidation-reduction potential and pH in Crystal Lake.

Figures 2 to 12 show some of the results obtained on the different lakes. In Crystal and Weber lakes, both oligotrophic, the Eh curves are similar and show little change from surface to bottom (Figs. 2 and 3). Both showed a somewhat larger oxygen content in the thermocline and the hypolimnion than in the epilimnion. A slight increase in Eh values was noted at depths of larger oxygen content. There was a rather marked difference in hydrogen ion concentration in Crystal Lake; it ranged from

pH 7.1 at the surface to pH 5.9 at the bottom. In Weber Lake, on the other hand, the range was from pH 6.8 at the surface to pH 6.4 at the bottom. Various fertilizers, including lime, have been added to Weber Lake during the past few years and this may account, in part at least, for the uniform condition.
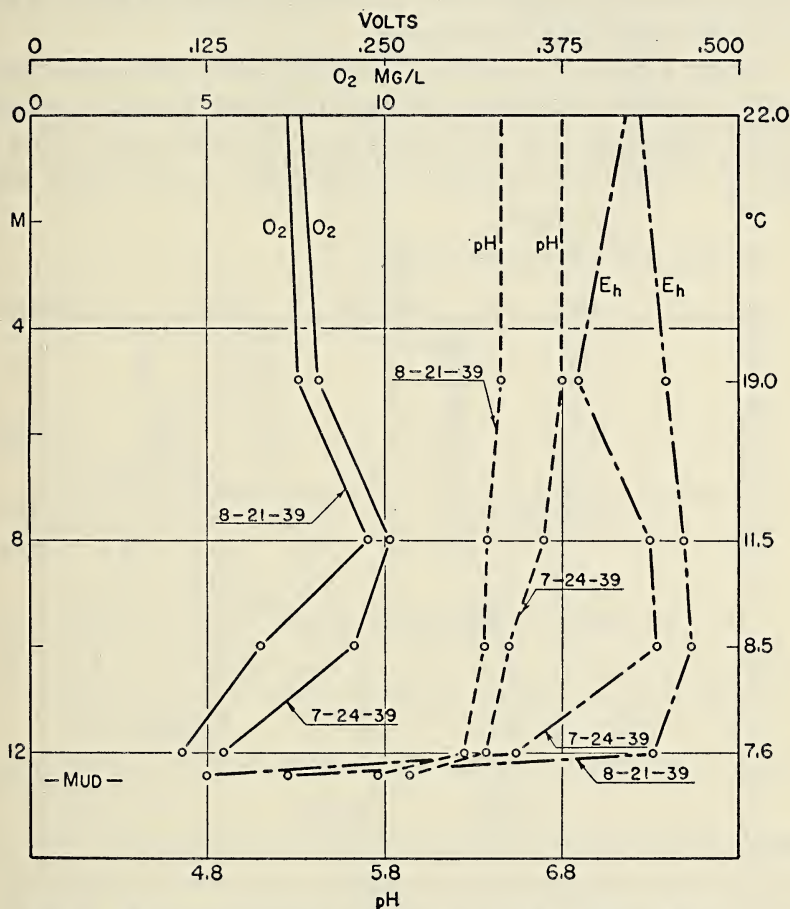
FIG. 3. Oxidation-reduction potential and pH in Weber Lake.

Trout Lake (Fig. 4) showed a distinct decrease in the oxygen content in the lower water; the quantity declined from 8.4 mg/l at the surface to 3.0 mg/l at the bottom. The oxidation-reduction potentials showed appreciable differences on the two dates represented in the curves; this was true especially in the thermocline and in the hypolimnion. The August series of readings

showed greater irregularity with depth than the July series. No hydrogen sulphide or ferrous iron was found in the lower water although the reading of the bottom mud indicated very reduced conditions at that level; at 34 meters the reading of the water was Eh + 0.388 volt and that of the mud was Eh + 0.074 volt. The pH readings ranged from 7.7 to 7.9 at the surface to 6.6 to 6.8 in the upper part of the mud.

Figure 5 gives the results for Silver Lake taken one month apart. The Eh curves are similar in form, but the readings obtained on August 29 were higher at all depths than those of July 28. The oxygen content of the water on the latter date,

FIG. 4. Oxidation-reduction potential and pH in Trout Lake.
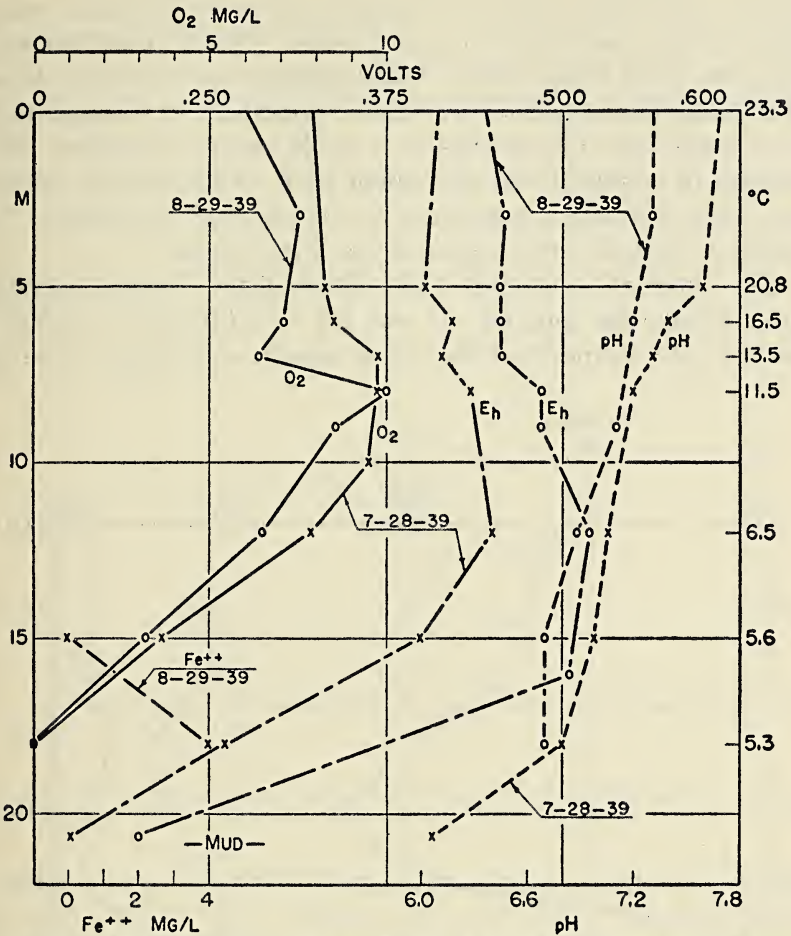
FIG. 5. Oxidation-reduction potential and pH in Silver Lake. Compare with Figs. 2-4.

however, was smaller at all depths, except 8 meters, than on the former date. There was a gradual decrease in the oxygen below 10 meters, but the change in the Eh did not begin until a depth of 12 meters was reached. Below 15 meters the Eh values declined very rapidly, thus indicating reduced conditions. Ferrous iron was found in this region of rapidly decreasing potential on August 29. The pH values fell within the range of those of Trout Lake (Fig. 4).

Only one set of observations was made on Anderson Lake. Figure 6 shows that there was a marked increase in dissolved

oxygen with depth down to 8 meters, below which there was a rapid decline, reaching zero at 15 meters. The Eh readings were about the same from surface to 10 meters, but below the latter depth there was a marked decrease in potential; it changed from Eh + 0.425 volt at 10 meters to + 0.125 volt at 19 meters. This decrease in potential was correlated with an increase in ferrous iron which showed a maximum of 8.1 mg/l at 18 meters. No hydrogen sulphide was found in the lower water.

The mud of Anderson Lake showed the lowest potential found during the summer; it was Eh − 0.140 volt. In fact it was the only sample that showed a negative potential. The pH
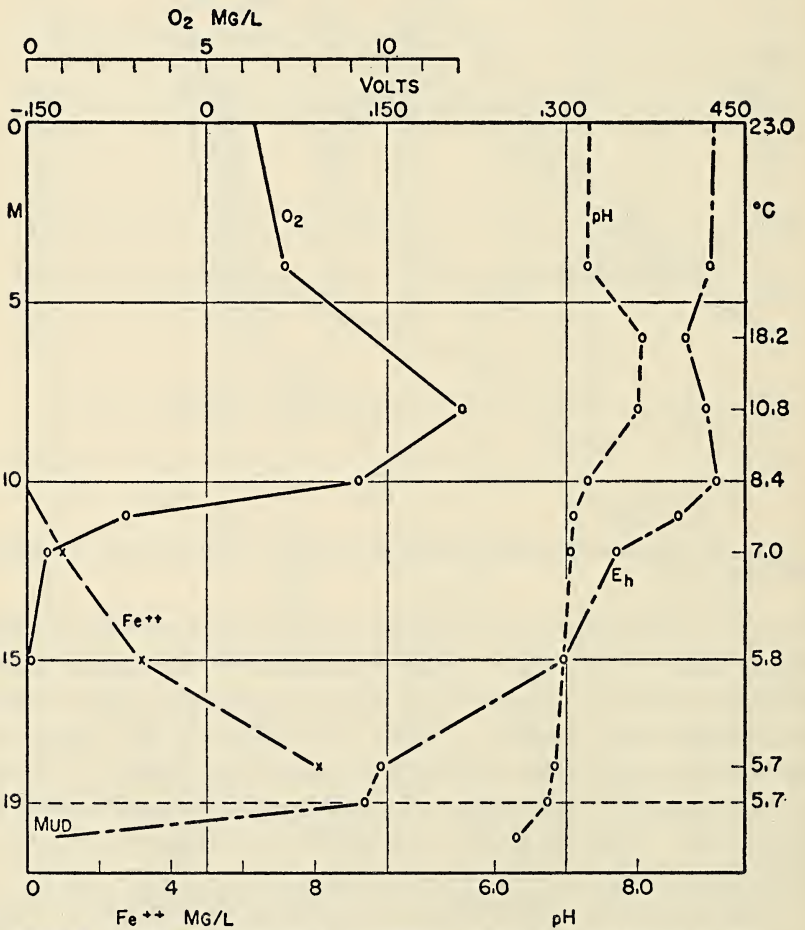
FIG. 6. Oxidation-reduction potential and pH in Anderson Lake.
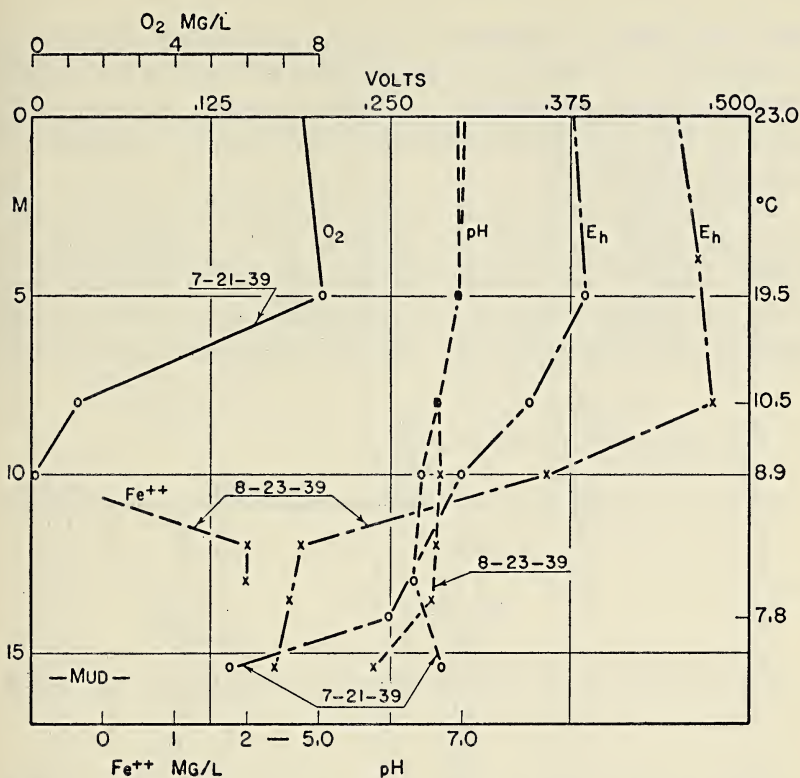
FIG. 7. Oxidation-reduction potential and pH in Nebish Lake. Compare with Fig. 6.

readings were somewhat higher in value in the high oxygen stratum, but the Eh readings did not show any appreciable change in that region.

The exidation-reduction potentials were higher in the upper water of Nebish Lake (Fig. 7) on August 23 than on July 21, but a marked decrease was noted in the lower water on both dates. No ferrous iron was found at any depth on July 21, but 2.0 mg/l were present at 12 and 13 meters on August 23. The pH readings were substantially the same down to a depth of 8 meters on both dates and the differences were not very great in the lower water. No oxygen samples were taken on August 23.

In Muskellunge Lake (Fig. 8), the potential readings were about the same on the two dates down to a depth of 8 meters, but

below this depth the decrease was more gradual on July 26 than on August 17. It will be noted that the Eh curves are roughly parallel to those representing dissolved oxygen. A trace of ferrous iron but no hydrogen sulphide was found at a depth of 19 meters on August 17.

Scaffold Lake (Fig. 9) is a rather small body of water with a maximum depth of about 11 meters. It is a difficult lake to classify since it has certain features of the dystrophic group but its very large production of plankton indicates that it really belongs to the eutrophic type. The lake has high wooded shores
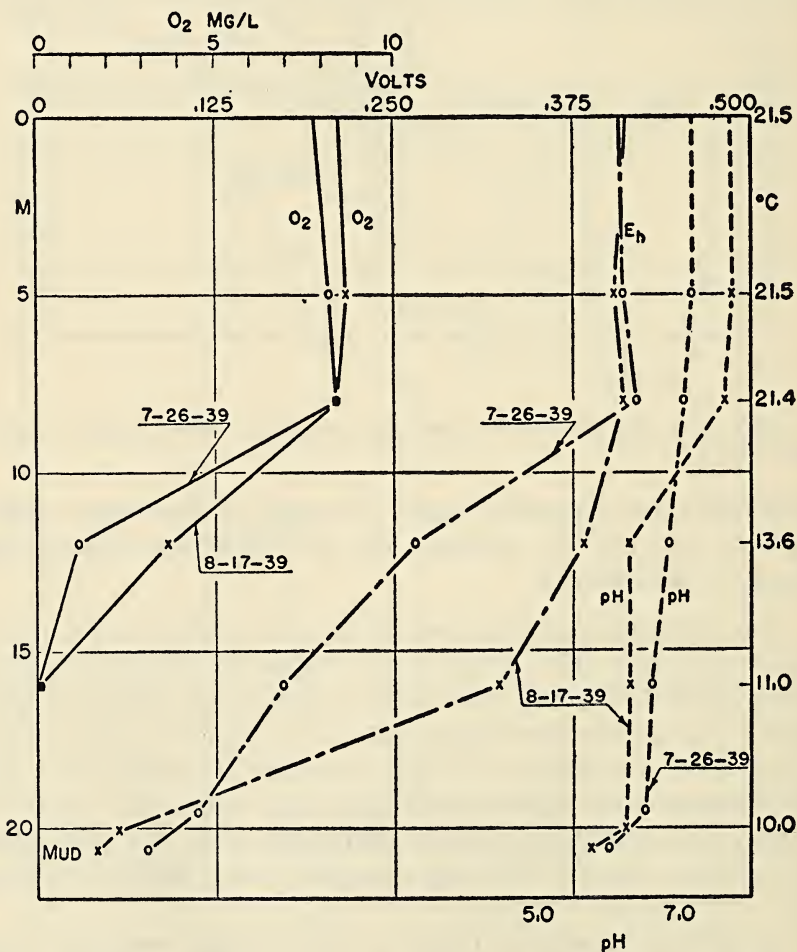
FIG. 8. Oxidation-reduction potential and pH in Muskellunge Lake.
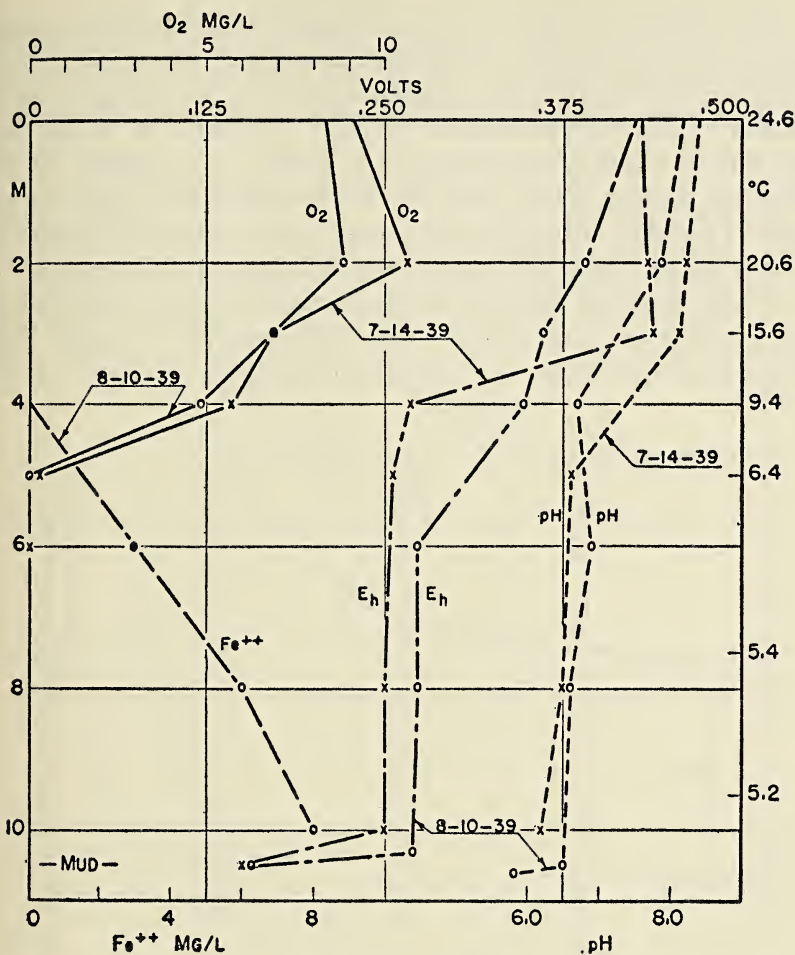
FIG. 9. Oxidation-reduction potential and pH in Scaffold Lake. Compare with Fig. 8.

for the most part so that the upper water is not greatly disturbed by wind during the summer. The temperature record in Figure 9 shows that the water had a sharp thermal stratification on July 14, 1939. The amount of dry organic matter in the centrifuge plankton catches on July 22 ranged from 9.4 mg/l at the surface to 19.2 mg/l at 10 meters. On August 11 the surface sample yielded 4.1 mg/l and the 10 meter sample 15.1 mg/l; this is the largest plankton production that has been found in any of the lakes of the Northeastern Lake District.

The dissolved oxygen curves of Figure 9 show that the phytoplankton was carrying on photosynthesis actively in the upper water on July 14 since the oxygen content at the surface and at 2 meters was above saturation, namely, 105 per cent at the former and 114 per cent at the latter depth.   On August 10 the dissolved oxygen was a little below the saturation point in the upper 2 meters.   On both dates there was a marked decrease in oxygen below 2 meters; the amount fell to zero at 5 meters.

It will be noted that the sharp decrease in redox potential on July 14 came one meter below that of the dissolved oxygen. Most of the fall in potential on that date took place between 3 and 4
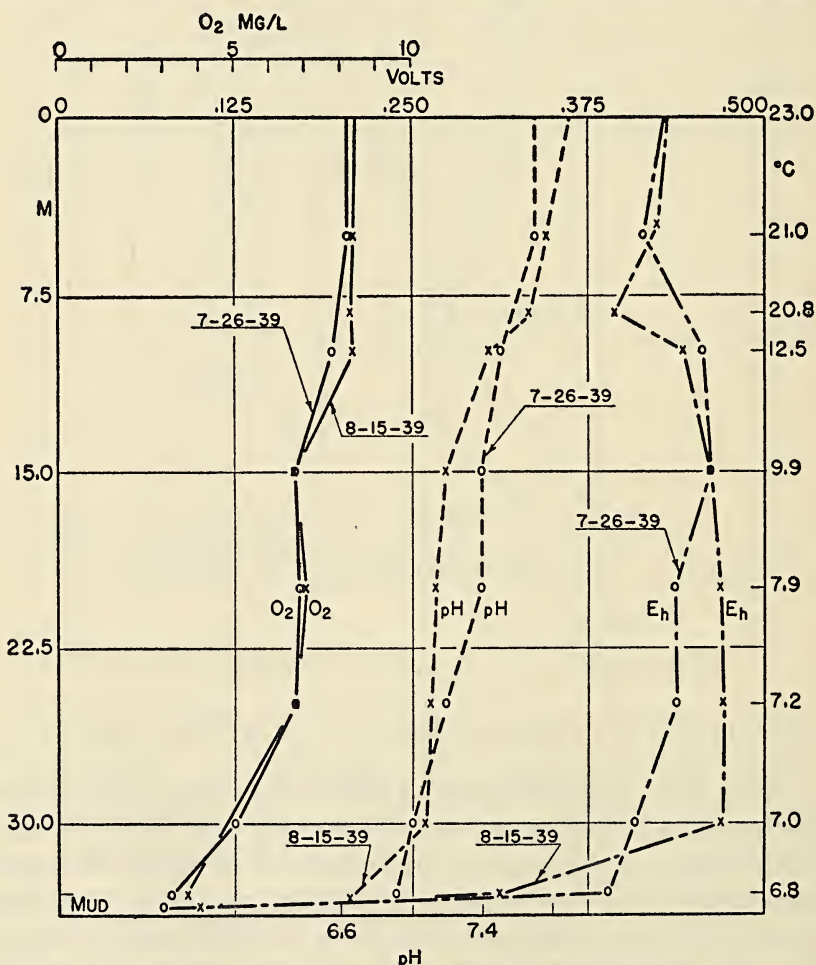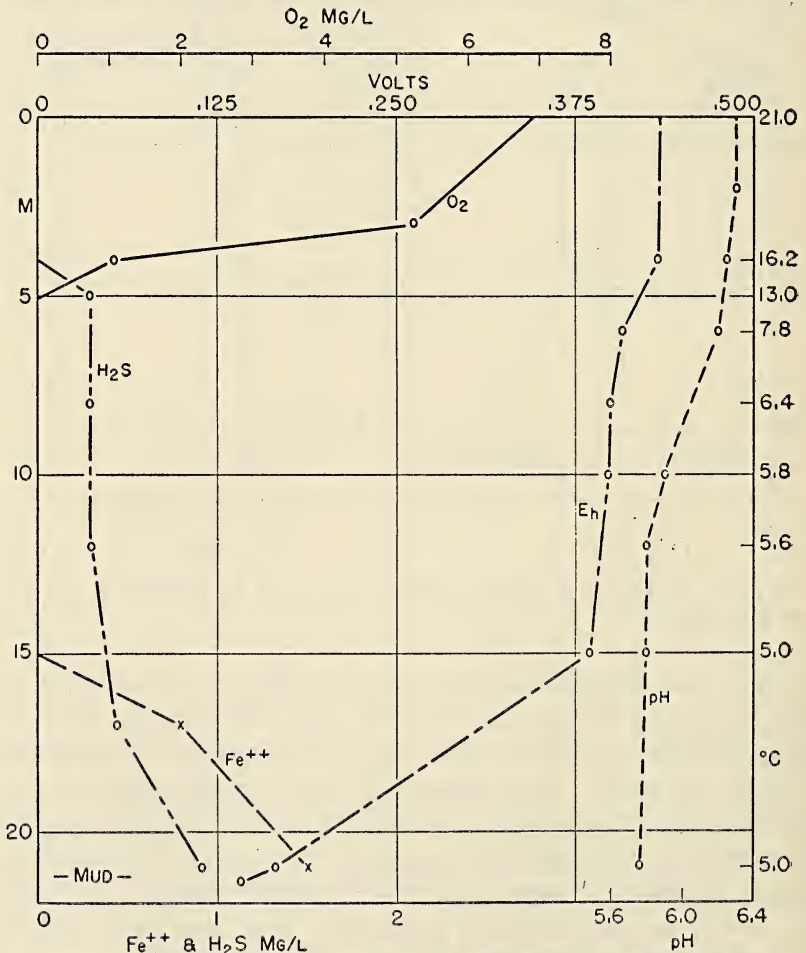

Fig. 10. Oxidation-reduction potential and pH in Adelaide Lake.
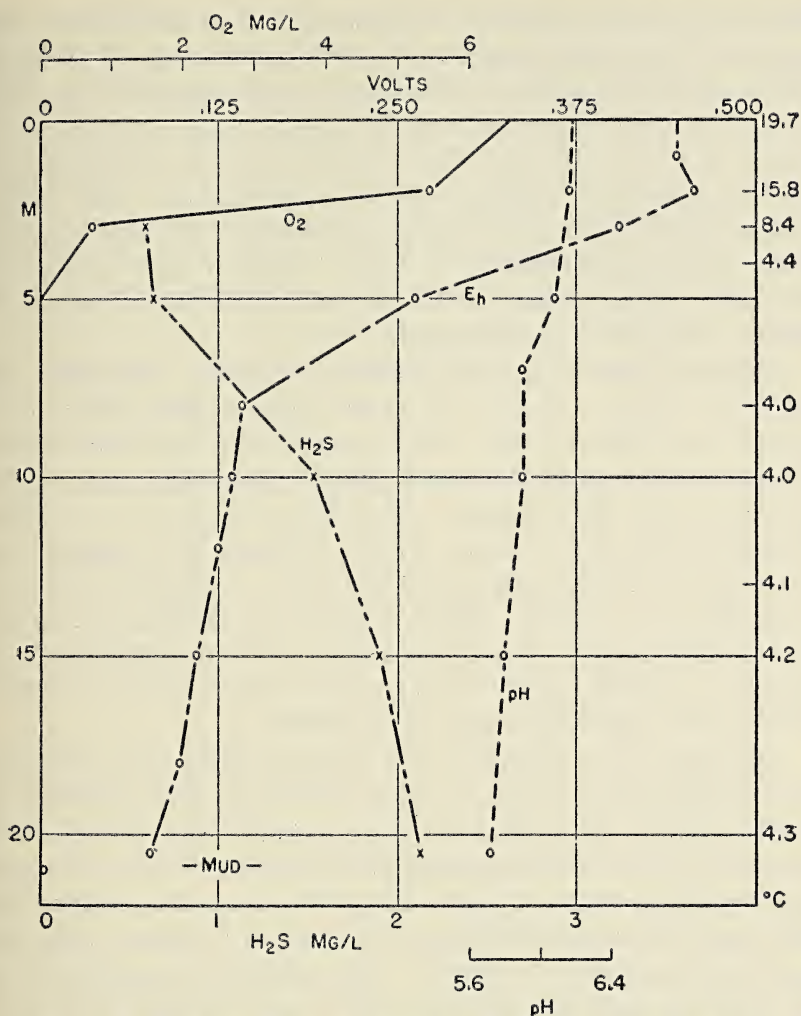
FIG. 11. Oxidation-reduction potential and pH in Lake Mary. Compare with Fig. 10.

meters, with only a small decline thence to the bottom. On August 10 there was a gradual decrease in redox potential from the surface to a depth of 6 meters, which was followed by only a small change between that depth and the bottom. On both dates the bottom deposits of Scaffold Lake showed a lower potential than the bottom water.

The curve for ferrous iron shows that it reached a maximum of 8.0 mg/l at 10 meters; Anderson Lake was the only other one

which had so large a quantity of ferrous iron at the bottom. The amount of hydrogen sulphide in the lower water of Scaffold Lake reached a maximum of 2.0 mg/l at the bottom. It is difficult to account for the constancy of the Eh values below 4 and 6 meters in view of the fact that both ferrous iron and hydrogen sulphide increased in amount below these depths. The results suggest that these two substances are not the controlling factors in the potential changes in this lake. The hydrogen ion in Scaffold Lake ranged from pH 8.4 at the surface to pH 6.2 at 10 meters, with pH 5.8 in the mud.

Adelaide Lake is on the borderline between eutrophic and dystrophic lakes. Figure 10 shows the results obtained on August 12, 1939, the only date on which the lake was visited. The dissolved oxygen decreased rapidly from 7.0 mg/l at the surface to zero at 5 meters. The Eh curve shows a uniform potential down to 4 meters; this is followed by a gradual decrease to 15 meters, below which there is a marked decline to the bottom, 21 meters. Small amounts of hydrogen sulphide were found between 5 and 12 meters, with an increase to 0.9 mg/l at 21 meters. No ferrous iron was found above 15 meters, but the curve shows 1.5 mg/l at 21 meters.

Lake Mary is a small bog lake situated only a short distance from Adelaide into which it drains when the water reaches an overflow stage. The water is soft and highly colored with stains extracted from the surrounding bog deposits. Figure 11 shows that the thermocline of Lake Mary lies near the surface and that dissolved oxygen is limited to the upper 5 meters, with only small amounts below 2 meters. The oxidation-reduction potential shows a rapid decrease between 2 and 8 meters and a more gradual decrease thence to the bottom, 20.5 meters. The rapid decrease in potential was found much nearer the surface in Lake Mary than in Adelaide Lake and the bottom potential was lower in the former than in the latter. Some hydrogen sulphide was found at 3 meters in Lake Mary (0.6 mg/l) and the quantity increased to 2.1 mg/l at 20.5 meters. No ferrous iron was found in the lower water of Lake Mary as compared with 1.5 mg/l in Adelaide. The pH curves of the two lakes are similar and cover about the same range between surface and bottom.

Results for two sets of observations on Helmet Lake are

given in Figure 12.   This is a typical bog lake with soft water which is highly colored with stains extracted from peat deposits.   During the summer of 1939, the color reached a maximum of 528 on the platinum-cobalt scale.   The maximum depth is 10 meters.

The upper water had relatively small amounts of dissolved oxygen, especially on August 3; very little was found below a depth of 4 meters.   The Eh curve for August 3 shows a gradual decrease in potential from surface to bottom.   On August 29 the potential values were higher in the upper 2 meters than in any other lake on which observations were made, namely,
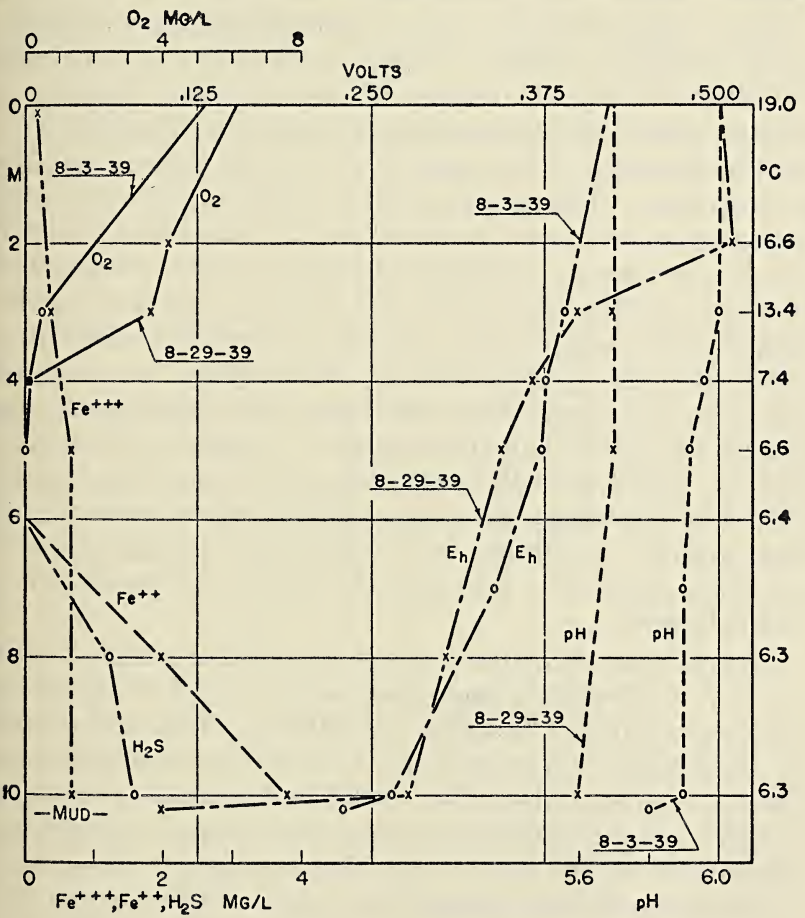
FIG. 12. Oxidation-reduction potential and pH in Helmet Lake. Compare with Figs. 10-11.

+ 0.510 volt. There was a sharp decrease of potential between 2 and 4 meters on this date and then a gradual decrease to the bottom. The low potential in the mud on August 29 (Eh + 0.100 volt) shows clearly the state of activity in the bottom sediments. A ferrous-ferric system was present; 4.0 mg/l of ferrous iron were found in the bottom water. Hydrogen sulphide was present in the lower water on August 29. The pH curves show that the hydrogen ion content of the water was higher at all depths on August 29 than on August 3.

DISCUSSION

The results obtained in this investigation show that there is a wide variation in these 11 lakes in oxidation-reduction potential, dissolved oxygen, ferrous iron and hydrogen sulphide. As pointed out by other investigators, the redox potentials of the systems present in lake waters do not depend entirely on oxygen concentration. The data show that complex systems of decomposing plant and animal material play an important rôle in the hypolimnion where no dissolved oxygen exists. Pearsall and Mortimer (1939) state that ferrous iron, hydrogen sulphide, ammonia and some of the nitrogen compounds present in the water play a part in the reduction phenomenon. It seems probable also that humus-like substances and lignocellulose compounds are involved in the problem. Hutchinson, Deevey and Wollack (1939) have also suggested that ferrous iron is responsible, in part at least, for the decrease in redox potential in the lower water. Brujewicz (1937) states that manganese, as well as iron, is a factor in the oxidation-reduction potentials of marine sediments.

Pearsall and Mortimer (1939) have called attention to the fact that relatively low concentrations of oxygen suffice to maintain predominantly "oxidized" conditions. They indicate that the change-over from reducing to oxidizing conditions takes place at a value of about E5 + 0.350 volt in natural waters and that this has considerable ecological significance. Such a sharp change-over was not found in the Wisconsin lakes. Table 1 gives the results for 8 lakes computed to a value of E5 at depths where the dissolved oxygen amounted to 0.5 mg/l. On a pH 5 basis the Eh values (E5) range from + 0.495 in Adelaide Lake to + 0.319

in Muskellunge Lake. The mean for the 8 lakes is + 0.405. Only one lake (Scaffold) gave a value of + 0.350 volt; Muskellunge had a lower value and the other 6 a higher value.

TABLE 1. Eh values calculated to pH 5 (E5) at depths where the dissolved oxygen was 0.5 mg/l in the various lakes.

Lake	Date	Depth, Meters	pH	Eh, volt	E5, volt
Adelaide	Aug. 12	4.5	6.2	0.424	0.495
Anderson	Aug. 19	12.0	7.0	0.327	0.445
Helmet	Aug. 3	3.0	6.0	0.388	0.446
Mary	Aug. 12	4.0	6.1	0.346	0.405
Muskellunge	July 26	14.0	6.7	0.220	0.319
Nebish	July 21	9.0	6.5	0.315	0.394
Scaffold	July 14	5.0	6.6	0.255	0.350
Silver	July 28	17.5	6.8	0.281	0.387

The differences between these E5 values and those reported by Pearsall and Mortimer are due, in part at least, to differences in the method of taking the readings; in addition also they may be due in part to the wide variations in the physical and chemical characterstics of the waters of the Wisconsin lakes.

Some experiments were run for the purpose of comparing the readings obtained *in situ* with those obtained by hauling samples to the surface from the same depths and taking readings immediately in the boat, with as little exposure of the water to the air as possible. The readings taken by the two methods checked very well in the epilimnion where there was an abundance of dissolved oxygen, but there were appreciable differences in the hypolimnion where there was little or no dissolved oxygen. The samples brought to the surface gave higher Eh values than the direct readings and there was a rather rapid drift in the values of the samples brought to the surface, due apparently to exposure to the air while making the readings.

The effect of oxygen has been observed in this investigation as well as that of ferrous iron and of hydrogen sulphide, but the effects of other reversible and irreversible reactions have not been analyzed because so little is known of the complex reactions which are undoubtedly taking place in the lower water under anaerobic conditions. More extended studies by this method of determining redox potentials in connection with more detailed chemical analyses of the water are planned for the future.

Summary

1. Apparatus is described for the determination of oxidation-reduction potentials and pH simultaneously *in situ* in lake waters.

2. Data are given for Eh, pH, dissolved oxygen, ferrous and ferric iron, hydrogen sulphide and temperatures at different depths in 11 lakes of northeastern Wisconsin.

3. The Eh values in the various lakes ranged from a maximum of $+$ 0.512 volt in the upper water of Helmet Lake to a minimum of $+$ 0.077 volt in the bottom water of Lake Mary. The lowest redox potential in the mud was Eh $-$ 0.140 volt in Anderson Lake.

4. Dissolved oxygen was not the only factor involved in decreasing the redox potential of the lower water; ferrous iron and hydrogen sulphide evidently played a part, and probably organic reducing systems as well.

5. In the oligotrophic lakes, there was either no decrease or only a small one in the redox potential of the lower water; the decrease in the lower water of the eutrophic and dystrophic lakes was much greater.

6. The 7 lakes on which two sets of observations were made about one month apart showed marked differences in redox potentials on the two dates. This indicates that these potentials are controlled by dynamic factors that are in a state of flux and not by static agents.

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THE LARGER AQUATIC VEGETATION OF TROUT LAKE, VILAS COUNTY, WISCONSIN

L. R. WILSON

INTRODUCTION

In the last eight years considerable attention has been given to the ecology of the larger aquatic vegetation in the lake region of northern Wisconsin. The present paper is the result of one summer of intensive work on Trout Lake and of several additional seasons during which the observations of 1934 were checked. The studies have been made in conjunction with the limnological studies of the Wisconsin Geological and Natural History Survey.

Trout Lake is located near the center of the Northern Highlands Lake District. Parts of it lie in T. 41 N., R. 6 and 7 E., and T. 42 N., R. 7 E.

One previous study dealing with the large aquatic plants of Trout Lake has been published (Fassett 1930), but it was of a reconnaissance nature and did not consider the ecological problems.

METHODS

The methods used in the present study were the same as those employed during earlier work in the region (Wilson 1935). These consisted of quadrat studies of 625 sq. cm. made with a modified Petersen dredge along transects of the bottom of the lake. The transects were chosen with reference to ecological conditions and quadrat collections were made at depth intervals of one-fourth meter. The total number of quadrats studied is 1696 (Fig. 1). The use of the Petersen dredge facilitated the collection of soil samples as well as the plants, and both were packeted for study in the laboratory. The plants were first separated into species and then air dried, weighed, and recorded.

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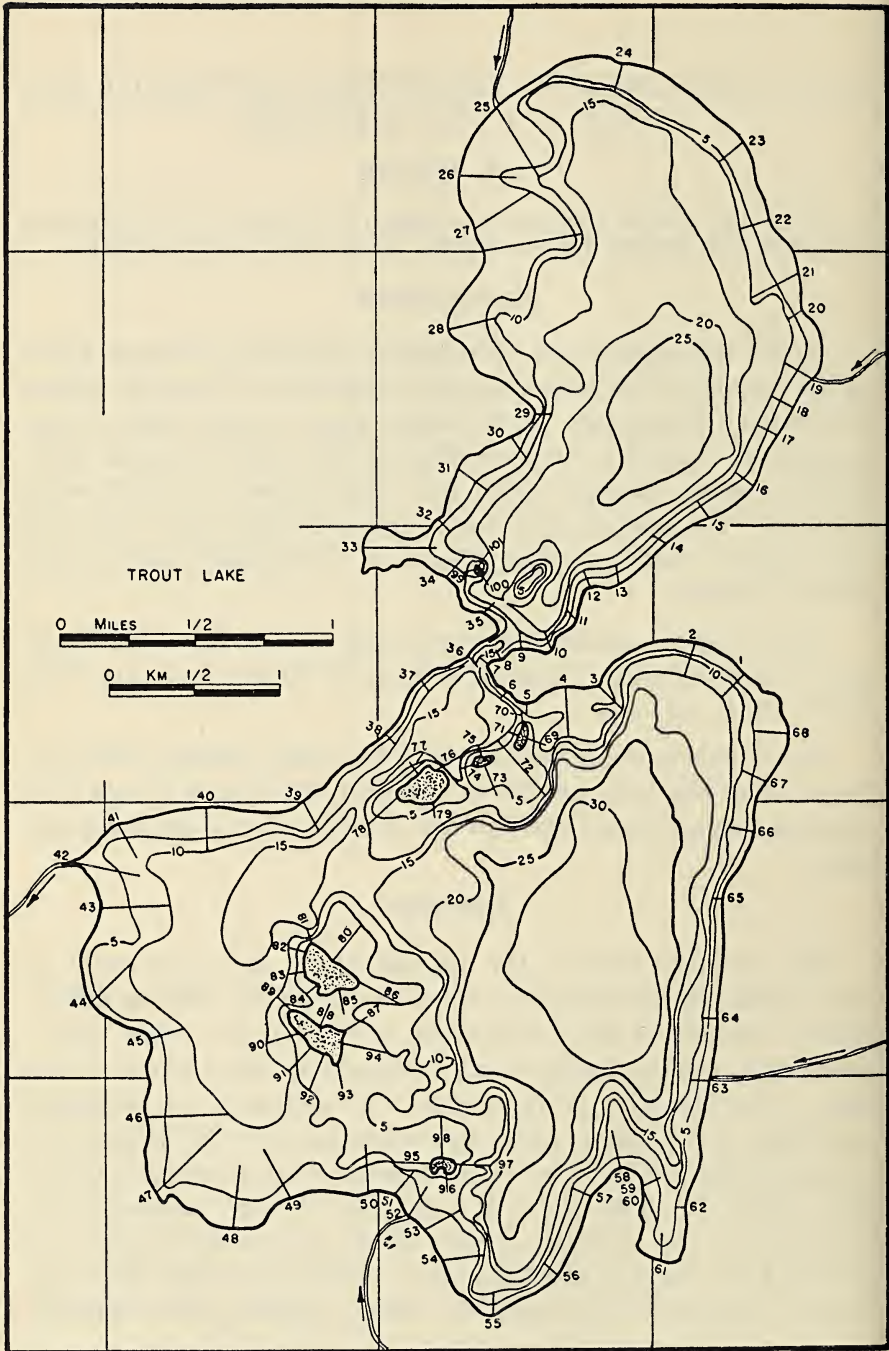
Fig. 1. Hydrographic map of Trout Lake showing the location of the transects along which quadrats were studied.

Fig. 2. Islands in the north end of South Trout Lake. The action of longshore currents has shaped and extended these islands. In the sheltered areas between them, a dense aquatic vegetation has developed.

Fig. 3. Shoreline of South Trout Lake at Station 1, showing the walled nature of the beach. Here the wave action is too great for the permanent establishment of littoral vegetation.

The soils were also air dried, but as yet have not been thoroughly studied.

The Geology and Water Properties of Trout Lake

Like most lakes in this region, Trout Lake was formed by melting of buried or partly buried ice masses in a pitted outwash plain. The ice involved in the formation of the lake appears to be of Early Mankato (4th Wisconsin) age. An examination of the map (Fig. 1) shows that the lake is constricted near its center and might almost be treated as two lakes rather than one. The ridge that forms the constriction is composed of drift materials which lack good assortment. This ridge has the structure of a recessional moraine. Though the two parts are considered as one, they are locally called North Trout and South Trout.

The length of Trout Lake is 7 kilometers and the width is 4 kilometers. The total area is 1583 hectares. North Trout is 533 hectares and South Trout is 1050 hectares in area. The mean depth is approximately 14 meters. The deepest portion of the lake is in South Trout and it is 35 meters. The volume of the entire lake has been estimated to be 218,037,000 cubic meters.

Four small streams enter the lake and one that is several meters wide drains it. In addition to the four streams entering the lake there is an area of springs in a bay on the west side of North Trout that must contribute considerable water to the lake. Springs are very few in this region, consequently these are of geologic interest.

In North Trout one small island exists, and in South Trout there are six (Fig. 2). A survey of the gravel bars in South Trout indicates that at least thirteen additional islands probably existed in the early history of the lake. These have been eroded by the waves and only the heavier gravels remain to indicate the former presence of islands.

Around many parts of the lake a walled character is well illustrated (Fig. 3). The walls are ramparts of sand and gravel built up by the ice while overriding the shoreline during the late spring. There are usually several well defined walls. This condition is also true for most of the lakes in the neighborhood and further study of these should lead to a better understanding of the lake development.

The shorelines range from the low swampy type to steep banks, with the last most abundant. Several bays exist in each of the two parts of the lake, but, with the exception of the bay containing the springs, comparatively little sedimentation of organic soils has taken place in them. The large size of the lake and the bays has allowed the winds to form waves that have eroded the embankments. Shorework has been accomplished in many parts of the lake and it has had an important effect on the aquatic vegetation.

The early history of the lake has to some extent determined the present distribution of the lake soils and the shore line features. There is evidence of shore work at approximately ten feet above the present level of the lake. The erosion of the former shore line and the deposition of sediments in deeper water, or in bays, has formed submerged terraces upon which rooted aquatics grow. The presence of such features indicates that the level of water remained high for some time.

It appears probable that most of the islands that are now gravel bars in South Trout were not, if at all, very high out of the water when it was deeper. It is possible that as the water level dropped, the islands or bars were likewise reduced in height by the waves eroding them. The drop in water level may be due to several circumstances of which three may be suggested. (1) The disappearance of the glacial ice and the shrinkage of the swollen drainage channels; (2) the cutting down of the outlet, and (3) a change in climate. Of the three hypotheses the second appears the most probable, though the first may have been important for a short time. That a marked change in climate took place in the last thousand or more years has been suggested by several writers. The evidence for a more arid ("xerothermic") climate than now exists in the region is not entirely agreed upon by ecologists. If such a period did exist it would have had most effect upon the seepage lakes, and drainage lakes, such as Trout Lake, might not have suffered greatly. In many of the nearby lakes, there is, in the shallow waters, a definite leaching and enrichment of the sandy soils, which is not unlike the podsol soil of the region. If the lake levels were lower than they are at present, the sandy beaches would be subjected to soil water leaching, resulting in a soil profile like the upland. Subsequent

Fig. 4. West shore of North Trout Lake showing *Scirpus acutus* growing where sand is an abundant sediment.

rise of the water level in the lakes would submerge the beaches, and account for the puzzling distribution of this soil type.

The soils of Trout Lake are for the most part gravel, sand, and silt in the shallow water. Only in bays, between certain of the islands, and near several of the inlets is an organic sediment present in the shallow water. Beyond the depth of six meters the common sediment is an organic deposit often referred to as limnic peat.

The water of Trout Lake is clear. The pH ranges from 6.8 to 8.2, and the bound carbon dioxide content varies from 17.8 to 20.0 parts per million. These properties place Trout Lake well within the catagory of the medium hard water lake, as defined by the Wisconsin Geological and Natural History Survey. The lake may also be described as oligotrophic, and the sum total of its characteristics indicate that it is hydrographically in a youthful or early mature stage of development (Wilson, 1939).

THE VEGETATION AND ITS DISTRIBUTION

During the present study, 36 species of aquatic plants were observed (Table I) and several others that are swamp or bog inhabitants might be added to this list. Also to the above number might be added *Potamogeton dimorphus* and *P. filiformis*, var. *borealis*, which were collected and recorded by Fassett 1930), but not seen by the author.

Trout Lake is relatively rich in its number of aquatic plant species, but it does not produce an unusually large crop. This might be explained in part by the fact that Trout Lake is hydrographically a young lake with only a narrow zone about the shore in which aquatics can grow. Except for a few bays, the remainder of the lake is either too deep for rooted plants or the shorelines are subjected to strong wave action, which prevents an abundant growth of attached hydrophytes.

The weight of the total crop of the larger plants is estimated to be 320.874 kilograms (Table I). With the exception of *Ceratophyllum demersum* the plants are rooted forms that grow between the zero and six meter contour lines. The above species is not a rooted form and has been found in great masses close to the six and one-half meter depth in the north end of South Trout.

TABLE 1. *Specific crops and their zonal distribution in Trout Lake.*

Species	Total dry weight of specific crops (kilograms)	Average dry weight per hectare (grams)	Per cent of crop Zones		
			I (0-1 m.)	II (1-3 m.)	III (3-6.5 m.)
Anacharis canadensis	1.265	4.84	1	20	79
Bidens Beckii	.284	1.24	43	54	3
Castalia odorata	3.363	3.36	100	0	0
Ceratophyllum demersum	72.064	200.86	0	0.5	99.5
Chara sp.	4.073	10.88	26	38	36
Eleocharis acicularis	.446	3.84	70	30	0
Eleocharis palustris	10.109	260.56	100	0	0
Equisetum limosum	4.248	217.92	100	0	0
Gratiola aurea, f. pusilla	.031	1.64	100	0	0
Isoetes macrospora	15.760	81.32	71	29	0
Juncus pelocarpus, f. submersus	.972	49.92	100	0	0
Littorella americana	.391	20.20	100	0	0
Lobelia Dortmanna	.219	11.24	100	0	0
Myriophyllum alterniflorm	.719	3.72	87	13	0
Myriophyllum tenellum	2.088	6.88	68	31.5	0.5
Myriophyllum verticillatum	1.128	4.92	30	65	5
Najas flexilis	26.084	64.92	25	61	14
Nitella sp.	.124	.69	0	0.5	99.5
Potamogeton amplifolius	22.696	68.92	2	83	15
Potamogeton epihydrus	.441	22.64	100	0	0
Potamogeton gramineus var. graminifolius	7.158	19.12	75	24.5	.5
Potamogeton natans	3.935	29.00	80	20	0
Potamogeton obtusifolius	3.555	8.52	4	27	69
Potamogeton pectinatus	5.937	42.64	87	13	0
Potamogeton praelongus	9.098	26.84	3	88	9
Potamogeton pusillus	2.788	6.48	18	34	48
Potamogeton Richardsonii	14.332	38.28	32	59	9
Potamogeton Robbinsii	83.946	195.68	2	54	44
Potamogeton spirillus	.002	.12	100	0	0
Ranunculus aquatilus, var. capillaceus	2.201	14.20	99.5	0.5	0
Ranunculus reptans	.098	5.04	100	0	0
Sagittaria cuneata	.062	.64	98	2	0
Sagittaria graminea	2.185	7.20	59	40	1
Scirpus actus	14.286	367.92	100	0	0
Sparganium angustifolium	.149	7.68	100	0	0
Vallisneria americana	4.637	13.68	42	46	12
Totals	320.874	748.3	61	23	16

Many of the plant species show a marked preference for certain soils, and occur abundantly wherever these soils are found. The soil relationship was given considerable attention and an attempt has been made in the chart below, to summarize the plant communities and soil types. The area of plant growth has been divided into three vertical zones following the practice of Rickett (1922 and 1924), who worked in southern Wisconsin. Zone I extends to a depth of one meter and represents a zone of maximum wave action, or in sheltered places, the last stages of open water and the formation of the swamp or bog habitat. Zone II extends from one meter to three meters in depth. In water of this depth the sedimentation is not very rapid if the location is opposite an exposed shoreline, but if it is in a bay or otherwise shelted location the sedimentation of finely divided inorganic and organic materials may be rapid. Zone III extends from three meters downward to the limit of rooted aquatics, or growing unrooted forms as *Ceratophyllum.* This is usually between five and six meters. The sedimentation in this zone depends upon the size, depth, outline, and hydrographic age of the lake. In Trout Lake organic soils occur in this zone but are seldom more than a few inches thick.

Another vital factor in the distribution of aquatic vegetation is the light relationship. At present there are few published observations of this nature. A few growing depths of aquatic plants have been checked in the field with observations of solar transmission in water. Pearsall and Hewitt (1933) and Pearsall and Ullyott (1934) working in the Lake District of England found that aquatic vegetation grew to a depth where only two per cent of full daylight existed. In three lakes of Vilas County, Wisconsin, the limit at which plants grew was observed to be 4.4 to 6.8 per cent of the total solar radiation (Wilson, 1935). The following table is a more complete study of this subject. It must be realized that many of the plant species grow only on certain soils whose distribution in Trout Lake is not always the distribution for other lakes. This difference will materially change the depth distribution of the plants and light relationship. Further observations in other lakes, made with consideration to plant succession should finally give definite information on the light requirements of aquatic plants. Sev-

Summary of plant distribution in Trout Lake

Zone I (0-1 meter) Gravel, sand, silt	Zone II (1-3 meters) Sand, silt	Zone III (3-6.5 meters) Sand, silt
Chara sp. *Eleocharis acicularis* *E. palustris* *Equisetum limosum* *Gratiola aurea*, f. *pusilla* *Isoetes macrospora* *Juncus pelocarpus*, f. *submersus* - - - - *Littorella americana* *Lobelia Dortmanna* *Myriophyllum tenellum* *Najas flexilis* *Potamogeton gramineus*, var. *graminifolius* *P. spirillus* *Ranunculus reptans* *Sagittaria cuneata* *S. graminea* *Scirpus acutus* *Sparganium angustifolium* *Vallisneria americana* - - - - - -	*Anacharis canadensis* *Bidens Beckii* *Chara* sp. *Eleocharis acicularis* *Isoetes macrospora* *Myriophyllum tenellum* *Myriophyllum verticillatum* - - - - *Najas flexilis* *Potamogeton amplifolius* *P. epihydrus* *P. graminens*, var. *graminifolius* *P. obtusifolius* *P. praelongus* *P. pusillus* *P. Richardsonii* *Ranunculus aquatilus*, var. *capillaceous* *Sagittaria graminea* *Vallisneria americana* - - - -	*Anacharis canadensis* *Chara* sp. *Myriophyllum tenellum* *M. verticillatum* *Najas flexilis* *Potamogeton amplifolius* *P. obtusifolius* *P. praelongus* *P. pusillus* *P. Richardsonii* *Vallisneria americana* - - - - - - - - - - - -
Sand, silt, organic soil (well decomposed)	Organic Soil (well decomposed)	Organic soil (well decomposed)
Anacharis canadensis *Bidens Beckii* *Castalia odorata* *Chara* sp. *Eleocharis acicularis* *Isoetes macrospora* *Juncus pelocarpus*, f. *submersus* *Lobelia Dortmanna* *Myriophyllum alterniflorum* *M. tenellum* - - - - - - - - - - *M. verticillatum* *Najas flexilis* *Potamogeton amplifolius* *P. epihydrus* *P. graminens*, var. *graminifolius* *P. natans* *P. obtusifolius* *P. pectinatus* *P. praelongus* *P. pusillus* *P. Richardsonii* *P. Robbinsii* *Ranunculus aquatilus*, var. *capillaceus* *Sagittaria graminea* *Sparganium angustifolium* *Vallisneria americana* - - - -	*Anacharis canadensis* *Bidens Beckii* *Ceratophyllum demersum* *Chara* sp. *Isoetes macrospora* *Myriophyllum alterniflorum* *M. verticillatum* - - - - - - *Najas flexilis* *Nitella* sp. *Potamogeton amplifolius* *P. natans* *P. obtusifolius* *P. pectinatus* *P. praelongus* *P. pusillus* *P. Richardsonii* *P. Robbinsii* *Ranunculus aquatilus*, var. *capillaceus* *Vallisneria americana*	*Anacharis canadensis* *Bidens Beckii* *Ceratophyllum demersum* *Chara* sp. *Najas flexilis* *Nitella* sp. *Potamogeton amplifolius* *P. praelongus* *P. pusillus* *P. Richardsonii* *P. Robbinsii* *Vallisneria americana*
Organic soil (not well decomposed)		
Anacharis canadensis *Bidens Beckii* *Castalia odorata* *Myriophyllum alterniflorum* *Najas flexilis* *Potamogeton natans* *P. pectinatus* *P. Robbinsii* *Sparganium angustifolium* *Typha latifolia* *Vallisneria americana* - - - - Swamp and bog		

DIAGRAM OF PLANT SUCCESSIONS
IN TROUT LAKE

Wave action great   Wave action slight   Wave action almost none
(Gravel, sand)   (Fine sand, silt,   (Mineral silts,
     organic sediments)   organic sediments)

SWAMP or BOG

Depth of water in meters

Diminishing wave action

0
1
2
3
4
5
6

Barren

Eleocharis-Scirpus-Equisetum

Typha-Sparganium Sagittaria

Isoetes-Lobelia-Juncus

Potamogeton Najas-Anacharis

Castalia-Potamogeton Sagittaria

Najas-Vallisnaria-Chara

Najas-Potamogeton-Chara

Myriophyllum Potamogeton-Nitella

Potamogeton (linear-leaved) Ceratophyllum

NOTE
    Arrows indicate successions and sedimentation, the type of which is shown by the column.

TABLE 2. *Depth and light relationship of plants in Trout Lake.*

Species	Max. depth in meters	Per cent of incident radiation*
Sparganium angustifolium	¼	70
Potamogeton epihydrus	¼	70
Ranunculus reptans	¼	70
Gratiola aurea, f. *pusilla*	¼	70
Potamogeton spirillus	¼	70
Lobelia Dortmanna	¼	70
Littorella americana	¼	70
Equisetum limosum	½	50
Juncus pelocarpus, f. *submersus*	½	50
Eleocharis palustris	½	50
Scirpus acutus	½	50
Castalia odorata	1	28
Sagittaria cuneata	1¼	25
Eleocharis acicularis	1½	23
Potamogeton natans	1¾	20
Ranunculus aquatilis var. *capillaceus*	2	18
Myriophyllum alterniflorum	2½	16
Isoetes macrospora	2½	16
Potamogeton pectinatus	2½	16
Bidens Beckii	3½	11
Myriophyllum verticillatum	3½	11
Myriophyllum tenellum	4	6.6
Sagittaria graminea	4	6.6
Potamogeton gramineus, var. *gaminifolius*	4½	5.0
Potamogeton praelongus	4½	5.0
Vallisneria americana	4½	5.0
Anacharis canadensis	4½	5.0
Nitella	5	4.3
Potamogeton amplifolius	5	4.3
Potamogeton Richardsonii	5	4.3
Chara	5	4.3
Najas flexilis	5½	3.5
Potamogeton obtusifolius	6	2.7
Potamogeton pusillus	6	2.7
Potamogeton Robbinsii	6	2.7
Ceratophyllum demersum	6½	2.0

* Birge, E. A. and C. Juday. p. 397. Fig. 7.

eral of the species listed in Table 2 are plants with floating leaves, others have most of their green parts above the water, and at least one species is not rooted. All of these must receive separate treatment when their light relationships are studied.

Above, in the summary of plant distribution in Trout Lake, is a graphic presentation of the plant communities and their relationship to the soils and depth of water in which they grow. The dashes separating the various communities indicate relationship, but not necessarily trends of succession. Below, in the diagram

of plant succession the trends are indicated by arrows, and three important species in each community have been used to designate each assemblage. By comparing the two diagrams one may gain a more complete picture of the specific succession.

SUMMARY

1. Trout Lake is a medium hard water, oligotrophic lake located in the northcentral part of Wisconsin.
2. The larger aquatic vegetation consists of 38 species, which occupy the lake soils to a depth of six and one-half meters. The total dry weight of the crop is estimated to be 320.874 kilograms and the average dry weight per hectare of the colonized area is estimated to be 748.3 grams. Sixty-one per cent of the crop is restricted to the first meter (Zone I); 23 per cent to the area between one and three meters (Zone II), and 16 per cent of the crop occupies the area between three and six and one-half meters (Zone III).
3. The growing depth and light relationship of the plants was investigated. Some species do not grow where less than 70 per cent of the total sun light occurs, while others grow where as little as 2 per cent is present. All of these percentages are not suggested as vital factors in the distribution of the species.

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BATHYMETRIC DISTRIBUTION OF FISH IN LAKES OF THE NORTHEASTERN HIGHLANDS, WISCONSIN[1]

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INTRODUCTION

The present study of the bathymetric distribution of fish in the lakes of northeastern Wisconsin has been based on records of the catches of gill nets fished during the summers of 1930, 1931 and 1932. During the first of the three summers, soundings were made only of the general area in which each gang of nets was fished. In 1931 and 1932, however, individual records were made of the depths from which almost all of the nets were lifted. The more exact data obtained in these two years form the basis for most of the material that will be presented, although some references will be made to the fishing operations of 1930.

The limnological data of Table 1 indicate the general nature of the five lakes, the distribution of whose fish populations will be described. The location of four of the lakes (Nebish, Muskellunge, Trout and Silver) may be seen in Figure 1. Clear Lake lies about 13 kilometers (8 miles) southeast of Trout Lake. Trout Lake is the second largest and the deepest lake of the Northeastern highlands. In comparison with other Lakes of the region its waters are relatively hard. Muskellunge Lake and Clear Lake are of intermediate and similar size. Clear Lake has very soft water, particularly for a lake so large, whereas the water

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of Muskellunge Lake may be termed medium hard. Silver Lake and Nebish Lake are both small. They differ, however, as to the hardness of their waters; the concentration of bound CO_2 is 15.0 p. p. m. in Silver Lake as compared to 4.0 p. p. m. in Nebish Lake. Limnological data concerning all of these lakes have appeared from time to time in publications of the Wisconsin Geological and Natural History Survey.
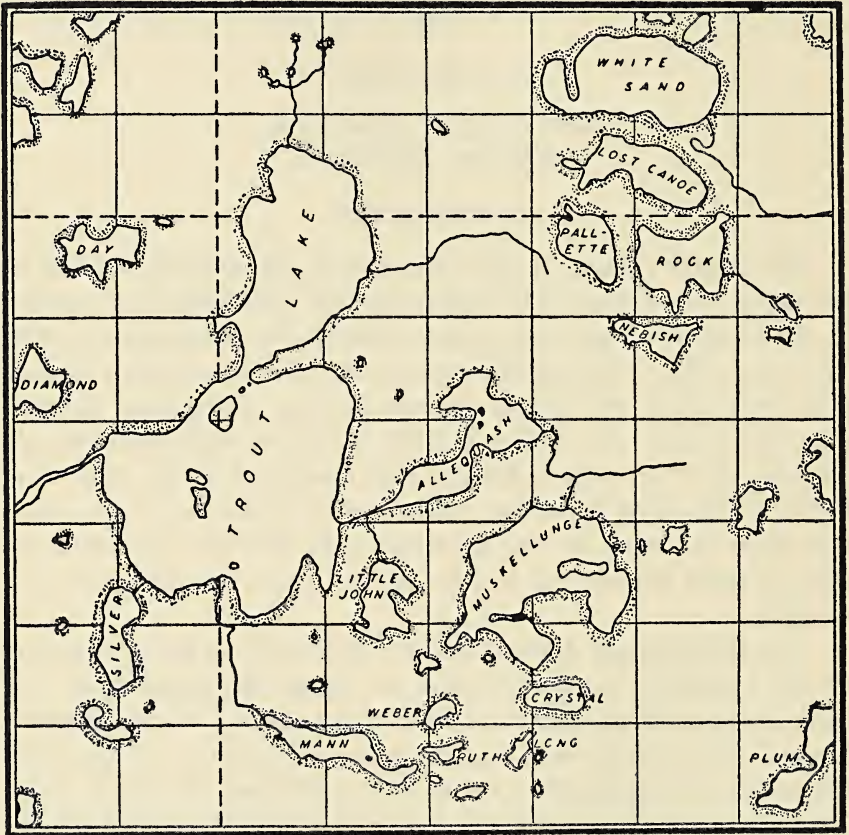
FIG. 1. Map of Trout Lake region.

TABLE 1. *Limnological data on five Lakes of the northeastern highlands, Wisconsin. The data for color, pH, conductivity, bound CO_2, and the organic matter of the plankton refer to average surface conditions in summer.*

Lake	Length in kilometers	Breadth in kilometers	Surface area (hectares)	Length of shore line in kilometers	Depth in meters Maximum	Depth in meters Mean
Nebish	1.32	0.66	38.5	4.2	15.8	5.2
Muskellunge	3.12	2.00	372.3	14.5	21.0	7.0
Trout North basin	7.00	4.00	533	25.9	31.0	12.9
Trout South basin			1,050		35.0	14.2
Silver	1.75	0.66	87.3	4.3	19.5	11.3
Clear	3.36	2.04	417.8	22.2	29.3	8.8

Lake	Secchi disc transparency (meters)	Color, platinum-cobalt scale	pH	Conductivity in reciprocal megohms	Bound CO_2 in milligrams per liter	Organic matter of plankton in milligrams per liter
Nebish	6.0	9	6.8	19	4.0	0.77
Muskellunge	4.0	4	7.2	40	10.0	1.16
Trout North basin	5.0	6	7.8	73	18.5	0.66
Trout South basin	4.5	3	7.6	77	18.7	0.92
Silver	5.5	4	7.5	62	15.0	0.85
Clear	6.3	0	6.6	17	2.2	0.84

Methods

The gill nets fished in 1930 and the early summer of 1931 included the following sizes of mesh (stretched measure in inches) : $1\frac{1}{2}$, 2, $2\frac{1}{2}$ and $3\frac{1}{4}$. The depth of these nets ranged from $3\frac{1}{2}$ to 4 feet. A complete replacement of gear was made July 22, 1931. The new nets included seven sizes of mesh (stretched measure in inches): $1\frac{1}{4}$, $1\frac{1}{2}$, $1\frac{3}{4}$, 2, $2\frac{1}{4}$, $2\frac{1}{2}$ and 3. Each of these nets was 50 yards long and approximately 6 feet deep. Thus the area of each net was roughly 100 square yards. All tabular material on the average catch per lift has been based on data from the "new" nets.

Ordinarily the gill nets were fished in gangs of seven nets, and were lifted daily. The different sizes of mesh were not arranged in a gang in any definite order. The sets were made along rather than across the contours of the lake since this procedure made possible a more accurate determination of the depth at which each net was set. The mean of the soundings at the ends of each net has been taken as the depth from which the net was lifted.

At the time the nets were lifted the catches from the different meshes were placed separately in labeled pails. Counts and measurements of the fish from each net were made later at the field laboratory.

The description of the bathymetric distribution of fish will include a consideration of the relationship between the length of fish and the depth of water inhabited. Since the data on which the discussion will be based will consist of records of the average numbers of fish captured in different sizes of mesh at the various depths of water, a knowledge of the relationship between the size of mesh and the average length of the fish captured is of considerable importance. Table 2 shows the relationship between the size of gill-net meshes and the average length of the fish taken for each species of each lake for which detailed tabular material will be presented in later sections[2]. It is apparent that the relationship between length of fish and size of mesh is sufficiently close to make valid the use of the numbers of fish captured in different sizes of mesh for the study of the bathymetric

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[2] The data of Table 2 relative to the perch of Nebish and Silver lakes were computed from tabulations given by Schneberger (1935). The remaining data were compiled originally for this report.

distribution of fish of different size. In other words, if small-mesh nets made their best catches in shallow water and large-mesh nets fished most successfully in deep water it may be concluded that the smaller fish were living in shallower water than were the larger individuals.

TABLE 2. *Average standard length in millimeters of fish taken by gill nets of different mesh size in four lakes of northeastern Wisconsin. Numbers of specimens in parentheses.*

Lake	Species	Average length of fish taken in mesh (stretched measure)						
		1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
Nebish	Rock bass	86 (17)	92 (172)	116 (79)	134 (92)	156 (70)	162 (224)	177 (350)
	Perch	122 (35)	144 (115)	165 (120)	182 (48)	202 (9)	222 (3)	... ...
	Smallmouth black bass	113 (38)	130 (23)	169 (12)	177 (25)	199 (22)	215 (14)	249 (10)
Muskellunge	Rock bass	83 (97)	92 (79)	121 (40)	142 (50)	149 (66)	158 (71)	175 (37)
	Perch	115 (493)	140 (95)	168 (39)	175 (51)	198 (51)	211 (36)	164 (7)
	Common sucker	133 (30)	143 (119)	169 (114)	196 (152)	221 (283)	236 (384)	277 (197)
	Bluegill	70 (29)	82 (87)	96 (98)	112 (30)	124 (102)	126 (80)	141 (23)
Trout	Rock bass	75 (6)	90 (28)	103 (20)	128 (93)	147 (6)	157 (7)	185 (3)
	Perch	116 (158)	137 (87)	160 (29)	183 (24)	201 (5)	191 (4)	... ...
	Common sucker	168 (2)	134 (20)	165 (12)	202 (25)	213 (15)	235 (43)	294 (32)
	Wall-eyed pike	... ...	189 (5)	266 (1)	227 (18)	310 (6)	308 (6)	338 (15)
Silver	Rock bass	... ...	89 (1)	102 (3)	... ...	132 (1)	160 (3)	157 (1)
	Perch	124 (463)	139 (102)	159 (63)	172 (4)	... ...	... ...	... ...
	Common sucker	123 (2)	144 (3)	169 (9)	219 (1)	222 (5)	267 (7)	289 (26)

NEBISH LAKE

The collections from Nebish Lake contained significant numbers of only three species—rock bass (*Ambloplites rupestris*), yellow perch (*Perca flavescens*), and smallmouth black bass (*Micropterus dolomieu*)—in that order of abundance. A fourth

species, the largemouth black bass (*Aplites salmoides*) was represented by two individuals. These fish most probably had been introduced, since there is no evidence that Nebish Lake was supporting a population of largemouth black bass at the time the collections were made.

Tables 3, 4 and 5 contain data relative to the bathymetric distribution of the rock bass, yellow perch and smallmouth black bass in Nebish Lake in late summer. The dates of the collections were July 29 to August 6, 1931, and August 6 to 11, 1932. Sets were made at various localities in the lake (for map of Nebish Lake see Fig. 2). The fishing intensity (number of lifts) was distributed more irregularly among the different depths of water than would be desirable for a careful study of the vertical distribution of fish. However, the primary purpose of the fishing in Nebish Lake and the other lakes as well was the collection of specimens in quantity; consequently, the majority of the nets was set at depths at which experience had shown the best catches
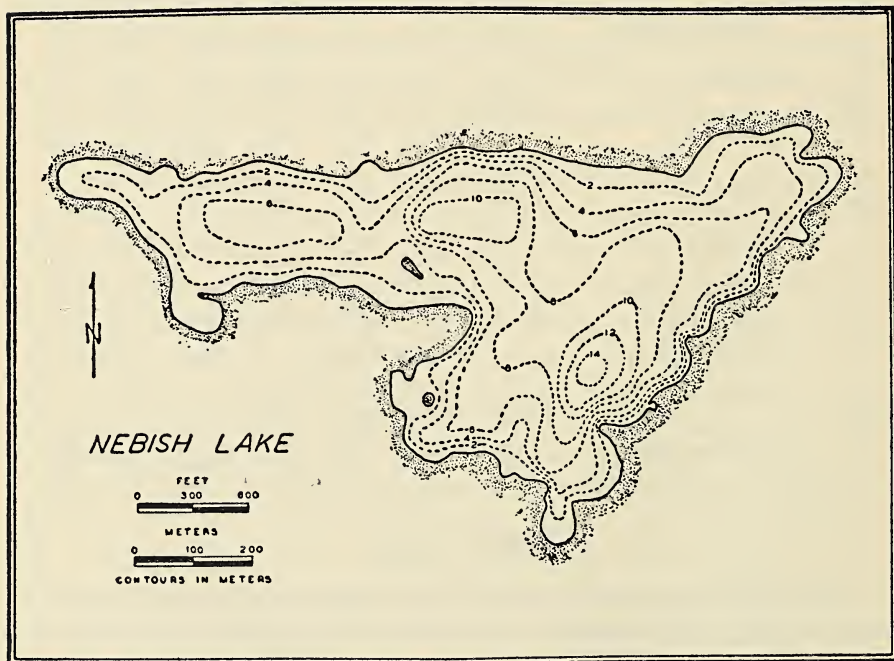
Fig. 2. Hydrographic map of Nebish Lake.

could be made. The combination of the data for 1931 and 1932 was made after an examination of the results for the two years separately failed to reveal significant differences.

The strata defined in Tables 3, 4 and 5 refer to the depths at which the nets were set on the bottom, not necessarily to the depths at which the fish were taken. Since the height of each net (distance between float-line and lead-line) was 6 feet as hung or approximately the depth of the strata of Tables 3, 4 and 5 (2 meters), a net set near the upper limit of an indicated stratum fished almost the entire stratum immediately above. On the other hand, the fishing of a net was confined to its own stratum only when it was set at the lower limit of that stratum. Consequently, nets set repeatedly and at random on the bottom within a 2-meter stratum actually fished on the average a water-stratum of nearly 4 meters. The average depth of the water-stratum fished corresponds approximately to the upper limit of the 2-meter stratum in which the nets were set. For example, the fishing of nets set in the stratum, 3.0 to 4.9 meters, extended through the stratum, 1.0 to 4.9 meters, and nets set at 5.0 to 6.9 meters fished the stratum, 3.0 to 6.9 meters. Because of the overlap in the depths fished by nets set in successive strata, the data of the type presented in Tables 3, 4 and 5 provide only an approximate measure of the bathymetric distribution of fish. It should be mentioned also that the depths employed in the analyses were the averages of the depths at the ends of the nets, (p. 150) and that different parts of the nets actually were set above and below the average depth. Errors from this source were reduced by the fact that nets were ordinarily set along rather than across the contours.

In order to avoid the too frequent use of such awkward expressions as "fish taken by nets set at 5.0 to 6.9 meters", the more simple term "fish taken at 5 meters" frequently will be employed. This latter phrase should be understood to refer to fish captured in a 4-meter stratum whose average depth was approximately 5 meters. In all tables of the type of Tables 3, 4 and 5 the upper limit of each stratum, which corresponds to the average depth at which the fish were captured by nets set in that particular stratum, has been printed in bold-face type. The average depth for the nets lifted from 11.0 meters and deeper is,

of course, indefinite. Nets fished in the stratum, less than 3.0 meters, took fish at an approximate average depth of 1.5 meters.

There is some evidence that in late July and early August large rock bass (Table 3) live in deeper water than do small ones. The best catches in all three of the smaller meshes ($1\frac{1}{4}$, $1\frac{1}{2}$, and $1\frac{3}{4}$ inches) were made at depths of 5 meters and less. The numbers of fish per lift were relatively low at 7 meters, and not one rock bass was taken in small-mesh nets at 9 meters or deeper. No lifts of the 2-inch mesh nets were made from the shallowest water and from 3.0 to 4.9 meters. The best catches (average of 6.4 fish per lift) were taken at 5 meters, but good lifts were made also at 7 meters (average of 4.5 fish). Nets of $2\frac{1}{4}$-inch mesh took more fish at 9 meters than at shallower depths. Data are lacking for the $2\frac{1}{2}$-inch mesh nets at 9 meters. The best lifts in this net were made at 5 meters, although good catches were taken also at lesser (3 meters) and greater (7 meters) depths. The catches of the 3-inch mesh net give the strongest support to the belief that the larger rock bass live in deeper water than do the smaller rock bass. The average catch at 7 meters (18.3 fish) was 3.2 times the average at 5 meters (5.7 fish), but was less than half the average at 9 meters (39.2

TABLE 3. *Average number of rock bass taken in Nebish Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters	Gill-net mesh (stretched measure)						
	$1\frac{1}{4}$ inches	$1\frac{1}{2}$ inches	$1\frac{3}{4}$ inches	2 inches	$2\frac{1}{4}$ inches	$2\frac{1}{2}$ inches	3 inches
<3.0	.. ..	3.0 (1)	.. ..	.. ..	.. ..	.. ..	1.0 (1)
3.0 to 4.9	2.0* (2)	6.1 (7)	6.7* (3)	.. ..	1.0 (1)	8.5 (2)	.. ..
5.0 to 6.9	1.0 (5)	13.6* (8)	5.1 (7)	6.4* (8)	2.7 (9)	11.4* (9)	5.7 (7)
7.0 to 8.9	0.2 (10)	1.3 (3)	2.6 (7)	4.5 (10)	3.0 (7)	8.6 (8)	18.3 (6)
9.0 to 10.9	0.0 (1)	.. ..	0.0 (2)	0.5 (2)	3.7* (3)	.. ..	39.2* (4)
>10.9	0.0 (1)	0.0 (1)	.. ..	.. ..	.. ..	0.0 (1)	0.0 (1)

fish). No rock bass were taken from nets of any mesh size set at depths in excess of 10.9 meters.

Differences in the vertical distribution of perch according to size of fish, if present, were small (Table 4). The best catches of every mesh size were made at 3 or 5 meters. Nets of three of the four larger mesh sizes took their greatest catches at the lower of the above two depths, but the 3-meter depth was not represented in the lifts of the 2- and 3-inch mesh nets. Catches of the nets of all mesh sizes were reduced at 7 meters (no fish in the 3-inch mesh). Perch were very scarce or totally lacking in nets set at 9 meters, and none were caught in lifts from depths greater than 10.9 meters.

TABLE 4. *Average number of yellow perch taken in Nebish Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters	Gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0	.. ..	5.0 (1)	.. ..	.. ..	.. ..	.. ..	0.0 (1)
3.0 to 4.9	6.5* (2)	11.7* (7)	10.7* (3)	.. ..	0.0 (1)	5.5* (2)	.. ..
5.0 to 6.9	4.0 (5)	9.2 (8)	7.7 (7)	3.6* (8)	1.2* (9)	1.1 (9)	0.3* (7)
7.0 to 8.9	2.8 (10)	2.7 (3)	6.7 (7)	3.1 (10)	0.7 (7)	0.4 (8)	0.0 (6)
9.0 to 10.9	0.0 (1)	.. ..	0.5 (2)	0.0 (2)	0.3 (3)	.. ..	0.2 (4)
>10.9	0.0 (1)	0.0 (1)	.. ..	.. ..	.. ..	0.0 (1)	0.0 (1)

The results for the smallmouth black bass (Table 5) resemble those for the perch. All but one (2¼-inch mesh) of the different mesh sizes made their best catches in water shallower than 7 meters. The absence of smallmouth black bass in the deep-water lifts is in agreement with the observations for rock bass and perch.

The catch records of Tables 3, 4 and 5 indicate that to a large extent the rock bass, yellow perch and smallmouth black bass of

Nebish Lake were occupying a common habitat in late July and early August of 1931 and 1932. The only suggestion of segregation is found in the relatively deeper habitat of large rock bass.

TABLE 5. *Average number of smallmouth black bass aken in Nebish Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters	Gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0	.. ..	5.0* (1)	.. ..	.. ..	.. ..	.. ..	0.0 (1)
3.0 to 4.9	0.5 (2)	1.3 (7)	1.7* (3)	.. ..	0.0 (1)	1.5* (2)	.. ..
5.0 to 6.9	2.4* (5)	0.5 (8)	0.6 (7)	1.2* (8)	0.9 (9)	1.1 (9)	0.9* (7)
7.0 to 8.9	0.2 (10)	0.0 (3)	1.1 (7)	0.8 (10)	1.0 (7)	0.1 (8)	0.5 (6)
9.0 to 10.9	0.0 (1)	.. ..	0.0 (2)	0.5 (2)	2.0* (3)	.. ..	0.0 (4)
>10.9	0.0 (1)	0.0 (1)	.. ..	.. ..	.. ..	0.0 (1)	0.0 (1)

The complete absence of fish in the four lifts from depths of more than 10.9 meters suggests the presence of some barrier that prevented fish from penetrating the greater depths. A better idea of the probable location of the "barrier" may be had from a more exact knowledge of the depths from which the deep-water lifts were made. The 1¼- and 2½-inch mesh nets were lifted from a depth of 11 meters and, therefore, on the average, fished approximately the 9- to 11-meter stratum. The 1½-inch mesh net was lifted from a depth of 11.5 meters and fished the 9.5- to 11.5-meter stratum. The 3-inch mesh net, lifted from 12 meters of water, fished the 10- to 12-meter stratum. The logical location to assume for the hypothetical barrier would then appear to be at or slightly below 9 meters.

The factors that may be expected to exert the greatest influence on the vertical distribution of fish in inland lakes are the distribution of food organisms and the physical and chemical

TABLE 6. *Relationship between depth of water and temperature, hydrogen-ion concentration and the concentrations (milligrams per liter) of dissolved oxygen and free carbon dioxide in Nebish Lake on three dates in the summers of 1931 and 1932.*

Depth in meters	August 11, 1931				July 21, 1932				August 23, 1932			
	Temperature in °C	O_2	CO_2	pH	Temperature in °C	O_2	CO_2	pH	Temperature in °C	O_2	CO_2	pH
0	22.3	7.7	0.7	7.5	19.5	8.2	1.5	6.6	22.1	8.2	1.6	6.8
2	21.8	..	..	..	..	..	..	..	..	..	..	..
3	21.0	..	..	..	19.5	7.9	1.5	6.6	22.0	8.3	1.6	6.8
5	20.8	8.1	0.7	7.5	19.4	8.2	1.5	6.6	21.3	8.0	1.6	6.6
6	20.6	..	..	..	19.3	..	..	..	..	7.9	1.6	6.7
7	20.3	8.1	1.0	7.5	15.0	8.4	2.0	6.5	20.8	7.8	2.1	6.4
8	13.7	7.6	1.2	7.3	13.0	7.4	4.5	6.2	17.7	3.3	10.6	6.2
9	13.2	..	..	..	11.2	5.7	6.5	6.2	13.5	1.0	13.6	6.1
10	12.5	0.7	10.2	6.7	10.2	3.1	8.5	6.1	12.2	0.65	15.1	6.0
11	11.2	..	..	..	9.6	2.6	9.0	6.1	11.0	0.55	15.6	6.1
12	10.4	0.2	13.5	6.7	9.0	1.45	10.0	6.1	10.1	0.4	16.6	6.1
13	..	..	..	..	..	0.4	11.0	6.1	9.6	0.4	20.6	6.1
14	¹9.9	0.2	16.0	6.7	8.8	0.9	11.0	6.0	..	0.2	21.6	6.1
15	..	..	16.0	6.7	..	..	..	..	..	..	..	..

¹ Temperature record for 15.5 meters.

conditions of the water.   Although the food habits of the rock bass, perch and smallmouth black bass of Nebish Lake have been investigated (Couey, 1935), the lack of published data on the distribution of food organisms prevents an examination of the relationship between the bathymetric distributions of fish and their food.   Neither is a vertical series of temperature readings and chemical determinations available for Nebish Lake during the periods in which the gill-net collections were taken (July 29-August 6, 1931, and August 6-11, 1932).   However, the vertical series taken after the dates of the 1931 collections (on August 11) and both before and after the time of collection of the 1932 materials (July 21 and August 23) make possible a fairly satis-factory estimate of the conditions in Nebish Lake with respect to temperature, hydrogen-ion concentration and the concentra-tions of dissolved oxygen and free carbon dioxide at the time the gill-net samples were taken (Table 6).

The 9-meter contour which marks the approximate lowest depth to which fish penetrated in Nebish Lake in late July and early August, 1931 and 1932, fell in the thermocline on July 21 and August 23, 1932, and was below the thermocline on August 11, 1931.   The thermal stratification of Nebish Lake on August 11 must be considered exceptional since a decline of 6.6° C. in temperature occurred between the depths of 7 and 8 meters whereas no other 1-meter stratum showed a decline of as much as 1° C. with the exception of the 10- to 11-meter stratum (de-crease of 1.3° C.).   It is not at all unlikely that a later disturb-ance of the water may have increased the thickness of the thermocline sufficiently to include the 9-meter contour.

The conditions in Nebish Lake at the time of the fishing operations were doubtless intermediate to those prevailing on July 21 and on the two August dates.   It is likely therefore that near the end of July and in early August the depth of 9 meters lay near the lower limit of the region of abundant dissolved oxygen and near the upper limit of the region with high concen-trations of free carbon dioxide.   The changes in the hydrogen-ion concentration near the 9-meter depth were so small that they may be disregarded as a factor in the vertical distribution of fish in Nebish Lake.   In fact, it appears that the variation in the hydrogen-ion concentration with depth of water is not suf-

ficiently great to affect significantly the bathymetric distribution of fish in any of the lakes considered in this study. Data on the hydrogen-ion concentration have been included chiefly to show the limited extent of the variations.

Low temperature of the water, a deficiency of oxygen or a high concentration of free carbon dioxide conceivably might limit the depth to which fish penetrate in Nebish Lake in mid-summer and late summer. More probably, a combination of some two or of all three factors played a deciding role. The "barrier" may have operated directly by calling forth an avoidance reaction on the part of the fish or indirectly through a control of the distribution of food organisms. The effectiveness of the barrier possibly may have been increased by the sharp gradients of temperature and/or of the concentrations of dissolved gases.

The observations of Pearse and Achtenberg (1920) have demonstrated that, for perch at least, a deficiency in oxygen does not constitute a barrier to movement into the deeper portions of a lake. On the basis of operations of experimental gill nets in Lake Mendota (Wisconsin) these authors reported that, "Though perch were usually most abundant immediately above the thermocline, large catches often occurred just below it, where there was no oxygen." The belief that perch could survive in oxygenless water over limited periods was substantiated by the experimental submersion (in cages) of a number of individuals in the region below the thermocline. Five of six specimens survived a period of 0.5 to 1.0 hour and two of six survived 2.0 to 2.5 hours, but none were alive after a 3-hour submersion. At the depth to which the cages were lowered, the oxygen content of the water was 0.05 cc. per liter (0.07 p. p. m.) and the concentration of free carbon dioxide was 5 cc. per liter (9.9 p. p. m.).

The observation of Pearse and Achtenberg that perch could not survive continued submersion in oxygen-deficient water was supported by the experiments of Smith (1924) who suspended fish in wire cages at various depths in Douglas Lake (Michigan). Smith employed a variety of species in his experiments, but perch were included in nearly all of the tests. Smallmouth black bass and rock bass were used only occasionally. Repeated tests indicated that the maximum depth at which fish can survive con-

tinued submersion is defined rather sharply; a distance of only 2½ feet may separate depths at which fish remain alive from depths at which conditions prove fatal. Smith stated that death occurred, "in water having decidedly less oxygen and less favorable acidity conditions, and these factors, rather than that of mere depth alone, determined the lowest limit at which fish could live." Although Smith made no definite statement as to the critical oxygen concentration, a careful examination of his data suggests that fish, particularly perch, were affected by oxygen concentrations of less than 3 or 4 p. p. m. The hydrogen-ion concentration in the shallowest water in which fish died did not fall below 7.1, and at no depth did the concentration fall below 6.8. Smith believed that the acidity conditions were not favorable at the depths at which fish died. It should be pointed out, however, that in Nebish Lake in 1932, perch, rock bass and smallmouth black bass were all abundant, indeed were compelled to live in waters that were more acid than those in which Smith held conditions to be unfavorable.

The experiments of Shelford and Allee (1913) on the reactions of fishes to gradients of dissolved atmospheric gases yielded direct evidence that fish do not exhibit a marked avoidance of water of low oxygen content, but that they do avoid high concentrations of free carbon dioxide. (Rock bass and smallmouth black bass were among the species with which the experiments were conducted.) From a long series of observations they concluded:

> "It appears * * * that the importance of oxygen in determining the distribution of fish has been too much emphasized. * * * Fishes react to oxygen gradients, though usually indefinitely."

In the next paragraph they continued:

> "On the other hand, the importance of carbon dioxide in fish distribution has been largely overlooked. It is significant that even in tap water, all the fish tried reacted very definitely to an amount of carbon dioxide that is scarcely greater than that often found in ponds. Increased carbon dioxide is usually accompanied in nature by low oxygen and it is to the combination of lack of oxygen * * * and increased carbon dioxide, that the fish react most definitely."

Wilding (1939) found the minimum amount of dissolved oxygen tolerated by perch to be 2.25 p. p. m. at temperatures of 20° to 26° C. He found, however, that "fish were capable of reducing the oxygen concentration to a lower level when the

temperature was reduced." The concentration of free carbon dioxide and the hydrogen-ion concentration were found to have no effect on the asphyxial oxygen concentration.

Powers (1938) pointed out that abnormally high concentrations of carbon dioxide may not be harmful to fish even at low concentrations of dissolved oxygen. He stated, "that the rock bass, *Ambloplites rupestris*, can absorb oxygen down to from about 0.40 to 0.30 milliliter per liter [0.57 to 0.42 p. p. m.] at pH 9.75 to 6.10 with the CO_2 tension from about 0.13 to about 21.00+ millimeters Hg [0.34 to 54.60+ p. p. m.]; the small-mouth bass, *Micropterus dolomieu*, down to about 0.40 to 0.30 milliliter per liter [0.57 to 0.42 p. p. m.] at pH 8.30 to 6.20± with the CO_2 tension from about 0.15 to 17.00+ millimeters Hg [0.40 to 44.21+ p. p. m.]; and the yellow perch, *Perca flavescens*, down to about 0.35± milliliters per liter [0.50± p. p. m.] at pH 8.60 to 6.50± with a CO_2 tension from about 0.15 to 14.00+ millimeters Hg [0.40 to 36.40+ p. p. m.]."[3]

In the same publication Powers emphasized the fact that, although fish can tolerate higher concentrations of free carbon dioxide than are ordinarily found in nature, they are nevertheless most sensitive to sudden changes in carbon dioxide tension. He considered the inability of fish to adjust themselves to alternating higher and lower carbon dioxide tensions an important source of sudden mortality in hatcheries and at times in natural waters.

It may be considered possible that the failure of fish to penetrate the deeper portions of Nebish Lake represents an avoidance reaction associated with the distress that accompanies the adjustment to a sharp change in carbon dioxide tension. On August 23, 1932, a marked upturn in the concentration of free carbon dioxide occurred at 8 meters and on August 11, 1931, an equally large upturn occurred between 8 and 10 meters. At the time of the collection of the samples, a similar gradient may have existed near the depth of 9 meters. Pearse and Achtenberg (1920) gave little information concerning the gradients of free carbon dioxide in the region of the thermocline and upper hypolimnion in Lake Mendota. However, their observations

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[3] The experiments upon which this statement was based are described in detail by Powers, Rostorfer, Shipe, and Rostorfer (1938).

that the concentrations of free carbon dioxide were 4.17 cc. per liter (8.2 p. p. m.) at 13.0 meters on August 10, 1916, and 5.0 cc. per liter (9.9 p. p. m.) at 13.5 meters from August 30 to September 4, 1916, indicate that the perch that entered the oxygen-deficient region below the thermocline were subjected to conditions that did not differ greatly from those in the upper part of the hypolimnion of Nebish Lake Unquestionably different stocks of fish may react in a different manner to similar conditions; nevertheless the comparison of carbon dioxide concentrations in Nebish Lake and Lake Mendota throws doubt on the assumption that the relatively high concentration of free carbon dioxide constituted the barrier that prevented the movement of Nebish Lake fish into the deeper portions of the lake.

MUSKELLUNGE LAKE

The records of extensive fishing operations conducted with gill nets in Muskellunge Lake in 1931 and 1932 provide information on the distribution of fish in a larger lake and one with a greater variety of species than is found in Nebish Lake. Sets were made in four general localities in the lake (Fig. 3) : (1) Crystal Bay; (2) Pearse Bay and the channel connecting it with the main body of the lake; (3) main body of the lake approximately off the northwest shore; and (4) extreme eastern portion of the main body of the lake. The species composition and the bathymetric distribution of fish in Pearse Bay and at the two stations in the lake proper agreed sufficiently well to warrant a combination of the data for the three localities. The data for the catches in Crystal Bay have been treated separately (p. 173). The dates of collection for the three stations that were combined were August 4 to 23, 1931, July 1 to July 16, 1932, and July 20 to August 5, 1932. Collections were taken in Crystal Bay, August 31 to September 4, 1931.

The significance of the arrangement of tabular material[4] (Tables 8, 9 and 10) is the same as described previously for Nebish Lake (p. 152). Originally the catch records for stations

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[4] It will be noticed in Tables 8, 9 and 10 that the total number of lifts of the 1¼-inch mesh net was considerably less than that of the nets of any other mesh size. Through a misunderstanding the 1¼-inch mesh net was, without our knowledge, omitted from the gangs during part of the 1932 season.
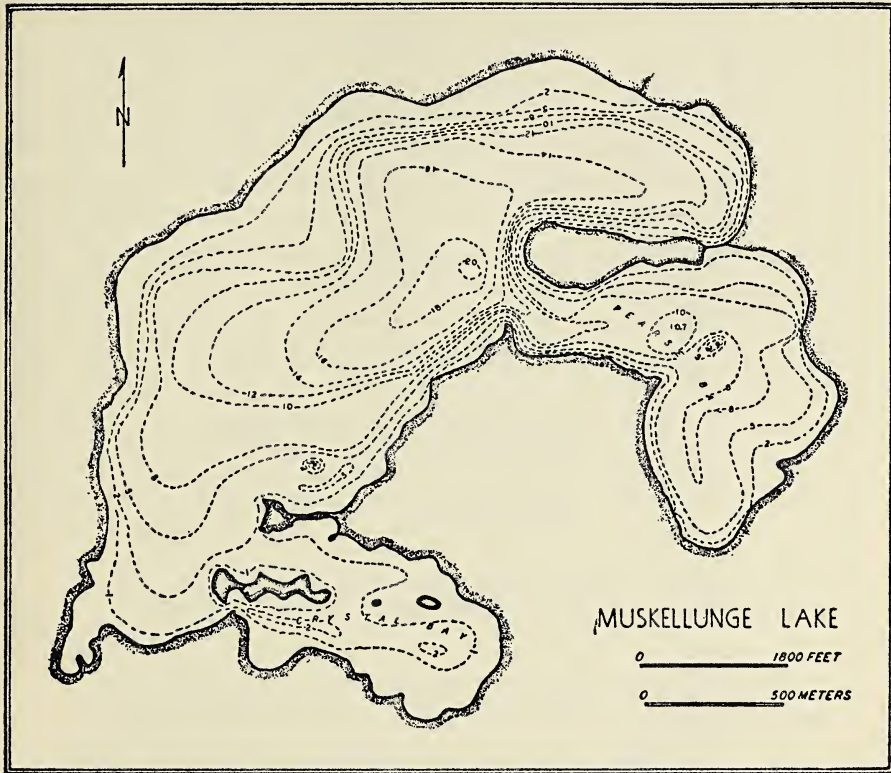
FIG. 3. Hydrographic map of Muskellunge Lake.

other than Crystal Bay were compiled separately for July and August. As no differences could be detected, the data for the two months have been combined.

Since the bathymetric distribution of fish in Muskellunge Lake will be discussed in relation to the physical and chemical conditions of the water, the presentation of distribution data for this lake will be preceded by the examination of vertical series of temperature readings and chemical determinations in July and August (Table 7). The thickness of the thermoclinal stratum was 3 or 4 meters on all four dates; however, the position of the thermocline was 2 meters deeper in late August than in early July. Dissolved oxygen was plentiful in the thermocline in July and was present in fair quantities in the upper 1 or 2 meters of the hypolimnion. Oxygen was relatively more abun-

TABLE 7. *Relationship between depth of water and temperature, hydrogen-ion concentration and the concentrations (milligrams per liter) of dissolved oxygen and free carbon dioxide in Muskellunge Lake on four dates in 1931 and 1932*

Depth in meters	July 10, 1931				August 26, 1931				July 5, 1932				August 25, 1932			
	Temperature	O_2	CO_2	pH	Temperature	O_2	CO_2	pH	Temperature	O_2	CO_2	pH	Temperature	O_2	CO_2	pH
0	21.2	8.6	1.0	7.1	20.2	8.6	0.2	7.5	18.6	8.3	1.2	7.4	21.3	8.0	1.0	7.5
3	...	...	...	...	...	...	...	...	...	8.7	1.2	7.4	...	...	1.0	8.0
5	21.0	8.5	1.0	7.1	...	8.5	0.2	7.5	18.6	8.1	1.2	7.4	21.3	8.7	1.0	7.6
6	21.0	8.6	1.0	7.1	20.2	8.8	...	...	18.5	8.7	1.2	7.4	...	...	1.0	...
7	19.6	8.6	1.0	...	20.0	8.5	0.3	7.5	16.6	8.4	1.7	7.3	...	...	1.2	...
8	16.5	8.6	1.2	7.1	19.7	6.7	0.5	7.4	13.5	9.4	2.2	7.2	20.7	8.2	2.0	7.4
9	14.0	5.7	...	...	17.8	7.6	3.0	7.3	12.6	8.8	2.7	7.2	17.8	...	4.5	7.1
10	12.9	5.6	6.5	6.3	14.8	1.6	7.5	6.8	11.8	6.6	4.5	6.9	14.5	5.3	8.0	6.7
11	11.8	5.4	6.7	...	13.0	1.1	10.0	...	11.3	...	...	...	13.8	2.7	12.5	6.5
12	11.2	3.6	8.6	6.3	12.0	0.2	11.5	6.7	10.9	0.7	11.5	6.7	10.5	0.4	16.5	6.4
13	10.9	...	...	...	11.2	...	...	...	...	...	...	...	...	...	16.5	6.4
15	10.2	...	...	6.3	10.2	0.0	13.5	6.7	10.2	0.6	11.5	6.5	...	0.6	20.0	6.4
17	10.0	0.3	11.0	6.3	...	...	...	...	...	0.2	12.0	6.5	...	...	...	...
18	...	...	...	...	...	0.0	14.0	6.7	...	...	...	...	...	...	...	...
19	...	...	...	...	...	...	...	...	9.5	0.2	13.0	6.5	...	0.2	21.5	6.4
20	...	...	...	...	...	0.0	15.5	6.7	...	...	...	...	...	...	21.5	6.4
20.5	...	...	...	...	9.8	...	...	...	...	...	...	...	10.1	...	...	...

dant at a greater depth on July 10, 1931, than on July 5, 1932. At 12 meters the concentration was 3.6 p. p. m. on the former date and only 0.7 on the latter. On August 26, 1931, a high concentration of dissolved oxygen was noted in only the upper meter of the thermocline. A day earlier in the next year, however, a pronounced deficiency was not found above the lowest meter of the thermocline. On all four dates the free carbon dioxide content of the water increased sharply in the thermocline; these increases were more rapid in August than in July. At almost all depths below 8 meters, for which the comparisons are available, the concentration of carbon dioxide was greater in August than in July and in 1932 than in the same month of 1931. The gradients of hydrogen-ion concentration in the thermocline were fairly sharp on all four dates. The total range of variation in hydrogen-ion concentration was much larger on August 25, 1932, than on the other dates.

The following general estimate of "average" conditions during the collecting season has been drawn from the data of Table 7:

(1) The thermocline, which lay at approximately 7 to 11 meters, was characterized by a drop in temperature of about 8° C. (20° to 12°).

(2) Dissolved oxygen was fairly plentiful at a depth as low as 10 meters (4 or 5 p. p. m.). A rapid decrease in oxygen content occurred below 10 meters, and the concentration was probably not in excess of 1 or 2 p. p. m. at 12 meters in 1931 and was below 1 p. p. m. in 1932. At lower depths oxygen was absent or in concentrations of less than 1 p. p. m. in both years.

(3) The amount of free carbon dioxide increased rapidly in the thermocline and reached a concentration of 10 p. p. m. or more at 11 or 12 meters. Below the thermocline the increase in free carbon dioxide was continuous but more gradual.

(4) There was a sharp gradient in the hydrogen-ion concentration in the thermocline. The total change in the thermocline nearly equalled the maximum difference between any two strata.

Tables 8, 9 and 10 contain the averages, according to mesh size and depth of water, of the numbers of individuals per lift for rock bass, perch and common suckers (*Catostomus commersonnii*), three of the four most abundant species in Muskellunge Lake. The data for the fourth species, the cisco (*Leucichthys artedi*),[5] and for minor species are presented in Table 11 in terms of the total catch of a complete gang of seven nets (except in the shallowest and deepest strata where some mesh sizes were not represented).

The rock bass of Muskellunge Lake exhibits a distinct preference for a shallow-water habitat (Table 8). The best catches were made in less than 7 meters of water (the maximum of 5.0 fish per lift at 7 meters by the 1¾-inch mesh was matched by an equally large catch in 1.5 meters and good catches at 3 meters), and almost no rock bass were taken at 9 meters or deeper. If it is remembered that some of the nets lifted from the 7.0- to

TABLE 8. *Average number of rock bass taken in Muskellunge Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters	Gill-net mesh (stretched measure)							Total
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches	
<3.0	.. ..	2.0 (1)	5.0* (1)	0.0 (1)	2.0 (1)	.. ..	3.0* (2)	12.0
3.0 to 4.9	1.8 (4)	8.1* (12)	4.3 (11)	1.8 (13)	2.3* (12)	5.3* (11)	2.3* (9)	25.9*
5.0 to 6.9	2.5* (11)	5.2 (20)	3.3 (21)	2.5* (21)	2.2 (21)	2.1 (20)	1.5 (19)	19.3
7.0 to 8.9	0.8 (6)	0.8 (5)	5.0* (3)	0.5 (4)	0.8 (4)	1.4 (10)	1.7 (9)	11.0
9.0 to 10.9	0.0 (8)	0.0 (6)	0.4 (11)	0.0 (8)	0.2 (6)	0.0 (6)	0.0 (5)	0.6
11.0 to 12.9	0.0 (1)	0.0 (5)	0.0 (2)	2.0 (1)	0.0 (1)	0.0 (1)	0.0 (1)	2.0
13.0 to 14.9	0.0 (2)	0.0 (1)	.. ..	0.0 (2)	.. ..	.. ..	.. ..	0.0

[5] The data on the bathymetric distribution of the cisco have been summarized from detailed information presented in an earlier paper (Hile, 1936). Only three sizes of gill-net mesh (1¼, 1½ and 1¾ inches) took ciscoes in Muskellunge Lake. The majority was captured by the 1½-inch mesh net.

8.9-meter stratum may have fished almost up to the 5-meter depth, it appears likely that the upper limit of the thermocline marks the approximate lower limit of the habitat occupied by the mass of the rock bass population.

The failure of any important portion of the rock bass stock to enter the region of the thermocline is in disagreement with the situation in Nebish Lake where large numbers of fish were captured near 9 meters, well into the thermocline. A second difference between the two lakes is to be found in the relationship of size of fish to the depth of water inhabited. There is little or no indication that size has any bearing on the depth of water in which Muskellunge Lake rock bass live. In Nebish Lake, on the contrary, there was a definite tendency for the larger rock bass to live at a greater depth than the small ones. This difference in the distribution of rock bass in the two lakes possibly may depend on differences in the distribution of the food organisms taken by rock bass of various sizes.

The outstanding feature in the bathymetric distribution of perch in Muskellunge Lake (Table 9) is the clear-cut relationship between the size of fish and the depth of water inhabited. The smallest perch caught, that is, those captured in the 1¼-inch mesh, were most abundant at about 11 meters. Each increase in mesh size from the 1¼-inch to the 2-inch mesh was accompanied by a 2-meter decrease in the depth at which the largest catches of perch were taken. There was no consistent relationship between size of mesh and depth of maximum catch in the four larger mesh sizes. However, three of the four larger mesh sizes took their best catches at 5 meters or shallower. The great difference between the distributions of large and small perch is brought out by the comparison of the total catch at different depths of the nets with the two smaller and the five larger mesh sizes. A difference of 6 meters separates the depths at which the two groups of nets made their maximum catches.

The pronounced tendency for the smaller perch to inhabit the deeper water of Muskellunge Lake stands in marked contrast to the distribution of perch in Nebish Lake. With the exception of a possible tendency for the smaller perch to inhabit slightly shallower water than the larger ones, there was no apparent correlation between the size of Nebish Lake perch and

TABLE 9. *Average number of yellow perch taken in Muskellunge Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters	Gill-net mesh (stretched measure)							Total for meshes		
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3	1¼ and 1½ inches	Above 1½ inches	All
<3.0	··	7.0 (1)	1.0 (1)	0.0 (1)	0.0 (1)	··	0.0 (2)	7.0	1.0	8.0
3.0 to 4.9	6.3 (3)	3.8 (12)	0.9 (11)	0.3 (13)	0.3 (12)	0.1 (11)	0.8* (9)	10.1	2.4	12.5
5.0 to 6.9	19.7 (11)	3.9 (20)	1.6 (21)	1.3* (21)	1.4* (21)	0.4 (20)	0.1 (19)	23.6	4.8*	28.4
7.0 to 8.9	51.2 (5)	9.4 (5)	2.0* (3)	0.8 (4)	1.0 (4)	0.8* (10)	0.1 (9)	60.6	4.7	65.3
9.0 to 10.9	159.9 (8)	17.0* (6)	0.7 (11)	0.4 (8)	0.2 (6)	0.3 (6)	0.4 (5)	176.9	2.0	178.9
11.0 to 12.9	181.0* (1)	15.8 (5)	0.0 (2)	1.0 (1)	0.0 (1)	0.0 (1)	0.0 (1)	196.8*	1.0	197.8*
13.0 to 14.9	43.0 (2)	0.0 (1)	··	0.5 (2)	··	··	··	43.0	0.5	43.5

the depth at which they occurred (p. 155). With the perch as with the rock bass, differences in the distribution of food taken by individuals of various sizes appear to offer the most logical explanation of the differences in the distribution of fish in the two lakes.

It is not known whether perch penetrate to greater depths than those fished by nets set at 13.0 to 14.9 meters. The only direct evidence on this question is contained in the records for a string of nets (including the mesh sizes, 1½ and 2 inches) lifted from 17.5 meters on August 27, 1930. The total catch was a single sucker, which was dead at the time the nets were lifted. The limnological data of Table 7 throw doubt on the ability of perch to maintain themselves continuously at depths in excess of, at most, 12 meters. The detailed records for the two lifts of 1¼-inch mesh nets from the 13.0- to 14.9-meter stratum offer evidence that some of the perch taken in these nets may have been captured during a temporary excursion into an oxygen-deficient region. The shallower of the two lifts, which contained 56 perch, was made off the north shore on August 4, 1932, from a depth of 13.2 meters. Since the net was 6 feet or nearly 2 meters deep it fished water as shallow as 11 meters. The deeper lift (containing 30 perch) was made on July 29, 1932, near the eastern end of the lake from a depth of 14.5 meters. Fish taken in this net were therefore captured at average depths in excess of 12.5 meters. If it is assumed that all perch were captured near the top of the net (no records were kept of the position of fish in the nets) it may be considered possible that the perch of the August 4 collection were captured in water with a sufficient supply of dissolved oxygen to maintain life. The perch from the deeper lift of July 29 were very probably taken in water that was deficient in oxygen (less than 1 p. p. m.). It is possible therefore that in Muskellunge Lake as in Lake Mendota (Pearse and Achtenberg, 1920) perch may spend short periods of time in oxygen-deficient regions.

Suckers were taken in greatest abundance at 7 and 9 meters, except in the 1¼-inch mesh nets whose catches were negligible (Table 10). There is indication that the larger suckers lived in the deeper water. Nets of the mesh sizes, 1½, 1¾ and 2 inches, took their largest catches at 7 meters. In the nets with

the three larger meshes, however, the averages at 9 meters were from two to four times as large as those for the nets with the same sizes of mesh at 7 meters. Very few suckers were taken at 11 meters or deeper.

TABLE 10. *Average number of common suckers taken in Muskellunge Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maxiumm average catches were taken.*

Depth in meters	Gill-net mesh (stretched measure)							Total
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches	
<3.0	.. ..	0.0 (1)	2.0 (1)	2.0 (1)	2.0 (1)	.. ..	2.0 (2)	8.0
3.0 to 4.9	0.0 (4)	2.3 (12)	1.6 (11)	2.0 (13)	2.5 (12)	3.4 (11)	3.1 (9)	14.9
5.0 to 6.9	0.3* (11)	2.0 (20)	2.0 (21)	2.2 (21)	3.7 (21)	4.7 (20)	2.2 (19)	17.1
7.0 to 8.9	0.0 (6)	6.8* (5)	5.0* (3)	4.7* (4)	7.2 (4)	7.4 (10)	1.8 (9)	32.9
9.0 to 10.9	0.1 (8)	0.0 (6)	2.6 (11)	4.4 (8)	14.4* (6)	14.7* (6)	7.2* (5)	43.4*
11.0 to 12.9	0.0 (1)	0.0 (5)	0.0 (2)	4.0 (1)	0.0 (1)	0.0 (1)	4.0 (1)	8.0
13.0 to 14.9	0.0 (2)	0.0 (1)	.. ..	0.0 (2)	.. ..	.. ..	.. ..	0.0

Diurnal inshore and offshore movements may have affected the data on the bathymetric distribution of suckers in Muskellunge Lake. Evidence for a daily migration of suckers in this lake was obtained by Spoor and Schloemer (1939) from a series of 10 sets of gill nets[6] (usually along the 6-meter contour) in the summers of 1933 to 1937. Examinations at 2- to 4-hour intervals revealed that from midnight to noon the majority of suckers had entered the nets from the shore side (that is, were moving toward deeper water), whereas from noon to midnight the majority had entered the nets from the lake side (were moving inshore). However, the clear-cut relationship between the depth of water and the number of suckers taken in 24-hour

[6] Except for the omission of the 1¼-inch mesh net the gear employed by Spoor and Schloemer included the same mesh sizes as those fished in 1931 and 1932.

sets (Table 10) indicates that the diurnal movements described by Spoor and Schloemer were either limited in their vertical extent or were undertaken by only part of the individuals in the population.

Spoor and Schloemer were unable to detect diurnal inshore and offshore movements in the Muskellunge Lake rock bass. They concluded that the movements of rock bass near the 6-meter contour were purely random.

Table 11 provides a composite picture of the bathymetric distribution of seven species of fish in Muskellunge Lake, exclusive of Crystal Bay. The values in the table represent the total catch of a complete gang of seven nets (except for the perch which were divided into groups of "small" and "large" fish—see Table 9) for all strata from 3 to 11 meters. Two mesh sizes are not represented in the lifts from less than 3 meters and four in the lifts from 13.0 to 14.9 meters.

Four species—rock bass, smallmouth black bass, bluegills (*Lepomis macrochirus*), and largemouth black bass—were most abundant at approximately 3 meters. All of these species may be said to inhabit the warm water of the epilimnion. The larger perch live in slightly deeper water than the four shallow-water species. The greatest numbers were captured at 5 meters but almost equally large catches were taken at 7 meters. Small perch, however, were most plentiful in deep water at 9 and 11 meters. It is of interest that the best catches of both perch and ciscoes were obtained at 11 meters. This situation emphasizes the apparent preference of small perch for deep, cold water. The presence of ciscoes at 13 meters indicates that this species as well as the perch may penetrate waters that are deficient in oxygen. Suckers were most abundant between the regions inhabited by the shallow-water species and by the small perch and ciscoes. The depths of greatest abundance of suckers (7 and 9 meters) correspond roughly to the upper portion of the thermocline.

The relationships indicated by the data of Table 11 apply, of course, to the summer only. At other seasons—in winter and at the periods of turnover—the distribution of the various species is probably much different.

TABLE 11. *Number of individuals of seven species taken in gill nets set at different depth in Muskellunge Lake in July and August, 1931 and 1932. The numbers represent the average catch of a complete gang of seven different mesh sizes in all strata except "less than 3.0" and "13.0 to 14.9 meters." The asterisks indicate the strata of maximum abundance.*

Depth in meters	Rock bass	Smallmouth black bass	Species[1] Perch Small	Large	Bluegills	Largemouth black bass	Suckers	Ciscoes	Total
<3.0	12.0	3.0	7.0	1.0	0.0	0.0	8.0	0.0	31.0
3.0 to 4.9	25.9*	4.1*	10.1	2.4	3.2*	0.6*	14.9	0.2	61.4
5.0 to 6.9	19.3	3.7	23.6	4.8*	1.8	0.3	17.1	0.1	70.7
7.0 to 8.9	11.0	3.2	60.6	4.7	0.4	0.0	32.9	12.5	125.3
9.0 to 10.9	0.6	0.4	176.9	2.0	0.0	0.0	43.4*	40.8	264.1
11.0 to 12.9	2.0	0.0	196.8*	1.0	0.0	0.0	8.0	135.9*	343.7*
13.0 to 14.9	0.0	0.0	43.0	0.5	0.0	0.0	0.0	18.5	62.0

[1]In addition to the catches listed in the table there were taken: four wall-eyed pike (*Stizostedion vitreum*) at depths less than 7 meters; one muskellunge (*Esox masquinongy*) at 6 meters; and one miller's thumb (Cottidae) at 3 meters.

The results of five lifts of complete gangs of gill nets[7] in Crystal Bay are summarized in Table 12. No separations of the catches as to depth were made since practically all of the Bay is less than 2 meters deep. Ecologically Crystal Bay is distinctly different from the remainder of Muskellunge Lake. The shallower water of most of the lake is characterized by a sand and gravel bottom, with a limited amount of submerged vegetation offshore. In Crystal Bay, on the contrary, the mucky bottom is covered with a dense growth of vegetation.

TABLE 12. *Average number of individuals of four species taken per day in different sizes of mesh of gill nets set in Crystal Bay, Muskellunge Lake, over the 5-day period, August 31 to September 4, 1931.*

Species[1]	Gill-net mesh (stretched measure)							Total
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches	
Rock bass	8.4	7.0	2.2	5.8	7.0	5.0	1.6	37.0
Perch	12.0	2.0	1.2	0.2	0.8	0.4	0.0	16.6
Sucker	5.6	2.2	1.4	1.8	5.0	6.6	7.0	29.6
Bluegill	1.6	2.4	11.2	3.0	11.4	5.6	2.2	37.4

[1] The total catches per gang per day of species other than those listed in the table were: golden shiner (*Notemigonus crysoleucas*)—2.8; mud minnow (Umbridae)—0.4; largemouth black bass—0.4; muskellunge—0.2.

The ecological nature of the Crystal Bay habitat is reflected in the generally greater abundance of fish and particularly in the presence of large numbers of bluegills. The total numbers of fish in Tables 11 and 12 for a gang of nets in shallow water are not comparable since two mesh sizes were lacking in the data for the lake proper. A more reliable comparison may be had from the following tabulation in which the catches of the 1¼-inch and 2½-inch mesh nets have been omitted from the totals for Crystal Bay:

Average Total Catch of Nets of Five Mesh Sizes

Species	Crystal Bay	Lake proper
Rock bass	23.6	12.0
Perch	4.2	8.0
Sucker	17.4	8.0
Bluegill	30.2	0.0

[7] The five lifts do not represent the total fishing effort in Crystal Bay in 1931 and 1932 but include merely the 24-hour sets. At the time of the earlier 1931 operations and in 1932 the number of persons in the State tourist camp, which is located on the Bay, made it inadvisable to leave gill nets unguarded in such shallow water. Consequently the nets were set for only short periods and on some occasions the fish were driven into them by beating the surface of the water with poles and by the noise of an outboard motor.

It is believed that the above data on the catches of fish in Crystal Bay and in the shallow water of the open lake (including Pearse Bay) are comparable in spite of the fact that the fishing operations in Crystal Bay were carried out somewhat later in the season than were those in the lake proper (August 31 to September 4, 1931, in the Bay as compared to August 4 to August 23, 1931, and July 1 to July 16, 1932, and July 29 to August 5, 1932). Operations with gill nets set for short periods on August 17 and 28, 1931, and August 26 to 31, 1932, gave no indication that either the species composition or the abundance of fish in Crystal Bay was undergoing a change in late August. Rock bass and suckers were approximately twice as abundant in Crystal Bay as in the shallow water of the open lake but only half as many perch were taken in the Bay. Bluegills, which were absent in shallow water in the open lake and were scarce at greater depths (Table 11), were the dominant species in the Crystal Bay catches. The Crystal Bay catches were featured also by the total absence of smallmouth black bass and the presence of a number of golden shiners (total of 14 in all nets for the 5-day period).

OTHER LAKES

Records of fishing operations in 1930, 1931 and 1932 have made available a small amount of information on the bathymetric distribution of fish in three additional lakes (Trout, Silver and Clear) in the northeastern highland region. Although the data are extremely scanty, they do provide some instructive comparisons with the more detailed data from Nebish Lake and Muskellunge Lake.

Trout Lake. The average lifts of four species of fish—rock bass, perch, suckers and wall-eyed pike—in the shallower water of Trout Lake are listed in Table 13. The nets on whose catches the table was based were set in both basins a short distance from the channel connecting the two. The dates of collection were July 23 and 24, 1931, and August 10 to 13, 1932. In spite of the low fishing intensity the rock bass may be said to occur in greatest abundance in relatively shallow water at approximately 3 meters. (The only net set in still shallower water took no rock bass.) The single individual that was taken in a net lifted

from 10.0 meters may be considered a straggler. Perch were taken in greater numbers at 3 than at 5 meters. The nets set in deeper water had too large meshes to sample the perch stock satisfactorily. Suckers exhibited differences in distribution correlated with the size of the fish. Nets with the four smaller meshes made their best catches at 3 meters but those with the larger meshes were most successful in water 2 to 4 meters deeper (*cf.* Muskellunge Lake, p. 170). The smaller mesh nets, in gen-

TABLE 13. *Average number of each of four species of fish taken in Trout Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based. Asterisks show strata at which the maximum average catches were taken.*

Depth in meters[1]	Rock bass in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0	.. ..	.. ..	.. ..	0.0 (1)	.. ..	.. ..	.. ..
3.0 to 4.9	6.0* (1)	1.5* (4)	14.0* (1)	14.5* (2)	4.0* (1)	0.0 (1)	0.0 (1)
5.0 to 6.9	0.2 (4)	0.0 (2)	0.8 (5)	0.3 (3)	0.3 (3)	0.0 (3)	0.3 (3)
7.0 to 8.9	.. ..	.. ..	.. ..	.. ..	0.0 (1)	0.0 (1)	0.0 (1)
9.0 to 11.9	.. ..	.. ..	.. ..	.. ..	.. ..	0.0 (1)	1.0* (1)

Depth in meters	Perch in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0	.. ..	.. ..	.. ..	2.0 (1)	.. ..	.. ..	.. ..
3.0 to 4.9	32.0* (1)	17.5* (4)	17.0* (1)	6.0* (2)	3.0* (1)	1.0* (1)	0.0 (1)
5.0 to 6.9	16.8 (4)	6.5 (2)	2.2 (5)	2.3 (3)	0.3 (3)	0.3 (3)	0.0 (3)
7.0 to 8.9	.. ..	.. ..	.. ..	.. ..	0.0 (1)	0.0 (1)	0.0 (1)
9.0 to 11.9	.. ..	.. ..	.. ..	.. ..	.. ..	.. ..	0.0 (1)

[1] The sets at 9.0 to 11.9 were: 2½-inch mesh net at 11.8 meters; 3-inch mesh net at 10.0 meters. The 2½-inch mesh net took nine whitefish. Other fish not listed in the table were one largemouth black bass at 3 meters and one redhorse sucker (*Moxostoma*) at 4 meters.

Depth in meters	Suckers in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0	.. ..	.. ..	.. ..	0.0 (1)	.. ..	.. ..	.. ..
3.0 to 4.9	1.0* (1)	0.8* (4)	4.0* (1)	4.5* (2)	3.0 (1)	2.0 (1)	5.0 (1)
5.0 to 6.9	0.0 (4)	0.0 (2)	1.6 (5)	1.0 (3)	1.0 (3)	5.7* (3)	6.0* (3)
7.0 to 8.9	.. ..	.. ..	.. ..	.. ..	6.0* (1)	1.0 (1)	2.0 (1)
9.0 to 11.9	.. ..	.. ..	.. ..	.. ..	.. ..	0.0 (1)	0.0 (1)

Depth in meters	Wall-eyed pike in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
<3.0	.. ..	.. ..	.. ..	0.0 (1)	.. ..	.. ..	.. ..
3.0 to 4.9	0.0 (1)	0.0 (4)	0.0 (1)	1.0* (2)	0.0 (1)	0.0 (1)	3.0 (1)
5.0 to 6.9	0.0 (4)	0.0 (2)	0.2* (5)	0.0 (3)	1.0 (3)	0.3 (3)	0.7 (3)
7.0 to 8.9	.. ..	.. ..	.. ..	.. ..	3.0* (1)	2.0* (1)	4.0* (1)
9.0 to 11.9	.. ..	.. ..	.. ..	.. ..	.. ..	0.0 (1)	1.0 (1)

eral, failed to take wall-eyed pike. Nets with the three larger mesh sizes were most successful at 7 meters (only one lift of each mesh size).

The rock bass of Trout Lake inhabits approximately the same depth of water as in Muskellunge Lake (greatest abundance at about 3 meters), but lives in shallower water than do the larger rock bass of Nebish Lake. On the other hand, perch were most plentiful in lifts from approximately 3 meters in both Trout Lake and Nebish Lake but were most abundant at greater depths in Muskellunge Lake. The smaller Muskellunge Lake perch in particular appeared to prefer deep water (9 to 11 meters). Suckers live in shallower water in Trout Lake (about 3 to 5 meters) than in Muskellunge Lake (7 to 9 meters). The

two lakes show a similar correlation between the size of suckers and the depth at which they live (with the larger fish in the deeper water).

Fishing operations were carried on in 1930 with the "old" nets (see p. 150) in Blaisdell's Bay at the extreme southeast corner of Trout Lake at depths of about 5 meters and shallower. Records of depth were not obtained for the individual nets, but the catch indicates a species composition in the shallow water similar to that in the neighborhood of the channel connecting the two basins of the lake. The total 1930 catch in Blaisdell's Bay consisted of 93 perch, 27 common suckers, 20 rock bass, 12 wall-eyed pike and 1 smallmouth black bass.

Fishing operations were carried on in the hypolimnion of the south basin of Trout Lake in July, 1930 and 1931, at depths of from 15 to 33.5 meters. Only typically deep-water forms—ciscoes, whitefish (*Coregonus clupeaformis*), lake trout (*Cristivomer n. namaycush*) and burbot (*Lota maculosa*)—were taken.[8] Since the conditions with respect to the dissolved gases,

TABLE 14. *Relationship between depth of water and temperature, hydrogen-ion concentration and the concentrations (milligrams per liter) of dissolved oxygen and free carbon dioxide in Trout Lake, August 10, 1931.*

Depth in meters	Temperature in °C.	O_2	CO_2	pH
0	20.6	8.3	1.0	7.7
5	..	8.5	1.0	7.7
8	20.6	8.4	1.0	7.7
9	20.2	8.5	1.0	7.7
10	16.2	8.4	1.5	7.5
11	13.4	..	..	..
12	11.7	..	..	..
14	10.3	..	..	..
15	9.8	8.5	3.7	7.4
18	8.6	..	..	..
20	8.3	6.2	5.5	7.1
25	7.7	5.0	7.5	7.0
28	..	3.6	8.5	7.0
30	..	3.4	9.7	..
31	..	3.0	9.7	6.9
32	..	2.1	11.0	6.9
32.5	7.2	..	11.0	6.9

[8] The actual numbers were: ciscoes—1,197; whitefish—32; lake trout—32; burbot—1 (Hile 1936).

oxygen and carbon dioxide, are satisfactory in most of the hypolimnion in the summer (Table 14), the absence of shallow-water fish was probably due to the low water temperatures, or the scarcity or absence of their favorite food organisms.

Silver Lake.   The scarcity of rock bass and suckers in Silver Lake together with the small number of gill nets lifted renders the formation of conclusions as to the bathymetric distribution of these species[9] inadvisable.   The data of Table 15 serve chiefly to show the presence of a dense concentration of perch at 5 and 7 meters under late-summer conditions.   (The dates of collection were August 20 to 24, 1931, and August 16, 1932.)   Further information on the distribution of fish in Silver Lake was obtained from the catches of gill nets that were set in deeper water for the capture of ciscoes.   (The dates of these deep-water lifts were August 9, 10 and 15, 1930, and July 17 and August 22, 1931.)   These nets took 524 ciscoes—all from nets that were lifted from depths between 10.5 and 15.5 meters.   The only fish taken along with the ciscoes was a perch captured at 14.5 meters.

The Silver Lake cisco was most abundant at approximately the same depth of water in summer as the Muskellunge Lake cisco.   However, the Muskellunge Lake cisco is forced to share its summer habitat with other forms, particularly small perch, whereas in Silver Lake the cisco lives practically in isolation. This difference in the distribution of fish in the two lakes appears difficult to explain on the basis of temperatures and the concentrations of dissolved gases (Tables 7 and 16).   The conditions with respect to the dissolved gases in the lower thermocline and upper hypolimnion of Silver Lake in late August were distinctly superior to those in Muskellunge Lake.[10]   It is true that the temperatures in Silver Lake were somewhat lower than at corresponding depths in Muskellunge Lake.   However, this temperature difference appears less important when it is remembered that in Muskellunge Lake the small perch were taken in the coldest water that contained sufficient oxygen to support

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[9] In addition to the fish listed in Table 15, there were taken 10 smallmouth black bass at depths of 3 to 7 meters and one cisco (in 1932) at 6 meters.

[10] The most reliable comparison with the Silver Lake data of August 28, 1931, is to be had from the two Muskellunge Lake series taken in August (Table 7).

TABLE 15. *Average number of each of three species of fish taken in Silver Lake in nets set at different depths, 1931 and 1932 data combined. In parentheses, the number of lifts on which each average was based.*

Depth in meters	Rock bass in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
3.0 to 4.9	.. ..	.. ..	.. ..	0.0 (1)	0.3 (3)	0.0 (3)	0.2 (4)
5.0 to 6.9	0.0 (2)	0.0 (2)	0.0 (1)	0.0 (2)	0.3 (3)	0.0 (1)	.. ..
7.0 to 8.9	.. ..	1.0 (1)	1.5 (2)	.. ..	.. ..	1.5 (2)	0.0 (2)

Depth in meters	Perch in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
3.0 to 4.9	.. ..	.. ..	.. ..	1.0 (1)	0.3 (3)	0.0 (3)	0.0 (4)
5.0 to 6.9	128.5 (2)	64.0 (2)	5.0 (1)	3.5 (2)	0.0 (3)	2.0 (1)	.. ..
7.0 to 8.9	.. ..	77.0 (1)	38.0 (2)	.. ..	.. ..	0.0 (2)	0.0 (2)

Depth in meters	Suckers in gill-net mesh (stretched measure)						
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches
3.0 to 4.9	.. ..	.. ..	.. ..	0.0 (1)	1.0 (3)	1.0 (3)	3.0 (4)
5.0 to 6.9	0.5 (2)	0.0 (2)	4.0 (1)	0.0 (2)	0.7 (3)	2.0 (1)	.. ..
7.0 to 8.9	.. ..	3.0 (1)	2.5 (2)	.. ..	.. ..	1.5 (2)	7.5 (2)

life and may even have spent short periods of time at levels deficient in oxygen. In Silver Lake, again, the lack of data prevents an examination of the possible effects of the distribution of food organisms on the distribution of fish.

Clear Lake. Almost all of the fishing operations in Clear Lake were conducted in the deep water in July, August and early September, 1931 and 1932, for the capture of ciscoes. Individuals of this species were taken in Clear Lake in nets set as shallow as 8 meters, but most of them were captured in the

hypolimnion between the depths of 15 and 25 meters. The outstanding feature of the Clear Lake catches was the presence of wall-eyed pike at all depths at which the cisco occurred. Thirty-seven wall-eyed pike were taken in the same nets that captured 465 ciscoes. Although the summer conditions in deep water are generally similar in Clear Lake (Table 17) and Trout Lake (Table 14), wall-eyed pike were not taken in the hypolimnion of the latter lake. Other fish taken in the hypolimnion of Clear Lake were one rock bass (at 15.5 meters) and five perch (19.5 to 24.5 meters). These two species also were absent from the hypolimnion of Trout Lake. A short gang of "old" nets of mesh sizes 1½ and 2 inches set in shallow water on September 5, 1931, took 12 perch, 1 rock bass, 2 wall-eyed pike and 2 smallmouth black bass.

TABLE 16. *Relationship between depth of water and temperature, hydrogen-ion concentration and the concentrations (milligrams per liter) of dissolved oxygen and free carbon dioxide in Silver Lake, August 28, 1931.*

Depth in meters	Temperature in °C.	O_2	CO_2	pH
0	20.2	8.7	0.7	7.7
5	20.2	8.9	0.7	7.7
6	..	8.8	0.7	..
7	20.2	9.2	0.5	7.7
8	18.8	9.9	0.5	7.7
9	14.7	13.2	0.2	7.8
10	11.4	11.7	1.5	7.5
11	9.4	9.8	3.0	7.4
12	8.6	7.5	6.0	7.3
13	..	4.4	9.5	7.1
14	7.7	1.6	12.0	6.9
15	7.2	0.6	13.0	6.9
17	..	0.0	23.5	6.9
18	..	0.0	31.0	6.9
19	6.8	..	..	..

TABLE 17. *Relationship between depth of water and temperature, hydrogen-ion concentration, and the concentrations (milligrams per liter) of dissolved oxygen and free carbon dioxide in Clear Lake, August 19, 1932.*

Depth in meters	Temperature in °C.	O_2	CO_2	pH
0	20.9	8.1	2.0	6.5
5	20.9	7.9	2.0	6.5
10	18.5	8.1	2.0	6.5
12	12.4	9.5	3.0	6.4
15	9.9	7.9	5.5	6.2
20	8.6	6.0	7.5	6.1
23	8.4	4.5	10.0	6.0
26	8.0	3.2	11.0	6.0

SUMMARY OF OBSERVATIONS ON THE BATHYMETRIC DISTRIBUTION OF FISH IN WISCONSIN LAKES

The data of the preceding sections lead to the following general conclusions. The depth of water inhabited by a single species of fish in the lakes of the Northeastern Highlands of Wisconsin varies rather widely from one lake to another; the relationship between size of fish and depth of water inhabited varies from lake to lake; different species that live at the same depths in one lake may inhabit different depths in another. The variations from lake to lake in the bathymetric distribution of fish exhibit no clear-cut dependence on differences in temperature and the concentrations of dissolved oxygen and free carbon dioxide.

Rock bass of all sizes exhibited a preference for the warm waters of the epiliminion in Muskellunge Lake, and so far as evidence is available appeared to select a similar shallow-water habitat in Trout Lake and Silver Lake (data for Clear Lake not adequate). In Nebish Lake, however, large rock bass were most abundant in the upper portion of the thermocline at depths about 2 to 4 meters greater than those occupied by small fish. Conditions with respect to temperature and the concentrations of oxygen and carbon dioxide do not seem to explain this peculiarity in the distribution of rock bass in Nebish Lake. Penetrations into the deeper regions of the lake, such as those made by the individual taken in Clear Lake at 15.5 meters and by the two rock bass captured at 11 meters in Muskellunge Lake, are rare.

The bathymetric distribution of the perch was variable from one lake to another. In Nebish Lake, and apparently in Trout Lake and Silver Lake also, perch of all sizes inhabited shallow water at about 3 to 5 meters (probably a little deeper at 5 to 7 meters in Silver Lake). The depth of greatest abundance of perch corresponds rather well with that of rock bass (except the large Nebish Lake rock bass) in all three lakes. An entirely different situation exists in Muskellunge Lake. Here the small perch exhibited a marked preference for the deepest, coldest strata that contained sufficient dissolved oxygen to support life. Among the four smaller mesh sizes, each increase in mesh size was accompanied by a 2-meter decrease in the depth at which the best catches were made. Large perch were taken most abun-

dantly at 5 to 7 meters—in shallow water but still below the depth of the greatest abundance of rock bass. The reason for the deep-water habitat of the smaller Muskellunge Lake perch is obscure. The small perch avoided these same depths in Silver Lake in spite of more suitable oxygen conditions. The somewhat lower temperatures of Silver Lake, as mentioned previously (p. 178), do not seem to account satisfactorily for the avoidance of the deeper water by small perch since the small perch of Muskellunge Lake appeared to seek out the coldest strata available. The capture of five perch in the hypolimnion of Clear Lake indicates an occasional penetration of deep water by perch in that body of water.

In Muskellunge Lake suckers were most abundant near the lower limit of the epilimnion and in the upper part of the thermocline. The larger mesh nets took their best catches 2 meters deeper (at 9 meters) than the smaller mesh nets (best catches at 7 meters). The Trout Lake data indicate a similar relationship between the size of suckers and the depths of water in which they are most numerous. In general, however, suckers were taken in shallower water in Trout Lake than in Muskellunge Lake. Suckers were taken in Silver Lake down to 7 meters, but were absent from the deep-water lifts.

Of all species for which data were obtained, the smallmouth black bass occurred most consistently in shallow water. This species appears to be almost exclusively an inhabitant of the epilimnion.

Wall-eyed pike were taken only in Clear Lake, Trout Lake, and Muskellunge Lake. In Clear Lake wall-eyed pike were taken throughout the hypolimnion as well as in the single shallow-water lift. In Muskellunge Lake all of the four wall-eyed pike captured were taken in less than 7 meters of water (see footnote to Table 11). The best catches of wall-eyed pike were made at 7 meters in Trout Lake but only one individual was taken below that depth and none were captured in the hypolimnion. Conditions with respect to water temperature and the concentrations of dissolved oxygen and free carbon dioxide are so similar in Trout Lake and Clear Lake that they cannot explain the differences in the distribution of the wall-eyed pike in the two lakes.

The bathymetric distribution of the cisco in Trout Lake, Muskellunge Lake, Silver Lake, and Clear Lake was described in some detail in an earlier publication (Hile, 1936). The summer distribution of the cisco, contrary to the other species studied, appears to depend closely on temperature and the concentration of dissolved oxygen. Aside from the occasional movement of a limited number of individuals into shallower water (or their failure to enter deep water), the cisco normally inhabits the coldest strata that contain sufficient oxygen to support life.

The belief that the bathymetric distribution of the cisco is correlated closely with temperature and the concentration of dissolved gases is supported by Fry's (1937) detailed study of the summer migrations of the cisco in Lake Nipissing, Ontario. With the warming of the epilimnion in late spring and early summer the ciscoes move downward—most of them below the thermocline where they scatter throughout the hypolimnion. Later in the season (late August and September) as the oxygen concentration in deep water diminishes and the concentration of free carbon dioxide increases they become concentrated immediately below the thermocline. Before the autumn turnover most of them return to the shallow water of the epilimnion. Fry considered the increase in free carbon dioxide in deep water more significant than the decrease in dissolved oxygen as the cause of the concentration of ciscoes below the thermocline in late August and September.

The data on the bathymetric distribution of other species that occur in these northeastern Wisconsin lakes are too scanty to warrant treatment in this summary.

Certain of the conclusions as to the variability of the bathymetric distribution of fishes find support in the observations of Pearse (1921a)[11] on the distribution of fish in other Wisconsin lakes. Since Pearse's fishing operations were carried out be-

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[11] In this publication Pearse presented original data on the distribution of fish in three lakes, Lake Michigan (near Sturgeon Bay, Wisconsin), Lake Pepin, and Lake Geneva, and summarized earlier findings on Lake Wingra and Lake Mendota (Pearse and Achtenberg, 1920) and Green Lake (Pearse, 1921b). The data for Lake Pepin, an expansion of the Mississippi River are not comparable with those for glacial lakes. In Lake Wingra, whose maximum depth is only 4.3 meters, the bathymetric distribution of fish is not an important problem.

tween late June and early September, his data are comparable to those of the present investigation. In each of four lakes rock bass were most abundant at 5 to 10 meters (Lake Michigan, Lake Geneva) or were equally plentiful at 0 to 5 and at 5 to 10 meters (Green Lake, Lake Mendota). The 5- to 10-meter stratum marked the lower limit of occurrence of rock bass in Lake Michigan, Green Lake and Lake Mendota, but in Lake Geneva this species ranged down to the depth of 15 to 20 meters. Smallmouth black bass were taken as deep as 20 to 25 meters in Lake Geneva as compared with a maximum of 10 to 15 meters in Green Lake. Wall-eyed pike also were present in relatively deep water (as deep as 15 to 20 meters) in Lake Geneva. In Lake Mendota wall-eyed pike were taken only in the 0- to 5-meter stratum.

Perch were present in the greatest depths that oxygen conditions permitted in both Lake Mendota (greatest depth of occurrence—10 to 15 meters) and Lake Geneva (greatest depth of occurrence—30 to 35 meters) and even penetrated the oxygenless regions of the former lake. The greatest depth at which perch were taken in Lake Geneva exceeded even the maximum depth of occurrence of ciscoes (20 to 25 meters). In Lake Mendota, however, neither species was present below 15 meters. The association of perch and ciscoes in Lake Geneva and Lake Mendota is in contrast to the situation in Green Lake, where no ciscoes were captured in water less than 40 meters deep, while perch were taken only in the 5- to 10-meter stratum. Perch were captured in Lake Michigan at 25 to 30 meters, the greatest depth at which experimental gill nets were set. They were much more abundant, however, in shallower water (best catches at 5 to 10 meters).

The maximum depth of occurrence of common suckers varied from 5 to 10 meters in Lake Mendota to 10 to 15 meters in Lake Geneva and Green Lake and 15 to 20 meters in Lake Michigan.

Pearse's observations confirm the statement made previously (p. 181) that the relationship between the bathymetric distribution of fish in lakes and the conditions with respect to temperature and dissolved gases (especially oxygen) is not clear-cut. The perch provides an outstanding example of the looseness of this relationship. In some lakes (Geneva, Mendota, and Muskel-

lunge) perch appear to select the coldest water containing sufficient oxygen to support life, and may even penetrate strata in which the oxygen is deficient or lacking (Mendota, Muskellunge?). Under these conditions the perch is an associate of the typically cold-water form, the cisco. In other lakes (Silver, Trout, and Green) the perch exhibits a marked preference for shallow water in spite of an abundance of cold, well-oxygenated water in the thermocline and hypolimnion.

The perch shows also a wide variation in the relationship between the size of fish and the depth of water inhabited. Individuals of all sizes lived at approximately the same depths in Nebish, Trout, Silver, Geneva, and Mendota.[12] In Muskellunge Lake, however, the progressively larger perch inhabited the progressively shallower strata. As an example of a situation that is the reverse of the one found in Muskellunge Lake may be cited the bathymetric distribution of perch in Lake Wawasee in northern Indiana.[13] During the summer small perch were taken in large numbers in the weedy areas of the shallow water, but large individuals were taken only in deep water where they were captured by hook and line just above the bottom at a depth of approximately 40 feet or 12 meters.

The data of the preceding pages contain similar, if less striking, examples in which the bathymetric distribution of other species varied among lakes that were apparently closely similar, or in which the distribution failed to exhibit a close dependence on temperature and oxygen conditions. It is true that the cisco appears invariably to seek the coldest water that contains sufficient oxygen to support life.[14] Even this selection may be a matter of preference rather than necessity for it has been demonstrated that the cisco, which was formerly considered strictly a stenothermal species limited in its occurrence to the colder strata of the deeper lakes, can tolerate very high temperatures (Scott, 1931; Hile, 1936).

[12] This statement, as it refers to Lake Geneva and Lake Mendota, is based on the examination of the average catches of gill nets of different sizes of mesh.

[13] Statements relative to the bathymetric distribution of fish in Lake Wawasee are based on personal observations made by Hile in the summers of 1926, 1927, and 1928.

[14] This statement applies only to the smaller inland lakes. The Great Lakes herring is typically a shallow-water form, although it does move offshore to somewhat deeper water during the hot summer months.

The failure to correlate closely the bathymetric distribution of certain species with temperature and oxygen conditions should not be taken as an indication that these two factors are unimportant in the determination of the depth of water at which fish live.   Certainly a lack of oxygen constitutes a complete barrier to long-time occupancy.   Furthermore, the existence of temperature preference is too well established for even conspicuous exceptions to throw doubt on the general importance of temperature as a factor in distribution.   Nevertheless, it is apparent that the modifying or interfering effects of local conditions may go far toward obscuring the influence of temperature and oxygen conditions.   The precise nature of these "local factors" is to a large extent a matter for speculation.   Obviously, however, they exert sufficient influence to make the ecological aspect of the bathymetric distribution of fish a very complex problem and to show the importance of the recognition of pronounced "individualities" in lakes and their fish population.

Among the more important factors in addition to temperature and oxygen conditions that may be expected to affect the bathymetric distribution of fish are: hereditary physiological differences among stocks of the same species and resultant variation in the reactions to environmental conditions; distribution of food as to kind and quantity; the abundance of fish of the same and other species; configuration of the lake basin and the topography of the surrounding land especially as related to wind and wave action; the type of bottom as it affects the abundance of bottom organisms and rooted plants; the abundance and distribution of larger aquatic plants as sources of food and shelter.   These potential factors have many interrelationships.   A discussion of these interrelationships is beyond the scope of this paper.   However, a listing of certain probable contributing factors does serve to emphasize the fact that no simple explanation of variations in the bathymetric distribution of fish in lakes is to be expected.

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AGE AND GROWTH OF THE ROCK BASS,
AMBLOPLITES RUPESTRIS (RAFINESQUE),
IN NEBISH LAKE, WISCONSIN[1]

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INTRODUCTION

The present study of the age and growth of the Nebish Lake rock bass is another in a series of papers that have been based wholly or in part on materials collected in the course of investigations on the fishes of the lakes of the northeastern highlands, Wisconsin, conducted cooperatively by the Wisconsin Geological and Natural History Survey and the United States Bureau of Fisheries over the periods, 1927-1928 and 1930-1932. The publications have included studies of the age and growth of the rock bass (Wright, 1929), whitefish (Hile and Deason, 1934), yellow perch (Schneberger, 1935), cisco (Hile, 1936a), muskellunge (Schloemer, 1936, 1938), largemouth black bass (Bennett, 1937), common sucker (Spoor, 1938), and smallmouth black bass (Bennett, 1938). A total of five mimeographed reports on the growth of game fish in Wisconsin has been issued by Juday and Schneberger (1930, 1933), Juday and Bennett (1935), and Juday and Schloemer (1936, 1938). In addition there have appeared two publications on the morphometry of the cisco (Hile 1936b, 1937), three dealing with the parasites of fishes in the region (Cross 1934, 1935, 1938) and one on the food of fishes (Couey, 1935). A paper by Hile and Juday on the bathymetric distribution of fish will appear simultaneously with the present study of the rock bass. A contribution on the growth of the bluegill by Schloemer will be published in the near future.

The rock bass, *Ambloplites rupestris* (Rafinesque), occurs from "North Dakota to the southern parts of Ontario and Quebec, southward to Oklahoma, Arkansas and northern Alabama,

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[1] Published with the permission of the Commissioner of Fisheries.

and in the Atlantic drainage south to the Susquehanna in New York" (Greene, 1935). Earlier, the rock bass was reported from Louisiana and Texas (Jordan and Evermann, 1896). However, the southern rock bass was described as a new species, *Ambloplites ariommus,* by Viosca (1936). This form is probably typical of the Gulf coastal area.

The northern rock bass, *A. rupestris,* occurs abundantly both as a lake and as a stream fish. Forbes and Richardson (1920) stated that in Illinois the rock bass exhibits a "decided preference for clear rocky, streams" and for "swift water." (They emphasized the close association of the rock bass and the small-mouth black bass.) In Wisconsin, on the other hand, the rock bass appears to be characteristic of lakes rather than streams.
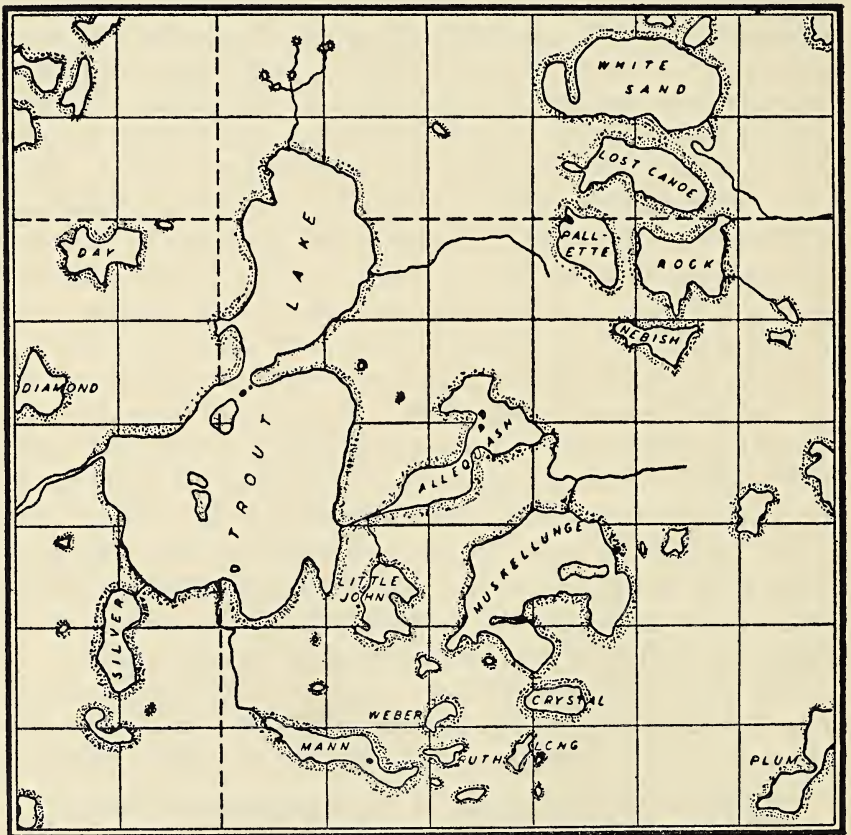
FIGURE 1. Map of Trout Lake region.

Greene (1935) stated that, "Considering its Wisconsin distribution alone, the rock bass could be included among the glacial lake species." Rock bass are particularly abundant in the soft-water lakes of the northeastern highland area.

Nebish Lake is situated in Vilas County, Wisconsin, about 4 kilometers or 2.5 miles east of Trout Lake (the location of the limnological laboratories of the Wisconsin Geological and Natural History Survey) at an elevation of 497 meters or 1,631 feet (Figs. 1 and 2). This small lake, which is completely landlocked, is surrounded by a rather dense second growth of mixed hardwoods and conifers. The water of Nebish Lake is exceptionally soft. Table 1 contains data on the morphometry of Nebish Lake and on the physical and chemical characteristics of its water. Data are given also for Muskellunge Lake and Silver Lake. Certain phases of the life histories of the rock bass populations in these two lakes are considered on pp. 276-288. Other limnological data on Nebish Lake—physical, chemical, and biological—have been presented from time to time in publications of the Survey.
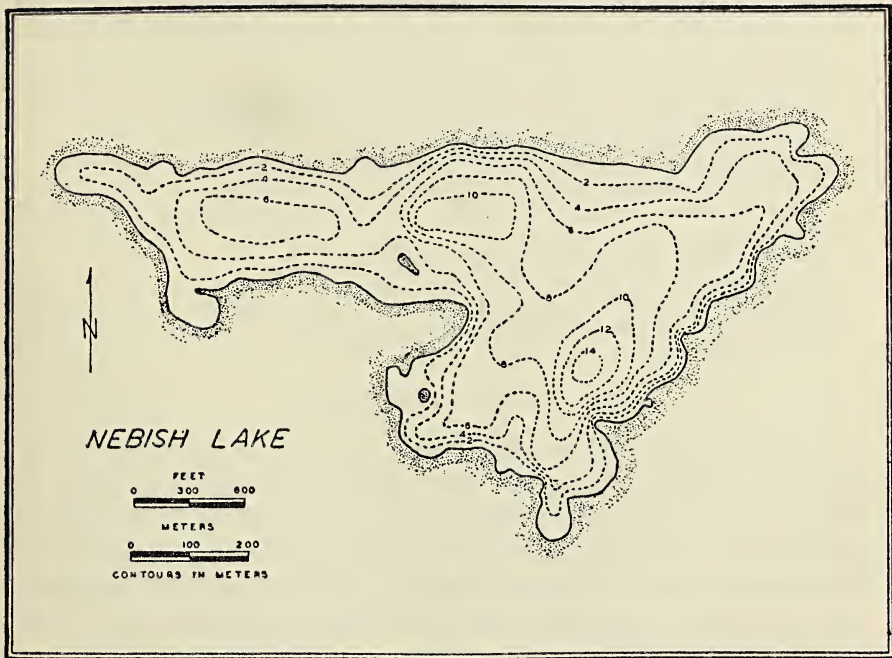
FIGURE 2. Hydrographic map of Nebish Lake.

TABLE 1. *Limnological data for three lakes of the northeastern highland lake district. The characteristics, transparency, color, pH, conductivity, concentration of bound CO_2, and organic matter of the plankton, refer to average surface conditions in summer.*

| Lake | Length, km. | Breadth km. | Area, ha. | Depth in meters | | Volume in cubic meters |
				Maximum	Mean	
Nebish	1.32	0.66	38.5	15.8	5.2	2,015,000
Muskellunge	3.12	2.00	372.3	21.0	7.0	26,172,000
Silver	1.75	0.66	87.3	19.5	11.3	9,884,000

Lake	Trans-parency, meters	Color	pH	Conduc-tivity, recip. megohms	Bound CO_2, mg /l	Plankton, organic matter, mg /l
Nebish	6.0	9	6.8	19	4.0	0.77
Muskellunge	4.0	4	7.2	40	10.0	1.16
Silver	5.5	4	7.5	62	15.0	0.85

Throughout this paper repeated references will be made to certain species of fresh-water fishes by their common names. To avoid misunderstanding that might originate in local variations in the common names of some of these fish the following list of common and scientific names has been prepared:

Bluegill, *Lepomis macrochirus* Rafinesque.
Cisco, lake herring, *Leucichthys artedi* (Le Sueur).
Common sucker, *Catostomus commersonnii* (Lacépède).
Common sunfish, *Lepomis gibbosus* (L.).
Largemouth black bass, *Aplites salmoides* (Lacépède).
Long-eared sunfish, *Lepomis megalotis* (Rafinesque).
Lake Superior long-jaw, *Leucichthys zenithicus* (Jordan and Evermann).
Muskellunge, *Esox masquinongy* Mitchill.
Sheepshead, *Aplodinotus grunniens* Rafinesque.
Smallmouth black bass, *Micropterus dolomieu* Lacépède.
Whitefish, *Coregonus clupeaformis* (Mitchill).
Yellow perch, *Perca flavescens* (Mitchill).

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MATERIALS

The study of age and growth of the Nebish Lake rock bass has been based on the determination of age and the calculation of growth histories of 1,215 specimens (Table 2). In addition, the data for 238 fish whose ages were not determined have been employed, when applicable, for the investigation of gill-net selectivity and for the study of the length-weight relationship. The study of the body-scale relationship has included also data for 218 rock bass taken in Muskellunge Lake (p. 207). In addition to the 218 Muskellunge Lake rock bass employed in the study of the body-scale relationship, certain other materials on the fluctuations in the growth and the strength of year classes of rock bass in Muskellunge and Silver Lakes have been presented for comparison with data on the Nebish Lake rock bass.

TABLE 2. *Dates and methods of collection of Nebish Lake rock bass.*

Gear	Date of collection					Total
	July 5 and 6, 1930	August 16 to 21, 1930	July 29 to August 6, 1931	July 12 and August 6 to 11, 1932	August 28, 1935	
Gill nets	..	144	513	492	105	1,254
Hook and line	154	18	2	25	..	199
Total in collection	154	162	515	517	105	1,453
Number aged	..	152	469	493	101	1,215

Certain discrepancies in the number of fish employed in different tabulations should be explained. For example, weights were lacking for 2 of the 154 rock bass collected in July, 1930. Consequently, the table of the length-weight relationship in this collection (Table 56) included only 152 specimens. All 154 were included, however, in the tabulation of the length frequencies of rock bass taken by hook and line (Table 5). Again, the acci-

dental omission of the record of the size of mesh for one fish taken in a gill net reduced the number of fish in Table 3 to 1,004 as compared to the number of 1,005 fish listed in Table 2 as taken in gill nets in 1931 and 1932. The reasons for certain other irregularities in the numbers of specimens will be given later in the paper. It was believed, however, that a preliminary statement as to the occurrence of the discrepancies might save the reader possible annoyance.

METHODS

COLLECTION OF SAMPLES

The collections of the Nebish Lake rock bass were made by hook-and-line fishing and by means of gill nets, as indicated in Table 2. The hook-and-line catches of the different years may be considered roughly comparable, but a complete change of the gill-net equipment was made before the start of the 1931 collecting season.

Nets of only three mesh sizes (1½, 2, and 2½ inches, stretched measure) were fished[2] in 1930. The approximate total number of square yards of nets of each size lifted was: 1½-inch mesh net—954; 2-inch mesh net—1,323; 2½-inch mesh net—159. All of the gill nets fished in 1930 were in a poor state of repair. The webbing contained many holes and could be torn easily.

The gill nets fished in 1931 and 1932 included the following seven sizes of mesh (stretched measure in inches): 1¼, 1½, 1¾, 2, 2¼, 2½, and 3. Each of these specially constructed nets was approximately 50 yards long by 6 feet deep or had an area of 100 square yards. Lifts were made of 16 gangs of seven nets each in 1931 and of 10 gangs in 1932; thus the fishing efforts for each mesh size in the two years were total lifts of 1,600 and 1,000 square yards, respectively.

The 1935 collection is known to have been taken by means of gill nets, but there are no records[3] of the sizes of mesh fished.

All nets were set on the bottom. In 1931 and 1932 the gangs were set, in general, along rather than across the contours, since

[2] A net of mesh size, 3¼ inches, failed to take rock bass.
[3] Dr. Clarence L. Schloemer who, along with Dr. William A. Spoor, collected the 1935 materials assures me that several sizes of mesh were included in the gear fished in Nebish Lake in that year.

this procedure gave more reliable information as to the average depth at which the nets were fished. No record was kept in 1930 of the depth at which different nets fished. The nets were lifted every day.

In the collection of fish for biological studies, it is of great importance to know the selective action of the gear employed. Consequently, the Nebish Lake rock bass samples were subjected to detailed analyses which included (1) the tabulation of length frequencies (sexes separately) of the hook-and-line catches and of the catches of gill nets of each size of mesh in each year's collection, and (2) the determination of the average length of the representatives of each age group in the samples taken by nets of each size of mesh and by hook and line. The detailed results of these analyses can not be presented here. However, certain summarizations of the data will give a good idea of the size range of the fish that can be taken by hook and line and by nets of different sizes of mesh.[4]

The gill-net collections of 1931 and 1932 which made up 69 per cent of the total collection (77 per cent of fish used in the study of age and growth) will be considered first. Table 3 shows for the combined collections of the two years the length distribution of the rock bass taken in each mesh size. It is at once apparent that the lower limits of the length ranges of fish that can be taken in different sizes of mesh are rather sharply defined, and that these limits increase regularly with increase in mesh size. The distributions for the smaller mesh sizes, especially those of the 1½-, 1¾-, and 2-inch meshes, are skewed sharply at the lower ends. The absence of this skewness in the distributions of fish taken in the nets with the larger meshes possibly may have depended on the nature of the length distribution of rock bass in the population as a whole (see totals at right of table). Other conclusions to be drawn from the distributions are that nets of each size of mesh fished were able to take fish over a large length range, and that the length-frequency distributions of fish from nets with successively larger mesh sizes have a high percentage of overlap.

[4] In an earlier paper (Hile, 1936a) data were presented relative to the selective action of gill nets in the collection of samples of ciscoes from lakes of northeastern Wisconsin. This same paper contains a discussion of the general question of gill-net selectivity and gives a review of part of the literature on the subject.

The ineffectiveness of the 1¼-inch mesh for the capture of small fish and the large overlaps among the frequency distributions constitute strong evidence for the adequacy of the sampling over the length range, 75 to 194 millimeters. However, the circumstance that the greatest number of fish was taken in the largest mesh (350 in the 3-inch mesh) suggests the possibility that the use of a net of still larger mesh size would have been advisable.[5] There is reason to believe, nevertheless, that the use of nets with larger meshes would have increased the number of

TABLE 3. *Length frequencies of Nebish Lake rock bass taken in different sizes of gill-net mesh, sexes and all age groups (including fish not aged) combined for 1931 and 1932.*

Length interval in millimeters	Gill-net mesh (stretched measure)							Total
	1¼ inches	1½ inches	1¾ inches	2 inches	2¼ inches	2½ inches	3 inches	
200—204	..	..	..	..	1	1	1	3
195—199	..	..	..	..	..	..	3	3
190—194	..	1	2	..	..	2	13	18
185—189	..	..	..	3	..	5	40	48
180—184	..	1	1	1	4	14	70	91
175—179	..	..	2	..	6	13	100	121
170—174	..	..	1	5	8	34	84	132
165—169	..	..	..	3	5	24	30	62
160—164	..	..	1	9	10	45	5	70
155—159	..	1	1	2	6	36	2	48
150—154	..	..	1	2	6	32	..	41
145—149	..	..	..	1	4	12	1	18
140—144	..	2	..	4	5	5	..	16
135—139	..	..	..	3	6	1	..	10
130—134	..	..	1	2	6	..	..	9
125—129	1	1	1	6	2	..	..	11
120—124	1	..	7	22	1	..	..	31
115—119	..	1	7	21	..	..	1	30
110—114	1	2	15	6	..	..	..	24
105—109	..	2	12	1	..	..	..	15
100—104	..	7	17	1	..	..	..	25
95— 99	..	10	8	..	..	..	..	18
90— 94	..	53	2	..	..	..	..	55
85— 89	1	69	..	..	..	..	..	70
80— 84	6	22	..	..	..	..	..	28
75— 79	5	..	..	..	..	..	..	5
70— 74	2	..	..	..	..	..	..	2
Total number	17	172	79	92	70	224	350	1,004
Average length	86	92	116	134	156	162	177	147

[5] A 3¼-inch mesh net fished in 1930 failed to take rock bass; however, the older age groups were represented more strongly in 1931 and 1932 than in 1930.

large fish taken but would not have brought about any important upward extension of the general length distribution. The frequency distribution of fish captured by the 3-inch mesh net is much more compact than are the distributions for nets of smaller mesh. Seemingly the 3-inch mesh net did not share the capacity of nets of other mesh sizes to take fish of lengths well above the lower limit of effectiveness. The compact distribution of the lengths of rock bass from the 3-inch mesh gill net can be explained, however, on the logical assumption that the absence of larger fish in the catch was caused by their absence from the lake. This assumption is supported by the observation that fish longer than 190 millimeters usually are very old (p. 223). It seems valid to conclude, therefore, that the use of nets with meshes larger than 3 inches might have changed somewhat the numerical representation of the older age groups but would not have affected the determination of their growth histories.

Among the smaller fish the growth data for age-group II (this age group was the youngest in the collections—see Tables 12 and 13 for the frequency distributions of the group) were discarded as unreliable, but the rejection was based on direct observations of the fishing action of gill nets rather than on the analysis of gill-net catches. It was observed repeatedly that small fish appeared to penetrate the meshes of gill nets with difficulty, and that ordinarily the smaller the fish the less securely it was held. Possibly these small fish do not swim with sufficient vigor to force their way into the meshes. At any rate, the suspicions concerning the reliability of the II-group samples were verified by the comparison of the growth of II-group rock bass with the growth of older age groups of the same year classes. The II group was the only age group excluded from the computation of general growth curves.

The collection of August, 1930, (Table 4) which was taken with nets of only three sizes of mesh is admittedly less satisfactory than the gill-net samples of 1931 and 1932. Particularly unfortunate was the low fishing intensity of the 2½-inch mesh net (p. 194). The addition of the 18 rock bass taken by hook and line in August, 1930, (Table 5) doubtless strengthened the representation of the larger fish. Since the growth data obtained from the collection of August, 1930, did not disagree seri-

ously with those of other years (Tables 14 and 15) this collection was retained as part of the general growth material.

The hook-and-line catches formed an unimportant part of the general growth material. Their length distributions (Table 5) resemble those of the rock bass from the gill nets with the larger meshes (2¼ and 2½ inches).

TABLE 4. *Length frequencies of Nebish Lake rock bass taken in different sizes of gill-net mesh in August, 1930, with the sexes and all age groups combined (including fish not aged).*

Length interval in millimeters	Gill-net mesh (stretched measure)			Total
	1½ inches	2 inches	2½ inches	
170—174	2	5	1	8
165—169	..	4	1	5
160—164	1	5	1	7
155—159	..	3	6	9
150—154	..	14	5	19
145—149	2	12	3	17
140—144	2	7	3	12
135—139	..	5	..	5
130—134	..	7	..	7
125—129	..	2	..	2
120—124	..	10	..	10
115—119	..	12	..	12
110—114	2	..	..	2
105—109	2	..	..	2
100—104	1	..	..	1
95— 99	2	..	..	2
90— 94	1	..	..	1
85— 89	4	..	..	4
80— 84	10	..	..	10
75— 79	8	..	..	8
70— 74	1	..	..	1
Total number	38	86	20	144
Average length	99	142	154	132

As stated previously (p. 194), there are no records concerning the meshes of the gill nets fished in 1935. The age composition of the collection was unusual (p. 245), but the good agreement of the data on the growth of the different age groups with data for corresponding age groups of earlier collections (Tables 14 and 15) appears to justify the retention of the 1935 sample as part of the general growth material.

TABLE 5. *Length frequencies of rock bass taken by hook and line, 1930 to 1932, with the sexes and all age groups combined (including fish not aged).*

Length interval in millimeters	Date of collection				Total
	1930		1931	1932	
	July[1]	August			
180—184	2	1	..	..	3
175—179	14	..	..	3	17
170—174	30	1	2	3	36
165—169	24	1	..	7	32
160—164	36	3	..	5	44
155—159	28	3	..	2	33
150—154	13	4	..	2	19
145—149	2	2	..	..	4
140—144	3	3	..	1	7
135—139	2	..	..	..	2
130—134	..	..	..	..	..
125—129	..	..	..	1	1
120—124	..	..	..	..	..
115—119	..	..	..	1	1
Total number	154	18	2	25	199
Average length	164	156	172	161	163

[1] This collection not employed in the study of age and growth.

RECORDS FOR INDIVIDUAL SPECIMENS

Scale samples were taken at the field laboratory from all rock bass except those preserved for a study of the body-scale relationship. (For treatment of preserved specimens see p. 207.) The scales were removed from the left side of the body in the region between the lateral line and the spinous portion of the dorsal fin, and were stored in Bureau of Fisheries scale envelopes. On each serially numbered envelope were recorded the date, name of the lake, length, weight, sex, state of maturity, and gear.

The standard length (from the tip of the snout to the base of the caudal peduncle) was measured for every fish. Measurements of total length (from the tip of the snout to the line connecting the tips of the extended caudal fin[6]) were made for the 1930 collections only. All length measurements were made with

[6] Subsequent experiences have convinced me that the most reliable and practical measurement of total length is the maximum measurable length, that is, the length from the extreme anterior point of the head to the extreme end of the caudal fin with its upper and lower edges parallel. This maximum length is the only one admissable when questions of legal minimum total length are concerned.

a steel tape in a straight line between the points indicated and were recorded to the nearest millimeter.

The fish were weighed on a Chatillon spring platform balance with a 500-gram capacity and calibrated by 2-gram intervals. Weights were estimated to the nearest gram. During the latter part of the 1931 season the balance developed a fluctuating error that at no point exceeded 2 grams. No corrections were attempted for the error, but the defective balance was replaced by a new instrument at the start of the 1932 season. This new balance was still in use in 1935.

In 1930 and 1931 the smaller individuals with poorly developed gonads were designated as immature without record of sex. A more careful examination provided sex records for every individual of the 1932 and 1935 collections.

PREPARATION AND EXAMINATION OF SCALE SAMPLES

The scales were soaked in water and cleaned by means of a dissecting needle and a small brush. Three scales from each fish were mounted on a microscope slide in a glycerin-gelatin medium.[7] Care was taken to avoid scales with regenerated centers or of highly asymmetrical or otherwise irregular form. On the label of each slide were recorded field number, slide number, length, weight, sex, maturity, and gear. The scales of all of the 1930 and 1931 samples and of about one-third of the 1932 collection were examined at a magnification of $\times$ 40.5 by means of the projection apparatus described by Van Oosten (1923). The remaining scales of the 1932 collection were studied at a magnification of $\times$ 40.7 with the aid of the apparatus described by Van Oosten, Deason, and Jobes (1934).

DETERMINATION OF AGE

The determination of the age of the rock bass from scale examinations has been based on the counting of the number of annuli or lines of discontinuity between the growth areas of successive years. Fish whose scales are without annuli, that is, fish in the first year of life, are designated as members of the O group. The ages of the older fish are expressed by Roman

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[7] The formula for the medium was given by Van Oosten (1929).

numerals corresponding to the number of annuli or completed years of life. Thus a fish in its second year of life (with one annulus) is a member of age-group I, a fish in its third year of life (with two annuli) belongs to the age-group II. . . . Fish hatched in the same calendar year are members of the same year class regardless of their age at capture. For example, the 1930 VII group, the 1931 VIII group, and the 1932 IX group are all 1923 year-class fish.

Since the rock bass scale is typically ctenoid, the annulus ordinarily can be traced only through the anterior portion of the scale. A few scales were seen that had not yet formed ctenii as late as the sixth or seventh year of life, but many form ctenii in the first summer. Differential wear of the ctenii, dependent on the age of that portion of the scale on which they occur, sometimes gives a clue to the position of the year-mark in the posterior field. In general, however, the differential wear of the ctenii is of no assistance in the determination of age.

VALIDITY OF THE ANNULUS AS A YEAR-MARK

The validity of the annulus as a true year-mark has been proven for so many species of fish, both marine and fresh-water, that the examination of scales as a general method for the determination of age in fishes may be considered well established. Any historical or critical review of the subject in this paper would be without point. Theoretical considerations of the validity of age determinations from scale study will be limited, therefore, to a demonstration of the applicability of the method to the rock bass.

The following outline of the most important arguments in favor of the validity of the annulus in rock bass scales as a true year-mark is based on data that will be presented in later sections of this paper. Similar arguments have been given for so many species that discussion will be held to a minimum.

(1) *Correlation between age and size.*—(*a*) The regularity with which increase in the number of annuli is accompanied by increase in the size of the fish proves that the occurrence of annuli on the scales is not haphazard but that annuli are added systematically as growth proceeds. Furthermore, fish assigned to the same age group have similar lengths (Table 9 and 10).

(*b*) Modes in the length-frequency distributions of small fish coincide with the modal lengths of age groups based on scale reading. In the Muskellunge Lake collections of small fish (see p. 207 and Table 6) all individuals in the length interval, 15 to 39 millimeters, were without annuli, and all fish in the length interval, 50 to 59 millimeters, had one annulus. The smaller of these two groups could hardly be interpreted as other than the young of the year. (One 15-millimeter fish was without scales on a large portion of its body.) The next larger group would then logically be expected to be second-year fish, with one annulus. In the Nebish Lake collections (Tables 12 and 13) age-group II forms a distinct mode in the general length-frequency distribution of each sex.

(2) *Agreements among calculated growth histories.*—(*a*) Lengths at the end of the various years of life calculated from scale measurements[8] (Tables 14 and 15) agree well with the corresponding empirical lengths[9] of younger age groups whose ages were determined by the examination of scales. In general, this agreement serves merely to establish the annulus more certainly as a structure whose appearance on the scales follows a definite systematic pattern (*cf.* argument *1a*). However, the agreement of lengths calculated from scale measurements of older fish with the empirical lengths of younger fish whose ages were determined by modes in the length-frequency distributions (see argument *1b*) does provide an argument for the yearly formation of annuli.

(*b*) There is a generally good agreement among the data on the calculated growth of fish of the same age groups in different years' collections and among the data for different age groups of the same or different years' collections, but *a still better agreement is to be found among the growth histories of the different age groups of the same year class.* As a specific illustration, the agreement among the growth histories (Tables 14 and 15) for both the males and females of the 1930 VII group, the 1931 VIII

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[8] The method of calculation is described on pp. 206-217.

[9] Empirical lengths of age groups usually fall between two calculated lengths. For example, average actual lengths for IV-group fish usually will fall between the calculated lengths at the end of the fourth and fifth years of life. This situation is to be expected since all collections were made during the growing season.

group, and the 1932 IX group, all purportedly members of the 1923 year class, is closer than the agreement among the VII groups, the VIII groups, or the IX groups of the same sex collected in different years. In fact, the corresponding calculated lengths of the heavily represented age-groups VIII and IX of the 1923 year class are well-nigh identical. That the growth data for different age groups of the same year class should agree so closely is understandable, indeed is to be expected, since all age groups were hatched in the same year and were, therefore, subjected to the same environmental conditions at the same periods of their life histories. The point to be stressed is that the identification of these so clearly homogeneous groups was based on scale readings. The 1932 IX group of each sex had a growth curve almost identical with that of the same sex of the 1931 VIII group but the IX-group fish had one more annulus. The obvious deduction is that an annulus was laid down during the 1-year interim between the 1931 and 1932 collection dates. Further examination of Tables 14 and 15 will reveal a tendency for growth histories of other well represented age groups to conform to a more or less typical "year-class curve".

(c) The agreement among different year classes as to the goodness or poorness of growth in certain calendar years provides another argument for the interpretation of the annulus as a year-mark (see pp. 249-259). The growth in 1928 will serve as an example. In that year the growth of male rock bass (Table 24) in every year of life from the second to the eighth, inclusive,[10] was below average for fish of corresponding age. Thus the data for every year class from 1921 to 1927, inclusive, indicate 1928 to have been a poor-growth year. The results are similar for the female rock bass (Table 25). Here again the 1928 growth was below average for all years of life from the second to the eighth (represented by year classes 1921 to 1927). The relatively good ninth-year growth of the females of the sparsely represented 1920 year class provides an unimportant exception to the trend of the data.

The designation of 1928 as a poor-growth year was based on scale readings that assumed the annulus to be a true year-mark.

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[10] First-year growth must be considered separately from growth in later years (p. 259).

Consequently, the uniformity of the results obtained independently from seven year classes, each of which was represented by two or more age groups, must be construed as a powerful argument for the contention that annuli are formed at the rate of one per year. The argument is strengthened materially by the close agreement between the data for the sexes.

The continued examination of Tables 24 and 25 will reveal similar general agreement among year classes as to goodness or poorness of growth in other calendar years. Furthermore, the data for the sexes agree well for the individual years.

(3) *Persistent abundance or scarcity of certain year classes.* —The persistent abundance or scarcity of a year class in the collections of successive calendar years provides possibly the most convincing evidence for the interpretation of the annulus as a year-mark. In the rock bass data the exceptionally rich 1923 year class offers the outstanding example of continued high abundance (Table 23). This year class as age-group VII was dominant (38.2 per cent) in the 1930 samples. Now, if the scale readings are accurate measures of age, this same year class should be strong in the 1931 collections also, but the number of annuli should be eight. The 1931 data conform precisely with this expectation, for in that year the 1923 year class as age-group VIII made up 45.8 per cent of the total collection. The unusual numerical strength of rock bass of the 1923 year class extended into 1932, in which year as age-group IX they were exceeded in abundance only by age-group II and were by far the strongest of the older age groups.

The great abundance of the 1923 year class in the collections of three successive calendar years is important not only for its contribution to the proof that the annulus on the rock bass scale is a true year-mark, but also as a demonstration that the determination of age in the Nebish Lake rock bass is practicable up to a relatively high age.

Other year classes, in contrast to the 1923 year class, were consistently weak at all ages at which they were collected. The 1927 year class provides an outstanding example.

The evidence outlined in the preceding pages leaves little room for doubt concerning the validity of the annulus on the

scales of rock bass as a true year-mark. However, the demonstration of the general reliability of age determinations in the rock bass does not mean that fully dependable readings can be made from the scales of every individual. The difficulties that were encountered in the interpretation of some scales will be discussed in the following section.

DIFFICULTIES ENCOUNTERED IN THE DETERMINATION OF AGE

False annuli or accessory checks, which cause so much difficulty in the interpretation of the scale structure of some fish, are of rare occurrence in the scales of the Nebish Lake rock bass. This situation is most fortunate in view of the abundance of old fish in the collections. Nevertheless, a few fish were discarded because of the inability to decide whether certain checks were actually annuli.

The erosion or resorption of portions of the scales of certain older individuals accounted for a large part of the difficulties experienced in the determination of age. The appearance of these defective scales suggested that the periphery had been resorbed at some earlier age. In some of the eroded scales only the lateral regions were affected, but in others erosion evidently had occurred along the entire periphery of the imbedded portion of the scale. The former, less severe, type of erosion made it impossible to trace certain annuli throughout their entire courses, but frequently did not prohibit a reasonably reliable assessment of age. On the other hand, all scales with the more complete erosion had to be discarded. Not only were the age readings of these scales questionable, but the earlier loss of portions of the scales along the anterior edge made their measurements worthless for the calculation of growth.

The examination of the scales failed to connect the occurrence of erosion with any particular calendar year, although most of the erosion appears to have occurred prior to 1931. It was observed also that scale erosion ordinarily does not occur before the sixth year of life. None of the fish had scales whose edges were eroded at the time of capture.

Late formation of the annulus may be a source of difficulty in the scales of fish that are caught early in the growing season. The collection of July 5 and 6, 1930, contained some fish whose scales obviously had newly-formed annuli or annuli in the proc-

ess of formation, and others whose scales had developed bands of growth of varying width outside the last visible annulus. Since it was uncertain for many of the latter group whether the band of growth represented growth made in 1930 subsequent to annulus formation, or whether the 1930 annulus had not yet been formed, the collection was rejected for purposes of age determination. The only other collection taken in the first half of July was one of 25 fish captured by hook and line on July 12, 1932. All of the individuals of this collection had recently-formed annuli lying just inside the margins of the scales. There is no reason to believe that late annulus formation had any effect on the accuracy of the age determinations for fish taken in late July or in August.

In all the collections combined (exclusive of the July, 1930, sample), 95.5 per cent of the scales were read. The percentages for the different years were: 1930 (August collection)—95.6 per cent; 1931—93.6 per cent; 1932—96.7 per cent; 1935—99.0 per cent. These percentages are higher than would be obtained from the data for "Number aged" and "Total in collection" listed in Table 2. The discrepancy has its origin in the exclusion from consideration of those fish represented by regenerated scales in the sample.

Body-Scale Relationship and the Calculation of Growth

Scale measurements for the purpose of computing individual growth histories were made for every rock bass whose age was determined. The distance from the center of the focus to each annulus and to the extreme anterior edge of the scale was measured on the projected image of one scale[11] from each rock bass. The measurements were made by means of an accurately graduated ruler, whose edge was laid along the radius most nearly collinear with the focus, and were recorded to the nearest millimeter (occasionally to the half-millimeter).

Computations of individual growth histories from scale measurements have been made for many species and by a variety of methods. Although a review of the general problem of the computation of growth from scale measurements would not be

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[11] Three scales were measured for most of the fish employed in the study of the body-scale relationship (p. 209).

desirable in this paper[12], it may be stated that the cumulative experience of numerous investigators points more and more to the conclusion that there is no general solution of the problem. The relationship between body growth and scale growth appears to vary widely from one species to another. Consequently each species of fish (and possibly different varieties or populations within a species) presents its own special problem as to the method to be followed for the calculation of growth. Accordingly a detailed study of the body-scale relationship in the rock bass was undertaken in order to determine the most satisfactory method for the computation of growth histories in this species.

The determination of the relationship between the body length of the rock bass and the length of the anterior radius of the scale was based on the measurements of selected or "key" scales from 318 fish. Of this total, 100 specimens were taken in Nebish Lake and 218 were captured in Muskellunge Lake (Fig. 1 and Table 1). All the specimens less than 86 millimeters long came from Muskellunge Lake. The Nebish Lake rock bass were taken by gill nets on August 6 and 8, 1932. The Muskellunge Lake fish of a length of 79 millimeters or more were taken in gill nets on July 24, 25, and 28, 1932. The smaller Muskellunge Lake rock bass were taken by means of a small hand seine on various dates during the latter half of August, 1932.

The fish from both lakes that were taken in gill nets were weighed and measured when fresh, provided with individual, serially numbered tin tags, and preserved in a 10 per cent solution of formalin. Upon their arrival at the Ann Arbor laboratory the specimens were soaked about 4 days in water and then transferred permanently to a 70 per cent solution of alcohol. The smaller Muskellunge Lake rock bass were not measured when fresh and were preserved directly in alcohol. The length measurements of these smaller preserved fish were corrected for shrinkage produced by the preservative.[13]

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[12] Excellent historical and critical reviews of the subject may be found in publications by Van Oosten (1929), Graham (1929), and others.

[13] It was assumed that the correction factor, 1.015, which was determined from the remeasurement of the larger (79 millimeters and longer) Muskellunge Lake specimens was applicable to the smaller preserved fish. At the time of the remeasurement of the large preserved fish (October 10 and 11, 1932) they had been in alcohol about 5 weeks. The measurements of both the fresh and preserved fish were made by the same individual (Dr. Edward Schneberger).

TABLE 6. *Average length of the anterior radius (×40.5) of key scales of rock bass at different body lengths as determined from the combined collections from Nebish and Muskellunge Lakes, 1932.*

Number of fish	Standard length in millimeters	Anterior scale radius in millimeters (×40.5)	Number of fish	Standard length in millimeters	Anterior scale radius in millimeters (×40.5)	Number of fish	Standard length in millimeters	Anterior scale radius in millimeters (×40.5)
5	18.3	4.5	15	96.9	53.9	6	151.0	103.0
10	23.2	8.9	22	101.6	59.9	9	156.3	113.3
41	28.0	9.8	8	106.1	63.6	8	162.4	125.1
32	32.0	11.8	13	110.9	70.1	10	167.9	125.3
9	53.2	24.7	4	117.5	79.9	10	171.7	114.2
1	58.9	31.5	12	121.6	80.7	5	176.6	127.8
1	72.1	38.5	7	126.9	83.4	8	182.2	135.8
1	79.0	42.5	6	130.9	95.2	5	186.4	146.2
12	82.3	46.0	2	139.0	102.4	2	190.5	133.1
20	87.1	47.5	10	141.8	94.4	2	197.5	143.5
16	91.1	50.3	4	146.5	101.0	2	203.5	160.8

The key scales taken from each specimen were removed from the second scale row above the lateral-line row, and were the three scales immediately posterior to the scale lying directly above the twelfth lateral-line scale. It was from this general region that the unselected scales of the general collections were taken. Ordinarily the key scales were taken from the left side, but in those specimens whose scales on this side had regenerated centers, the key scales were removed from the right side. Even so, a few fish had only one or two measurable key scales or none at all. The method of mounting and measuring the key scales was the same as that described previously (p. 206) for the scales in the general collection. The scale length for each fish was determined as the mean of the measurements of its key scales.

In the O-group fish, whose length ranged from about 15 to 35 millimeters, the individual scales were so small that it was not possible to remove and mount the key scales individually. In these fish a small patch of scales from the key area was detached with a dissecting needle and mounted. The number of measurable scales (scales not folded or torn) obtained by this method varied from two to five and all were measured and the measurements were averaged for each individual.

Table 6 shows the relationship between body length (averages for 5-millimeter intervals) and the length of the magnified anterior scale radius of the Nebish Lake and Muskellunge Lake rock bass, with the sexes and all ages combined. This general combination of data was made only after a detailed examination of the variation of scale length with body length by age and by sex for the lakes separately failed to reveal consistent differences among the several categories.

The plotting of the original data on both absolute and logarithmic scales suggested at once that the mathematical relationship between body length and scale radius in the rock bass might be described by the equation for the parabola:

$$L = cS^n, \qquad (1)$$

where
$$L = \text{body length},$$
$$S = \text{anterior scale radius},$$

and
$$c \text{ and } n = \text{constants}.$$

Accordingly, an equation of this type was fitted to the em-

pirical data on body length and scale radius. The resulting equation was:

$$L = 5.84011\ S^{0.695992},\tag{2}$$

or in the logarithmic form,

$$\log L = 0.7664210 + 0.695992 \log S.\tag{3}$$

A comparison of the curve for equation (2) with the averages[14] of the empirical data may be had from the examination of Figure 3. It may be seen that the theoretical curve fits the empirical data rather closely. The most serious disagreement is
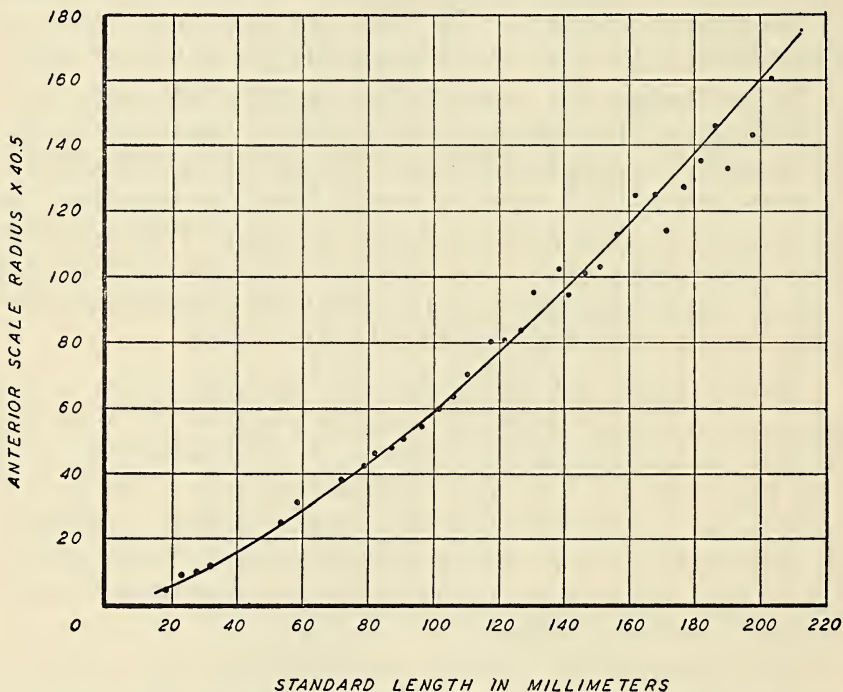
FIGURE 3. Relationship between the length of Nebish Lake rock bass and the length of the anterior radius of (magnified) key scales. The curve is the graph of the equation fitted to the data on body length and scale length (radius). The dots represent the empirical averages of body length and scale length (radius).

[14] Equations (2) and (3) were not derived from the averages presented in Table 6. In the derivation of the equations the measurements for each individual fish were considered as a point, and a straight line was fitted to the logarithms of the individual body lengths and anterior scale radii. It does not appear desirable, however, to present the data for the individual specimens.

to be found in the region where the fish length exceeds 170 millimeters. At these higher lengths the empirical points tend to lie to the right of the curve, but most of these points are represented by very small numbers of fish.

Since the parabolic equation (1) describes satisfactorily the body-scale relationship of the rock bass from Nebish and Muskellunge Lakes, it may be stated for these populations that from the time of scale formation[15] (at a body length of about 15 millimeters): (1) The growth of the scale with increase in the length of the fish proceeds along a curve whose backward continuation passes through the origin; and (2) the relative rates of growth of body and scale maintain a constant ratio.

For the computations of individual growth histories of rock bass a table of solutions of equation (2) was prepared. This table contains the body lengths (computed to the nearest tenth of a millimeter) corresponding to half-millimeter intervals of scale length.[16] Although the computed lengths in individual growth histories were recorded only to the nearest millimeter, the tabular solutions to the nearest tenth of a millimeter facilitated the reading of lengths corresponding to the "corrected" scale measurements, to be described presently. It has not been considered desirable to present this detailed table of solutions.

The procedure followed in the computation of growth histories will be illustrated by two examples (Table 7). The fish selected were both VIII-group males from the 1931 collection, and both were 183 millimeters long (standard length) at capture. For convenience they may be designated by their slide numbers, 263 and 322.

The magnified radius of the scale measured from the slide for fish No. 263 was 128 millimeters. The radial measurements to the first, second, third, ... annuli were 17, 33.5, 52, ... millimeters respectively. However, the scale that was measured was

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[15] The "time of scale formation" as used here refers to the time at which the scale has attained sufficient size that it can be removed from the fish, mounted, and measured.

[16] Actually equation (1) was solved for 5-millimeter intervals of the magnified scale radius and the solutions for the intervening points were obtained by interpolation. For a large part of the curve only linear interpolation was needed in order to arrive at solutions that were accurate to the nearest tenth of a millimeter. At the lower lengths, however, the use of second differences—and for a few intervals, third differences—proved necessary.

TABLE 7. *Original scale measurements, corrected scale measurements, and calculated lengths at the end of each year of life for two rock bass of the 1931 VIII group.*

Year of life	Specimen No. 263			Specimen No. 322		
	Scale measurement	Corrected scale measurement	Calculated length	Scale measurement	Corrected scale measurement	Calculated length
1	17	18.7	45	15	12.7	34
2	33.5	36.9	72	41	34.6	69
3	52	57.3	98	75	63.4	105
4	64	70.5	113	100	84.5	128
5	86	94.8	139	116	98.0	142
6	106	116.8	160	138	116.6	160
7	116	127.8	171	152	128.4	171
8	125	137.8	180	161	136.0	178
8+	128	141.1	[1]183	167	141.1	[1]183

[1] Length at capture.

smaller than would be expected, on theoretical grounds, on a fish 183 millimeters long. Consequently, these several measurements require correction before they can be employed for the determination of the lengths of fish No. 263 at the end of the different years of life. The table of solutions for equation (2) contains the following solutions for fish whose lengths are approximately 183 millimeters long:

Scale radius	Fish length
141.0	182.9
141.5	183.4

It is obvious therefore that the theoretical length of the scale from fish No. 263 is 141.1 millimeters as compared with the measured length of 128 millimeters. The ratio between the two scale lengths, $141.1/128 = 1.102$, may be used as a factor to "correct" or adjust the original scale measurements to the theoretical level. For example, $1.102 \times 17 = 18.7$; $1.102 \times 33.5 = 36.9$; $1.102 \times 52 = 57.3$; . . . and finally to verify the accuracy of the correction, $1.102 \times 128 = 141.1$. The use of the "correcting factor" involves the assumption that the percentage or relative deviation of the length of the anterior radius of any single scale from the theoretical length of the radius is constant at the time of formation of all annuli. There appears to be no alternative to this assumption although admittedly it is unproven.

The calculated lengths of fish No. 263 at the end of different years of life are simply the solutions of equation (2) corresponding to the corrected scale measurements. For example, the solution at $S = 18.7$ (end of first year) falls between the tabular solutions, $L = 44.5$ when $S = 18.5$, and $L = 45.4$ when $S = 19.0$. The length of fish No. 263 at the end of the first year of life may therefore be seen at a glance to have been 45 millimeters. Similarly the solution for $S = 36.9$ falls between the points (36.5, 71.4) and (37.0, 72.1), and $L_2 = 72$ millimeters. The remaining solutions are read from the table in the same manner.

Precisely the same procedure was followed in the calculation of the growth history of fish No. 322. Here, however, the scale that was measured proved to be larger than the theoretical scale (167-millimeter anterior radius as compared with the theoretical radius of 141.1 millimeters). The original measurements were reduced therefore by the factor, $141.1/167 = 0.845$. Again the solutions corresponding to the corrected scale measurements are obtained from the table of solutions of equation (2).

In actual practice the corrected scale measurements need not be recorded. Instead, the correcting factor, theoretical scale length/measured scale length, is placed in the keyboard of a calculating machine and multiplied successively by the several scale measurements. The solutions (calculated lengths) corresponding to the corrected scale measurements are read from the table of solutions and recorded at the time each corrected measurement is obtained.

The correction of the original scale measurements can be made satisfactorily also by means of a simple nomograph (Fig. 4) which consists of a thin spring-steel ruler graduated by tenths of an inch lying on a background of 0.1-inch[17] cross-section paper. (The use of the nomograph involves only the horizontal rulings of the paper.) The slotted end of the ruler is mounted on a flat brass cylinder set flush in the board on which the paper is mounted and is held in position by a small bolt fitted with a washer and a wing nut. For the computation of the corrected scale lengths for fish No. 263 the ruler is placed in such a position that the 0 graduation of the paper coincides with the 0 grad-

[17] The use of rather large graduations guarantees greater accuracy and reduces fatigue.

uation of the ruler, and the 128 (= 12.8 inches) horizontal line falls slightly beyond the 141 (= 14.1 inches) graduation of the ruler. The wing nut is then tightened and the corrected scale measurements are read from the ruler at the points of intersection with the horizontal rulings corresponding to the original scale measurements. The procedure for fish No. 322 is similar. The 0 graduations are again made to coincide, and the 167 grad-
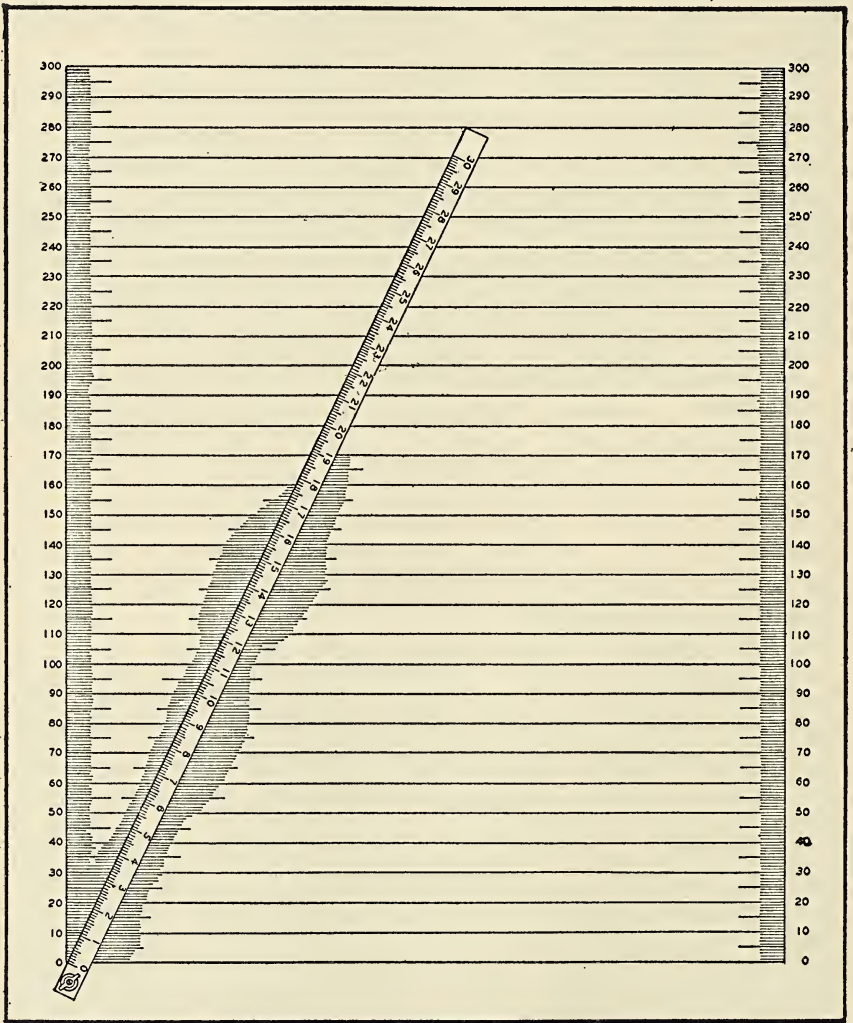
FIGURE 4. Diagram of nomograph employed for the correction of scale measurements. See text for explanation.

uation of the ruler is made to fall slightly beyond the 141 horizontal line. This time, however, the corrected measurements are read from the paper at the points of intersection with the original scale measurements along the ruler. The correcting factors discussed on p. 212 are merely the sines or cosecants of the angles at which the ruler in its different positions crosses the horizontal rulings.

Comparisons with machine calculations revealed that the nomograph gave accurate results. The only disagreements between the calculated lengths based on scale corrections from the nomograph and on scale corrections by machine occurred when the calculated lengths ended almost exactly in a half-millimeter.

The method employed for the calculation of individual growth histories of the rock bass may be considered in a sense a combination of methods used previously by Monastyrsky (1930) and Segerstråle (1933). The mathematical relationship assumed to exist between body length and scale radius in the rock bass (namely, that of a logarithmic straight line) is the one which Monastyrsky applied to several species and which he held to be generally applicable. However, Monastyrsky did not use a tabulation of corresponding body and scale lengths, but performed his growth calculations by means of a nomograph with logarithmic scales. Segerstråle made growth calculations with the aid of tables of body lengths and scale lengths (based on measurements of "normal" or key scales) and "normalized" his original scale measurements in a procedure identical with the "correction" of the measurements of rock bass scales. Segerstråle's tabulations of the body-scale relationship differed from that made for the rock bass in that his data were purely empirical and did not involve an assumption of any definite mathematical relationship between body length and scale length.

The only previously published growth calculations of rock bass (Wright, 1929) were made by the direct-proportion method, that is, on the assumption that the ratio, body length/scale radius, is constant for all lengths of fish beyond that at which the first annulus is laid down. Wright recognized the probable inaccuracy of his method of growth calculation and stated that it ". . . . is believed to give only approximate results . . . ."

The comparison of the growth histories of nine age groups of Nebish Lake rock bass (age-groups II to X of the males of the 1931 collection) as calculated by direct proportion and from equation (2) provides a measure of the error involved in the former method (Table 8). It may be seen that the extent of the error depends both on the length at capture of the fish for which the calculations are made and on the year of life for which the calculations are made. Although there are a few minor exceptions it may be said that in general the differences between "corrected" and "uncorrected" calculated lengths for corresponding years of life tended to decrease with a decrease in the size (at capture) of the fish on which the calculations were based. Within the individual age groups these differences tended first to in-

TABLE 8. *Comparison of the growth histories of nine age groups of male Nebish Lake rock bass captured in 1931 as computed from scale measurements by direct proportions (uncorrected lengths) and as computed on the assumption that the body-scale relationship takes the form of a parabola (corrected lengths). The lengths of the age groups at capture are designated by asterisks. All lengths are in millimeters.*

Age group	Item	Calculated length at end of year of life										
		1	2	3	4	5	6	7	8	9	10	11
X	Corrected lengths	35	66	102	128	145	156	168	174	180	186	190*
	Uncorrected lengths	17	42	78	106	126	143	160	167	176	185	190*
	Difference	18	24	24	22	19	13	8	7	4	1	..
IX	Corrected lengths	39	70	98	120	141	157	165	172	178	182*	..
	Uncorrected lengths	20	47	76	99	125	148	159	168	176	182*	..
	Difference	19	23	22	21	16	9	6	4	2	..	..
VIII	Corrected lengths	37	63	93	120	140	153	164	172	177*	..	..
	Uncorrected lengths	19	41	70	101	126	144	159	170	177*	..	..
	Difference	18	22	23	19	14	9	5	2	..	..	..
VII	Corrected lengths	40	72	102	129	149	162	172	177*	..	..	..
	Uncorrected lengths	21	49	80	113	138	156	170	177*	..	..	..
	Difference	19	23	22	16	11	6	2	..	..	..	..
VI	Corrected lengths	30	50	74	100	124	141	151*	..	..	..	..
	Uncorrected lengths	15	31	54	83	115	138	151*	..	..	..	..
	Difference	15	19	20	17	9	3	..	..	..	..	..
V	Corrected lengths	29	50	73	102	125	146*	..	..	..	..	..
	Uncorrected lengths	15	31	54	87	119	146*	..	..	..	..	..
	Difference	14	19	19	15	6	..	..	..	..	..	..
IV	Corrected lengths	30	54	82	112	135*	..	..	..	..	..	..
	Uncorrected lengths	16	37	66	103	135*	..	..	..	..	..	..
	Difference	14	17	16	9	..	..	..	..	..	..	..
III	Corrected lengths	32	61	92	116*	..	..	..	..	..	..	..
	Uncorrected lengths	18	46	84	116*	..	..	..	..	..	..	..
	Difference	14	15	8	..	..	..	..	..	..	..	..
II	Corrected lengths	31	63	89*	..	..	..	..	..	..	..	..
	Uncorrected lengths	20	55	89*	..	..	..	..	..	..	..	..
	Difference	11	8	..	..	..	..	..	..	..	..	..

crease and then to decrease. With the exception of age-group II the difference between the corrected and uncorrected calculated lengths always increased from the first to the second year of life. Beyond age-group III the differences tended to be approximately the same (within an age group) for the second and third years of life and to decrease progressively beyond the third year of life.

If the data of Table 8 are considered as a whole, it is apparent that the use of lengths calculated by direct proportion involves a high degree of error. For the earlier years of life, in particular, lengths calculated by direct proportion may give a seriously erroneous impression concerning the course of growth.

Average Lengths and Weights of the Age Groups

The average length (standard length in millimeters, total length in inches) and weight (in grams and ounces) of each age group (sexes separately) in each year's collection of the Nebish Lake rock bass are listed in Tables 9 and 10. The tables include also the grand average length and weight of each of the age groups for all collections combined.

TABLE 9. *Average length and weight of the age groups of male Nebish Lake rock bass in the different years of capture and for all years combined.*

Age group	Item	Year of capture				Grand average
		1930	1931	1932	1935	
XI	Standard length (millimeters)	..	..	195	..	195
	Weight (grams)	..	..	224	..	224
	Total length (inches)	..	..	9.3	..	9.3
	Weight (ounces)	..	..	7.9	..	7.9
	Number of fish	..	..	(3)	..	(3)
X	Standard length (millimeters)	..	190	188	171	187
	Weight (grams)	..	199	194	178	194
	Total length (inches)	..	9.1	9.0	8.2	9.0
	Weight (ounces)	..	7.0	6.8	6.3	6.8
	Number of fish	..	(4)	(10)	(1)	(15)
IX	Standard length (millimeters)	175	182	183	..	182
	Weight (grams)	161	179	180	..	179
	Total length (inches)	8.4	8.7	8.8	..	8.7
	Weight (ounces)	5.7	6.3	6.3	..	6.3
	Number of fish	(2)	(18)	(41)	..	(61)

TABLE 9 (continued)

Age group	Item	Year of capture				Grand average
		1930	1931	1932	1935	
VIII	Standard length (millimeters)	169	177	180	..	177
	Weight (grams)	141	164	167	..	164
	Total length (inches)	8.1	8.5	8.6	..	8.5
	Weight (ounces)	5.0	5.8	5.9	..	5.8
	Number of fish	(3)	(117)	(8)	..	(128)
VII	Standard length (millimeters)	166	177	174	..	173
	Weight (grams)	134	158	153	..	150
	Total length (inches)	8.0	8.5	8.3	..	8.3
	Weight (ounces)	4.7	5.6	5.4	..	5.3
	Number of fish	(15)	(27)	(5)	..	(47)
VI	Standard length (millimeters)	159	151	161	160	157
	Weight (grams)	114	99	120	150	120
	Total length (inches)	7.6	7.2	7.7	7.7	7.5
	Weight (ounces)	4.0	3.5	4.2	5.3	4.2
	Number of fish	(3)	(5)	(3)	(4)	(15)
V	Standard length (millimeters)	143	146	151	149	148
	Weight (grams)	84	93	98	116	104
	Total length (inches)	6.8	7.0	7.2	7.1	7.1
	Weight (ounces)	3.0	3.3	3.5	4.1	3.7
	Number of fish	(9)	(8)	(8)	(28)	(53)
IV	Standard length (millimeters)	125	135	146	128	133
	Weight (grams)	56	71	86	73	70
	Total length (inches)	6.0	6.5	7.0	6.1	6.4
	Weight (ounces)	2.0	2.5	3.0	2.6	2.5
	Number of fish	(9)	(3)	(7)	(5)	(24)
III	Standard length (millimeters)	..	116	121	..	120
	Weight (grams)	..	44	52	..	51
	Total length (inches)	..	5.6	5.8	..	5.7
	Weight (ounces)	..	1.6	1.8	..	1.8
	Number of fish	..	(6)	(43)	..	(49)
II	Standard length (millimeters)	..	89	93	..	93
	Weight (grams)	..	20	23	..	23
	Total length (inches)	..	4.3	4.5	..	4.5
	Weight (ounces)	..	0.7	0.8	..	0.8
	Number of fish	..	(10)	(78)	..	(88)

TABLE 10. *Average length and weight of the age groups of female Nebish Lake rock bass in the different years of capture and for all years combined.*

Age group	Item	Year of capture				Grand average
		1930	1931	1932	1935	
XIII	Standard length (millimeters)	..	..	193	..	193
	Weight (grams)	..	..	218	..	218
	Total length (inches)	..	..	9.2	..	9.2
	Weight (ounces)	..	..	7.7	..	7.7
	Number of fish	..	..	(1)	..	(1)
XII	Standard length (millimeters)	..	190	177	..	180
	Weight (grams)	..	210	167	..	178
	Total length (inches)	..	9.0	8.4	..	8.6
	Weight (ounces)	..	6.7	6.2	..	6.3
	Number of fish	..	(1)	(3)	..	(4)
XI	Standard length (millimeters)	..	182	180	177	180
	Weight (grams)	..	182	179	177	179
	Total length (inches)	..	8.6	8.6	8.4	8.6
	Weight (ounces)	..	6.4	6.3	6.2	6.3
	Number of fish	..	(2)	(13)	(1)	(16)
X	Standard length (millimeters)	154	176	175	..	175
	Weight (grams)	106	159	160	..	159
	Total length (inches)	7.4	8.4	8.3	..	8.3
	Weight (ounces)	3.7	5.6	5.6	..	5.6
	Number of fish	(1)	(17)	(33)	..	(51)
IX	Standard length (millimeters)	160	170	169	..	169
	Weight (grams)	125	149	144	..	146
	Total length (inches)	7.6	8.1	8.0	..	8.0
	Weight (ounces)	4.4	5.3	5.1	..	5.1
	Number of fish	(2)	(47)	(74)	..	(123)
VIII	Standard length (millimeters)	155	161	164	170	161
	Weight (grams)	113	124	129	174	124
	Total length (inches)	7.4	7.6	7.8	8.1	7.6
	Weight (ounces)	4.0	4.4	4.6	6.1	4.4
	Number of fish	(8)	(99)	(17)	(1)	(125)
VII	Standard length (millimeters)	149	159	159	..	153
	Weight (grams)	97	119	119	..	107
	Total length (inches)	7.1	7.6	7.6	..	7.3
	Weight (ounces)	3.4	4.2	4.2	..	3.8
	Number of fish	(43)	(24)	(9)	..	(76)
VI	Standard length (millimeters)	145	149	149	155	150
	Weight (grams)	88	96	96	129	103
	Total length (inches)	6.9	7.1	7.1	7.4	7.2
	Weight (ounces)	3.1	3.4	3.4	4.6	3.6
	Number of fish	(6)	(11)	(8)	(9)	(34)

TABLE 10 (continued)

Age group	Item	Year of capture				Grand average
		1930	1931	1932	1935	
V	Standard length (millimeters)	127	135	142	140	138
	Weight (grams)	62	74	82	96	89
	Total length (inches)	6.1	6.5	6.8	6.7	6.6
	Weight (ounces)	2.2	2.6	2.9	3.4	3.1
	Number of fish	(6)	(7)	(2)	(43)	(58)
IV	Standard length (millimeters)	118	125	137	130	128
	Weight (grams)	47	58	73	78	64
	Total length (inches)	5.7	6.0	6.6	6.2	6.1
	Weight (ounces)	1.7	2.0	2.6	2.8	2.3
	Number of fish	(9)	(5)	(9)	(8)	(31)
III	Standard length (millimeters)	..	112	114	111	114
	Weight (grams)	..	40	43	51	43
	Total length (inches)	..	5.4	5.5	5.3	5.5
	Weight (ounces)	..	1.4	1.5	1.8	1.5
	Number of fish	..	(7)	(59)	(1)	(67)
II	Standard length (millimeters)	..	89	90	..	90
	Weight (grams)	..	21	21	..	21
	Total length (inches)	..	4.3	4.3	..	4.3
	Weight (ounces)	..	0.7	0.7	..	0.7
	Number of fish	..	(9)	(59)	..	(68)

The agreement as to average length and weight of rock bass of the same age and sex but taken in different years is in general good. Some of the discrepancies that do occur are doubtless the result of the small numbers of fish in certain age groups. Others are traceable to differences in growth rate in different calendar years.[18] The high average weights of the age groups in the 1935 collection depend on the extremely good condition of the rock bass in late August of that year.

In spite of the general similarity of the size of fish of the same age and sex but taken in different years, there is nevertheless a noticeable tendency for the average lengths and weights of the age groups to increase from year to year over the period, 1930 to 1932. All ages below the VI-group follow this trend closely. Although the same general upward trend is detectable among the older fish, the data for the VI and older groups contain a number of exceptions. The observed upward trend in the average size of the age groups may be connected with the im-

[18] The question of annual fluctuations in growth is treated in detail in a later section (pp. 249 to 262).

provement that was occurring in the growth rate of the rock bass in 1930 and 1931.

Rock bass captured in 1935 usually were shorter but heavier than fish of the same age and sex in 1932. The only exceptions in age groups represented by more than one fish were the VI-group females which were 6 millimeters longer in 1935 and the IV-group males which were not only 18 millimeters shorter but also 13 grams lighter in 1935 than in 1932. The reason for the high weights of the 1935 age groups was mentioned two paragraphs previously. Their decreased length in comparison with 1932 age groups was correlated with a decline in growth rate in the years, 1932 to 1934 (p. 258).

The slow growth of the Nebish Lake rock bass prevents the attainment of a large size despite the fact that many of them survive to the age of 9 years or older. The age group with the greatest average size, the XI-group males of the 1932 collection, had an average length[19] of only 195 millimeters (9.3 inches) and an average weight of only 224 grams (7.9 ounces). Among the males no age group younger than the X-group had an average length as great as 187 millimeters (9 inches) and all age groups younger than the VII-group averaged less than 166 millimeters (8 inches). The small size attained by the females is even more striking. The grand average length of IX-group female rock bass was only 169 millimeters (8 inches) and no age group represented by more than one fish had a grand average length in excess of 180 millimeters (8.6 inches) or a grand average weight above 179 grams (6.3 ounces).

Data concerning the maximum average length and weight attained by age groups ordinarily do not provide information as to the maximum size attained by individual fish. It happens that the XIII-group female captured in 1932 not only was the oldest fish of that sex in the collections but also was the longest (193 millimeters, 9.2 inches) and the heaviest (218 grams, 7.7 ounces). However, males were captured whose size was greater than the average for any age group. The longest males taken were three 200-millimeter (9.6 inches) fish in the 1932 collection. One of these fish was also the heaviest (257 grams or 9.1

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[19] In this and later discussions all lengths given in millimeters are standard and those given in inches are total.

ounces). The age of this individual could not be determined. Of the remaining 200-millimeter male rock bass one was a member of age-group XI and weighed 253 grams (8.9 ounces) and the other of age-group X and weighed 242 grams (8.5 ounces).

The grand average lengths for the age groups show that males ordinarily attain the minimum legal length of 7 inches in the sixth year of life (age-group V) and females in the seventh (age-group VI). The averages for the age groups in the collections for the individual years indicate that with good or poor growth the age at which legal length is attained may be subject to some annual variation.

In order not to disturb the continuity of the preceding discussions, the standard and total lengths of rock bass have been presented without a statement of the relationship between the two measurements or of the conversion factors employed. Table 11 contains factors for conversions between standard and total length, as determined from measurements of 306 rock bass captured in 1930. The most noteworthy conclusions to be drawn from the data are: (1) small rock bass have relatively longer tails than large ones; and (2) among the largest rock bass the males have longer tails than the females. The observation as to the decrease in the relative length of the caudal fin with increase in body length is in agreement with the findings of Van Oosten on the Lake Erie sheepshead (1938), and the Lake Huron whitefish (1939).

TABLE 11.   *Factors for conversions between total length (T.L.) and standard length (S.L.) of rock bass according to sex and length group.*

Sex	Standard length interval	Number of fish	Factors for conversion of			
			T.L. to S.L. (No change of unit)	S.L. to T.L. (No change of unit)	T.L. (inches) to S.L. (millimeters)	S.L. (millimeters) to T.L. (inches)
Both	Less than 100 millimeters	29	0.818	1.222	20.78	0.0481
Male Female	100 millimeters or greater 100-159 millimeters	136 109	0.822	1.217	20.88	0.0479
Female	160 millimeters or greater	32	0.829	1.206	21.06	0.0475

RANGE OF LENGTH IN THE AGE GROUPS

The length-frequency distributions of the age groups of the Nebish Lake rock bass (Tables 12 and 13) have been based on the combination of the data for fish of corresponding age and

TABLE 12. *Length-frequency distributions of the age groups of the male rock bass of Nebish Lake.*

Length interval in millimeters	Age group										Total
	II	III	IV	V	VI	VII	VIII	IX	X	XI	
200-204	..	..	..	..	..	.	..	..	1	1	2
195-199	..	..	..	..	..	..	1	1	1	..	3
190-194	..	..	..	..	..	..	..	5	4	2	11
185-189	..	..	..	..	..	2	13	18	5	..	38
180-184	..	..	..	..	..	5	40	18	1	..	64
175-179	..	..	..	..	..	11	29	12	3	..	55
170-174	..	..	..	..	..	18	35	7	..	..	60
165-169	..	..	..	..	1	4	8	..	..	..	13
160-164	..	..	..	..	7	5	1	..	..	..	14
155-159	..	..	..	8	3	1	..	..	..	..	12
150-154	..	..	1	17	2	1	1	..	..	..	22
145-149	..	..	2	11	1	..	..	..	..	..	14
140-144	..	..	5	9	1	..	..	..	..	..	15
135-139	..	2	1	3	..	..	..	..	..	..	6
130-134	..	5	2	4	..	..	..	..	..	..	11
125-129	..	5	3	..	..	..	..	..	..	..	8
120-124	..	15	1	..	..	..	..	..	..	..	16
115-119	..	8	..	..	..	..	..	..	..	..	8
110-114	1	5	..	..	..	..	..	..	..	..	6
105-109	4	1	..	..	..	..	..	..	..	..	5
100-104	12	2	..	..	..	..	..	..	..	..	14
95- 99	9	..	..	..	..	..	..	..	..	..	9
90- 94	23	..	..	..	..	..	..	..	..	..	23
85- 89	24	..	..	..	..	..	..	..	..	..	24
80- 84	5	..	..	..	..	..	..	..	..	..	5
Average length	93	121	138	148	157	173	177	182	187	195	..
Number of fish	78	43	15	53	15	47	128	61	15	3	458

sex in the different years' collections, with the exception of those age groups for which records of sex were incomplete or lacking. The age groups that were excluded in the preparation of the tables were: II- and III-groups of 1930 and 1931; IV-group of 1930.

The data of Tables 12 and 13 give no evidence that the length range of an age group varies according to the age or sex of the fish involved. Among the 15 age groups that were represented by more than 20 fish the length range varied from 25 millimeters (II-group females) to 50 millimeters (VIII-group males). Ten of the 15 age groups had length ranges of 35 or 40 millimeters.

The generally high degree of overlap of the length-frequency distributions of the successive age groups of both sexes makes length a relatively poor index of age. The positions of the modal lengths of only the II-groups stand out distinctly in the length-frequency distributions for all ages combined. Larger rock bass at any particular length may belong to any one of several age groups. Among the males as many as five age groups were rep-

Among the females whose slower growth led to a greater overlap of the length-frequency distributions of the successive age groups, six age groups were represented in the intervals, 150-154 millimeters and 165-169 millimeters.

CALCULATED LENGTHS OF THE AGE GROUPS AND THE YEAR CLASSES

The calculated growth histories of the individual age groups in each year's collection of the Nebish Lake rock bass are recorded in Tables 14, 15, and 16. In the general arrangement of the data, fish of the same year class rather than of the same age have been grouped together. The data on the younger fish for which there were no sex records (Table 16) have been included largely for the sake of completeness, since the lack of these records renders the data of small value in the analysis of growth. The growth histories of the individual year classes, all ages combined, are presented in Tables 17 and 18.

The present section will be concerned only with variations in calculated lengths, and will not include the consideration of

TABLE 13. *Length-frequency distributions of the age groups of female rock bass of Nebish Lake.*

Length interval in millimeters	Age group													Total
	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII		
190-194	..	..	..	..	..	..	..	2	..	..	1	1		4
185-189	..	..	..	..	..	..	..	..	1	2	..	..		3
180-184	..	..	..	..	..	..	..	2	8	8	1	..		19
175-179	..	..	..	..	..	..	2	22	20	5	1	..		50
170-174	..	..	..	..	..	2	18	40	17	..	1	..		78
165-169	..	..	..	..	1	4	16	27	4	1	..	..		53
160-164	..	..	..	..	1	11	38	21	..	..	..	..		71
155-159	..	..	..	..	5	17	27	6	..	..	..	..		55
150-154	..	..	..	2	10	20	21	3	1	..	..	..		57
145-149	..	..	2	10	12	12	2	..	..	..	..	..		38
140-144	..	..	2	14	4	9	1	..	..	..	..	..		30
135-139	..	..	4	15	1	1	..	..	..	..	..	..		21
130-134	..	..	4	12	..	..	..	..	..	..	..	..		16
125-129	..	2	5	2	..	..	..	..	..	..	..	..		9
120-124	..	9	5	2	..	..	..	..	..	..	..	..		16
115-119	..	19	..	1	..	..	..	..	..	..	..	..		20
110-114	..	17	..	..	..	..	..	..	..	..	..	..		17
105-109	..	6	..	..	..	..	..	..	..	..	..	..		6
100-104	6	5	..	..	..	..	..	..	..	..	..	..		11
95- 99	3	2	..	..	..	..	..	..	..	..	..	..		5
90- 94	21	..	..	..	..	..	..	..	..	..	..	..		21
85- 89	22	..	..	..	..	..	..	..	..	..	..	..		22
80- 84	7	..	..	..	..	..	..	..	..	..	..	..		7
Average length	90	114	132	138	150	153	161	169	175	180	180	193		..
Number of fish	59	60	22	58	34	76	125	123	51	16	4	1		629

TABLE 14. *Average length in millimeters at capture and average calculated length at the end of each year of life for each age group of male Nebish Lake rock bass, arranged by year class and year of capture. Below, general growth data based on all age groups except the II-groups (designated by asterisks).*

Year class	Year of capture	Age group	Number of fish	Length at capture	Calculated length at end of year of life										
					1	2	3	4	5	6	7	8	9	10	11
1921	1930	IX	2	175	44	73	101	125	142	155	162	168	172		
	1931	X	4	190	35	66	102	127	145	156	163	174	180	186	
	1932	XI	3	195	38	72	101	123	143	157	167	173	178	183	190
1922	1930	VIII	3	169	37	65	93	118	139	152	161	166			
	1931	IX	18	182	39	70	98	120	141	157	165	172	178		
	1932	X	10	188	40	73	99	123	145	159	167	172	177	184	
1923	1930	VII	15	166	35	64	93	116	138	152	160	166			
	1931	VIII	117	177	37	63	93	120	140	153	164	172	178		
	1932	IX	41	183	36	63	94	121	141	153	163	171	179		
1924	1930	VI	3	159	34	61	86	114	133	151					
	1931	VII	27	177	40	72	102	129	149	162	172				
	1932	VIII	8	180	40	69	99	125	147	159	168	175			
1925	1930	V	9	143	34	57	83	107	128						
	1931	VI	5	151	30	50	74	100	124	141					
	1932	VII	5	174	35	60	88	112	136	154	170				
	1935	X	1	171	35	65	82	107	128	141	149	157	164	171	
1926	1930	IV	9	125	29	51	73	105							
	1931	V	8	146	29	50	73	102	125						
	1932	VI	3	161	37	62	88	114	132	151					
1927	1931	IV	3	135	30	54	82	112							
	1932	V	8	151	28	50	79	106	134						
1928	1931	III	6	116	32	61	92								
	1932	IV	7	146	30	56	89	122							
1929	1931	II*	10	89	31	63									
	1932	III	43	121	29	61	95								
	1935	VI	4	160	27	55	87	120	141	153					
1930	1932	II•	78	93	34	65									
	1935	V	28	149	31	59	89	117	137						
1931	1935	IV	5	128	29	55	81	103							
Average calculated length					35	62	92	119	139	153	163	171	177	184	191
Average growth increment					34.8	27.6	29.8	26.6	20.6	13.4	10.2	7.6	6.8	6.3	7.0
Number of fish					(395)	(395)	(395)	(346)	(322)	(269)	(254)	(207)	(79)	(18)	(3)

increments of growth in length or of annual fluctuations in growth rate. The detailed study of annual fluctuations in growth rate as determined from the analysis of the growth increments of the various year classes will be presented in a later section (pp. 249-262).

The calculated lengths of the age groups give little or no indication of the presence of Lee's phenomenon of apparent decrease in calculated length as it is determined from successively older groups of fish (Tables 14 and 15). In fact, the calculated lengths for the early years of life were usually greater among the older age groups (VI- or VII-group and older) than in the younger (III to V or VI). It is true that in some of the year classes represented by the age-groups III to VI the older fish had slightly lower calculated lengths than younger fish of the same year class. (The II-group probably was not represented adequately—see p. 197.) However, these discrepancies were usually small and did not occur consistently in all the year classes. Furthermore, the majority of the age groups involved contained only small numbers of specimens. The disagreements can not, therefore, safely be considered to represent Lee's phenomenon. Consequently, the general conclusion that Lee's phenomenon, if present at all, has no significant effect on the determination of calculated growths of the Nebish Lake rock bass appears to be justified.

The disagreements that occur among the calculated lengths of different age groups of the same year class can be attributed for the most part to the small numbers of specimens in the individual age groups. Gear selectivity may have played a rôle also. Usually, however, the agreement is good where the numbers of fish are large.

The differences between the calculated lengths of the age groups of a single year class are usually much less than the differences to be found between age groups of different year classes. As an illustration, the maximum difference[20] of 5 millimeters in the first-year length of female rock bass within a year class (year class of 1921) is much less than the 13-millimeter difference between the first-year lengths of the 1930 IX-group

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[20] Age groups represented by only one fish have been disregarded in the determination of the maximum discrepancies of calculated growth.

TABLE 15. Average length in millimeters at capture and average calculated length at the end of each year of life for each age group of female Nebish Lake rock bass, arranged by year class and year of capture. Below, general growth data based on all age groups except the II-groups (designated by asterisks).

Year class	Year of capture	Age group	Number of fish	Length at capture	1	2	3	4	5	6	7	8	9	10	11	12	13
1919	1931	XII	1	190	40	76	115	147	160	165	169	173	177	182	185	187	
	1932	XIII	1	193	40	68	107	141	158	163	166	170	175	177	180	185	192
1920	1930	X	1	154	32	68	102	124	131	138	142	148	151	153			
	1931	XI	2	182	33	60	92	125	140	150	157	163	171	175	178		
	1932	XII	3	177	32	57	86	113	132	140	146	152	159	164	168	175	
1921	1930	IX	2	160	41	67	94	117	130	139	149	154	158				
	1931	X	17	176	36	70	100	121	136	147	155	161	167	170			
	1932	XI	13	180	36	66	97	118	135	146	154	159	164	169	177		
1922	1930	VIII	8	155	35	69	90	109	129	141	147	152					
	1931	IX	47	170	35	65	94	116	134	146	154	160	165				
	1932	X	33	175	38	72	100	120	137	148	155	161	166	173			
1923	1930	VII	43	149	34	58	86	109	126	136	145						
	1931	VIII	99	161	36	63	90	113	130	141	149	156					
	1932	IX	74	169	36	62	91	114	131	142	151	157	165				
1924	1930	VI	6	145	34	60	86	110	127	139							
	1931	VII	24	159	36	65	93	116	132	144	153						
	1932	VIII	17	164	38	70	96	116	134	147	153	160					
	1935	XI	1	177	32	53	88	114	132	143	151	158	168				
1925	1930	V	6	127	34	54	75	95	114								
	1931	VI	11	149	35	60	84	107	126	140							
	1932	VII	9	159	37	61	87	108	128	141	153						
1926	1930	IV	9	116	29	52	73	98									
	1931	V	7	135	31	54	71	94	116								
	1932	VI	8	149	29	52	74	100	120	140							
1927	1931	IV	5	125	29	49	73	100									
	1932	V	2	142	32	55	80	104	126								
	1935	VIII	1	170	28	56	78	102	121	143	154	160					
1928	1931	III	7	112	31	55	87										
	1932	IV	9	137	30	54	84	114									
1929	1931	II*	9	89	32	64											
	1932	III	59	114	29	59	89										
	1935	VI	9	155	29	57	88	115	137	149							
1930	1932	II*	59	90	33	64											
	1935	V	43	140	29	57	86	111	129								
1931	1935	IV	8	130	28	55	84	109									
1932	1935	III	1	111	27	52	83										
Average calculated length					34	62	90	113	130	142	150	156	162	168	174	179	186
Average growth increment					33.9	27.8	27.9	23.0	17.5	11.4	8.2	6.3	6.3	5.3	6.2	5.6	7.0
Number of fish					(586)	(586)	(586)	(519)	(488)	(430)	(396)	(320)	(195)	(72)	(21)	(5)	(1)

and the 1935 IV-group.   Similarly the 10-millimeter discrepancy in the second-year lengths of the 1924 year class is less than the difference of 23 millimeters between the second-year lengths of the 1932 X-group and the 1931 IV-group.   A like relationship holds for the calculated lengths for other years of life and for the calculated growth data for the males.   The comparison of the growth histories of the age groups (Tables 14 and 15) with the average growth of the year classes (Tables 17 and 18) reveals that the relatively limited variation of calculated lengths within a year class is the result of a strong tendency for each age group to conform to the "style of growth" that is typical for the year class to which it belongs.

TABLE 16. *Average length in millimeters at capture and average calculated length at the end of each year of life for each age group of young Nebish Lake rock bass, based on fish for which there are no sex records.*

Year class	Year of capture	Age group	Number of fish	Length at capture	Calculated length at end of year of life			
					1	2	3	4
1926	1930	IV	6	118	28	53	74	99
1927	1930	III	9	99	26	50	75	..
1928	{ 1930	II	21	80	28	54	..	..
	{ 1931	III	1	118	28	56	92	..
1929	1931	II	41	85	32	61	..	..

TABLE 17. *Calculated length in millimeters at the end of each year of life of the males of each year class of the Nebish Lake rock bass.*

Year class	Number of fish	Calculated length at end of year of life										
		1	2	3	4	5	6	7	8	9	10	11
1921	9	38	70	101	125	144	156	166	172	178	184	191
1922	31	39	70	98	121	142	157	165	171	177	184	...
1923	173	37	63	93	120	140	153	163	171	179	...	...
1924	38	40	70	100	127	147	160	170	177	...	...	...
1925	20	33	56	82	106	129	146	161	[1]169	[1]176	[1]181	...
1926	20	30	52	75	105	127	146	...	...	...	...	...
1927	11	29	51	80	108	136	...	...	...	...	...	...
1928	13	31	58	90	123	...	...	...	...	...	...	...
1929	47	29	60	94	[1]127	[1]148	[1]160	...	...	...	...	...
1930	28	31	59	89	117	137	...	...	...	...	...	...
1931	5	29	55	81	103	...	...	...	...	...	...	...
Maximum difference		11	19	26	24	20	14	9	6	2	0	...
Maximum difference as percentage of lowest calculated length		37.9	37.2	34.7	23.3	15.7	9.6	5.6	3.5	1.1	0.0	...

[1] Calculated length excluded from the computation of the maximum difference because of inadequate representation.

TABLE 18. *Calculated length in millimeters at the end of each year of life of the females of each year class of the Nebish Lake rock bass.*

Year class	Number of fish	Calculated length at end of year of life												
		1	2	3	4	5	6	7	8	9	10	11	12	13
[1]1919	2	40	72	111	144	159	164	168	172	176	180	183	186	193
1920	6	32	60	91	119	134	143	149	155	162	166	170	177	..
1921	32	36	68	98	120	135	146	154	160	165	169	177	..	..
1922	88	36	68	96	117	135	146	154	160	165	172	..	..	..
1923	216	36	62	90	113	130	141	149	156	164	..	..	..	..
1924	48	36	66	93	115	132	144	152	159	[1]169	[1]174	[1]177	..	..
1925	26	35	59	83	105	124	138	150	..	..	..	..	..	..
1926	24	30	53	73	98	119	139	..	..	..	..	..	..	..
1927	8	30	51	75	101	122	144	[1]155	[1]161	..	..	..	..	..
1928	16	30	54	85	115	..	..	..	..	..	..	..	..	..
1929	68	29	59	89	116	138	150	..	..	..	..	..	..	..
1930	43	29	57	86	111	129	..	..	..	..	..	..	..	..
1931	8	28	55	84	109	..	..	..	..	..	..	..	..	..
[1]1932	1	27	52	83	..	..	..	..	..	..	..	..	..	..
Maximum difference		8	17	25	22	19	12	5	5	3	6	7	..	..
Maximum difference as percentage of lowest calculated length		28.6	33.3	34.2	22.4	16.0	8.7	3.4	3.2	1.9	3.6	4.1	..	..

[1] Year class or individual calculated length excluded from the computation of maximum difference because of inadequate representation.

The great extent to which the growth histories of the year classes may differ is brought out by the data of Tables 17 and 18. (See Figures 5 and 6.) These differences in the manner of growth led to a wide range of variation among the year classes in the relationship of length to age, particularly in the earlier years of life. In both sexes the differences between the largest and smallest calculated lengths of year classes at corresponding ages (maximum difference) increased rapidly from the first to the third year of life. Beyond the third year the maximum differences decreased continuously for the males and over a period of several years for the females. The data for the later years of life of the females were irregular. The relative advantages of the largest over the smallest calculated lengths at corresponding years of life (maximum differences as percentage of lowest calculated length) were much the same during the first three years. Beyond the third year the percentages as well as the absolute differences underwent a pronounced decline (continuous for the males and irregular for the females).

Differences in the growth of year classes may lead also to variations in different calendar years in the relationship of length to age. The light broken lines of Figures 5 and 6 that connect the calculated lengths for corresponding years of life

show, for example, that rock bass were smaller at most ages in 1929 than in the preceding and subsequent calendar years. In other years, as for example in 1924, the Nebish Lake rock bass were relatively large for their age.

The growth of both the males and females of the 1924 year class introduces irregularities into the general trend of the data on the fluctuations in the relationship of size to age in different calendar years. From Tables 17 and 18 and Figures 5 and 6, it may be seen that in some years, especially in 1926, 1927, and 1928, the calculated lengths as a whole tended to be smaller than those for fish in corresponding years of life in the calendar year immediately preceding. However, the regularity with which the calculated lengths of rock bass of the 1924 year class exceeded those of the 1923 year class introduced a series of exceptions to the general trend. At first these discrepancies suggested the
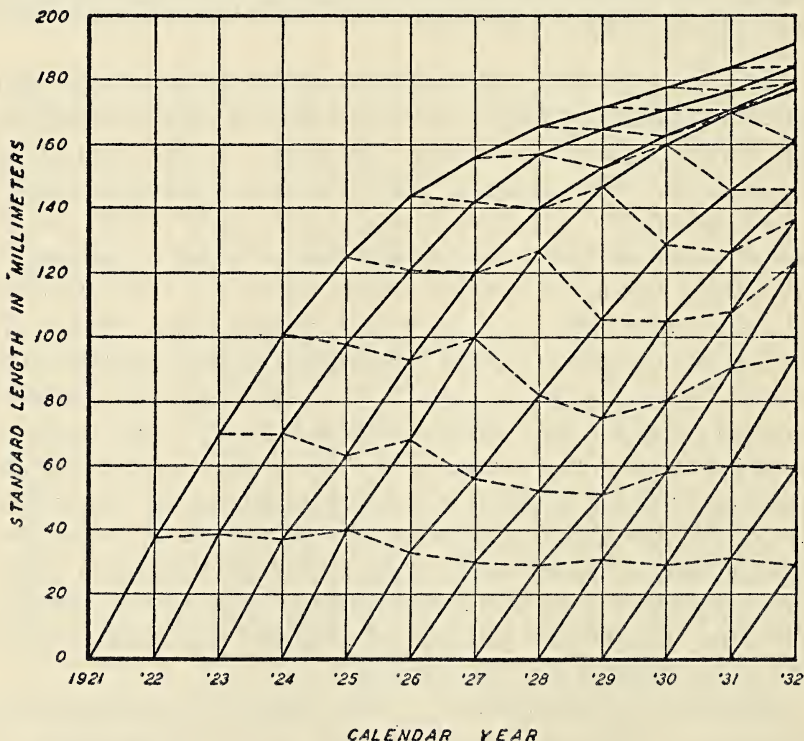

CALENDAR   YEAR

FIGURE 5. Calculated growth histories of the year classes of male Nebish Lake rock bass. The calculated lengths for corresponding years of life in different calendar years have been connected by light lines.

rather unpleasant possibility that erroneous age determinations of 1923 year-class fish (the overlooking of one annulus) might account for the large average calculated lengths of the 1924 year class. The 1923 year class was so very abundant that errors in the age determination of even a small percentage of them might well produce a serious distortion of the data for the much weaker 1924 year class.

There are strong arguments, however, against the belief that the high calculated lengths of the 1924 year class are the result of the erroneous inclusion of individuals of the 1923 year class. The discrepancies are not confined to the later years of life where the annuli may be difficult to detect, but occur also in the calculated lengths of the early years. The detection of the first five or six annuli is almost always a very simple matter. Consequently it appears that the 1923 and 1924 year classes exhibit differences in growth that can not well be attributed to errors in scale reading.
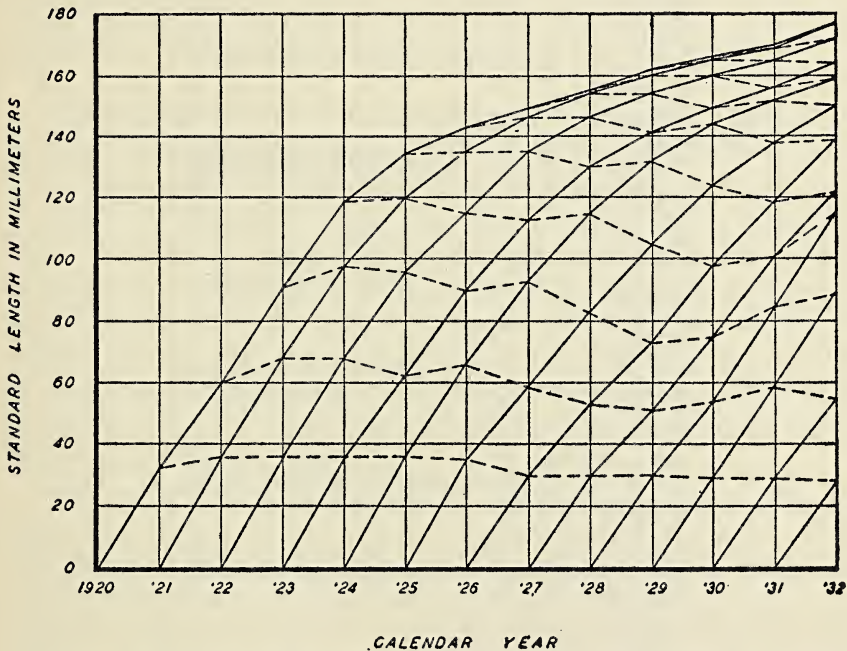

FIGURE 6. Calculated growth histories of the year classes of female Nebish Lake rock bass. The calculated lengths for corresponding years of life in different calendar years have been connected by light lines. Compare with Fig. 5.

TABLE 19. *Average calculated length at end of each year of life, annual increment of growth in length, and annual percentage increase in length of the Nebish Lake rock bass, all collections combined. The average calculated lengths are based on summations of the average increments of growth in length.*

Number of fish	Year of life	Males Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Number of fish	Year of life	Females Length in millimeters	ΔL	$\frac{100\Delta L}{L}$	Ratio of increments of sexes	Difference between increments of sexes
..	..	..	..	..	1	13	186	7.0	3.9	..	..
..	..	..	..	..	5	12	179	5.6	3.2	..	..
3	11	191	7.0	3.8	21	11	174	6.2	3.7	1.13	0.8
18	10	184	6.3	3.6	72	10	168	5.3	3.3	1.19	1.0
79	9	177	6.8	4.0	195	9	162	6.3	4.0	1.08	0.5
207	8	171	7.6	4.7	320	8	156	6.3	4.2	1.21	1.3
254	7	163	10.2	6.7	396	7	150	8.2	5.8	1.24	2.0
269	6	153	13.4	9.6	430	6	142	11.4	8.8	1.18	2.0
322	5	139	20.6	17.3	488	5	130	17.5	15.5	1.18	3.1
346	4	119	26.6	28.9	519	4	113	23.0	25.6	1.16	3.6
395	3	92	29.8	48.1	586	3	90	27.9	45.0	1.07	1.9
395	2	62	27.6	78.9	586	2	62	27.8	81.8	0.99	−0.2
395	1	35	34.8	..	586	1	34	33.9	..	1.03	0.9

With fish of such advanced age some errors in age determination almost certainly occurred. However, the rejection of all highly questionable scales must have minimized the possible effects of these errors. Although inaccurate scale readings may have contributed to the discrepancies between the calculated lengths of the 1923 and 1924 year classes, it is not believed that the observed differences are entirely the result of such errors.

<div align="center">GENERAL GROWTH</div>

<div align="center">GROWTH IN LENGTH</div>

The calculated lengths of all collections have been combined[21] to determine general curves of growth in length for the Nebish Lake rock bass (Table 19, Figs. 7, 8, and 9). The lengths of Table 19 are not the grand averages of the calculated lengths, but are rather the successive summations of the grand average increments ($\triangle$ L) of calculated growth in length. The use of grand average increments yields a smoother curve and one more in conformity with the actual data on growth in different years of life.

The data of Table 19 and Figures 7, 8, and 9 are general in the sense that they have been derived from all the reliable materials available. Information already presented on variations of growth among year classes (p. 229) and data to be presented later (p. 249) on annual fluctuations in growth rate are sufficient to prove that rock bass taken in another period of calendar years almost certainly would have yielded a slightly different general growth curve. The present general growth data must be recognized, therefore, as only roughly descriptive of the true typical growth, if indeed a clearly defined general growth curve can be said to exist at all.

The growth curves for the sexes have the same general form. The males nevertheless grow at a distinctly higher rate. The divergence of the growth curves for the sexes (Fig. 7) begins at the third year of life but is not distinctly noticeable until the fourth. The advantage of the males becomes more apparent in the light of comparisons as to the number of years required to

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[21] All II-group fish were excluded from the computations of general growth (p. 197).
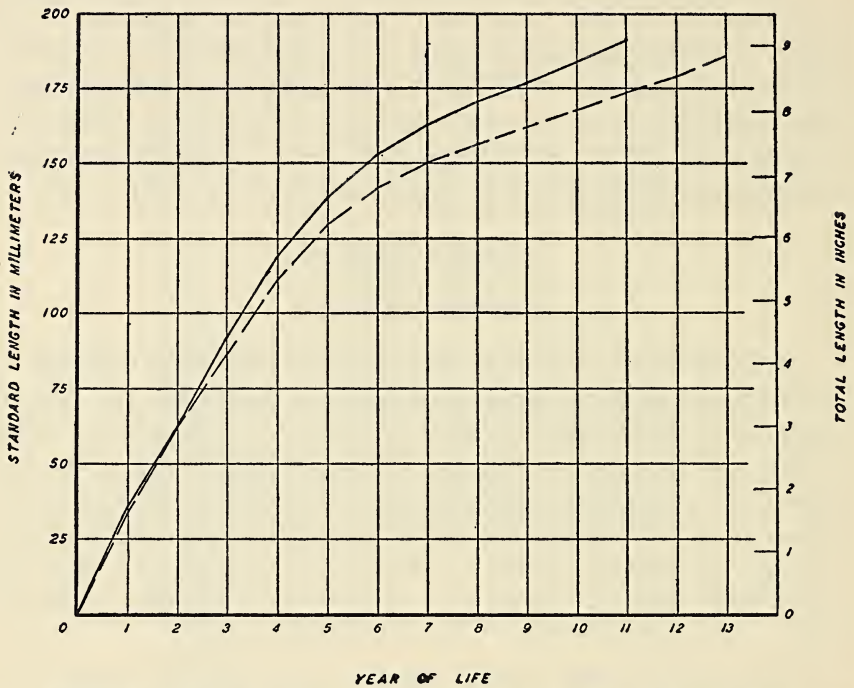
FIGURE 7. Grand average calculated length of the Nebish Lake rock bass at the end of each year of life. Solid line males, broken line females.

attain certain lengths. For example, males were 3 millimeters longer at the end of 6 years than females at the end of 7. At the end of 7 years of life the length of the males was 1 millimeter above the ninth-year length of females. In fact, at all ages beyond the sixth year, males were consistently longer than females that were 2 years older.

The ratios of the increments of the sexes and the differences between the increments (at extreme right at Table 19) show the relative and actual advantages of the growth of the males in different years of life. The greatest actual advantage of the males occurred in the fourth year (3.6 millimeters)—(See also, Fig. 8), but the relative advantage at that time was less than in all but two of the later years of life. The greatest relative advantage in the growth of the males was in the seventh year when the length increment of the males was 1.24 times that of the females.
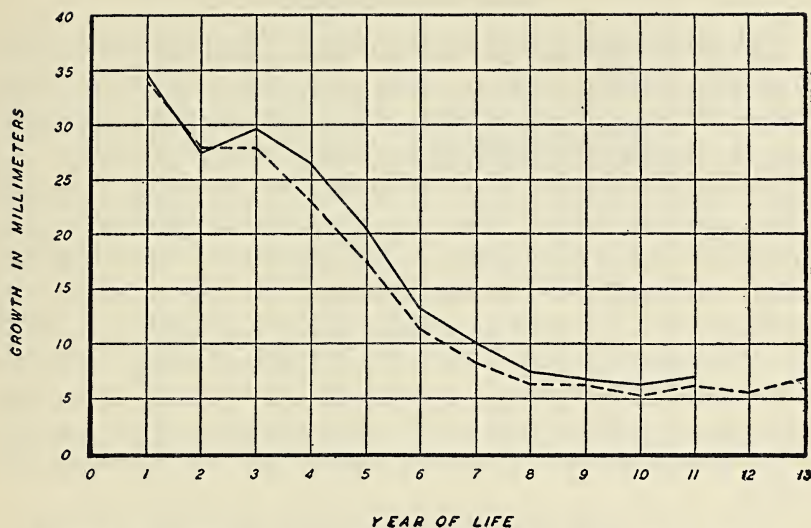
FIGURE 8. Calculated increments of the growth in length of the Nebish Lake rock bass in each year of life Solid line males, broken line females.

The growth of each sex in the first year was greater than in any other year of life. The length increment decreased in the second year and increased in the third. In the males this increase was sufficient to give the growth curve a definite inflection, but in the females it was too small to have any significance. The annual increments of growth in length of both sexes decreased continuously from the fourth to the eleventh year. (The equal eighth- and ninth-year increments of the females provide a single exception.) Both sexes showed improved growth in the eleventh year (only three male specimens). Only females were represented beyond the eleventh year; the increments of the twelfth and thirteenth years of life gave no indication of any pronounced further change in growth.

The rate of growth, as expressed by the annual percentage $\left(\dfrac{100\Delta L}{L}\right)$ increase (Fig. 9) declined continuously from the second to the eleventh year of life. The decrease was rapid in the earlier years. The annual percentage increase did not exceed 10 per cent beyond the fifth year in either sex, or 4 per cent beyond the eighth.

GROWTH IN WEIGHT

The data on general growth in weight (Table 20 and Fig. 10) correspond exactly with the data on general growth in length (Table 19) ; that is, the weights of Table 20 have been computed from the calculated lengths at the end of each year of life. The length-weight equation from which the computations were made is discussed on p. 311. The same equation was employed in the computations for both sexes. The positions of the empirical grand averages[22] for the age groups with respect to the computed curves of growth in weight also are indicated in Figure 10. (The lack of information on the length of males at the end of the twelfth year and of the females at the end of the fourteenth year makes impossible the determination of the positions of the points for the XI-group males and the XIII-group females.)
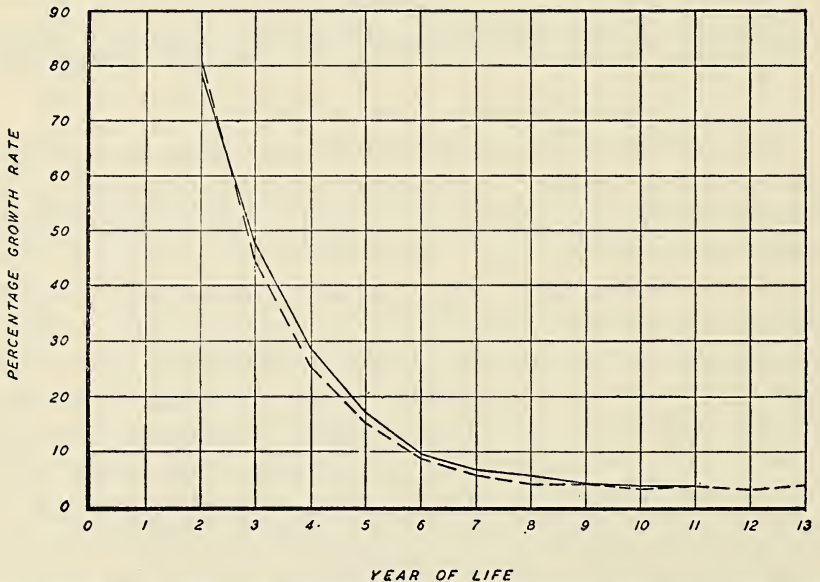
YEAR OF LIFE

FIGURE 9. Percentage increase in the calculated length of the Nebish Lake rock bass in each year of life. Solid line males, broken line females.

[22] The average weights of the age groups of the 1935 collection were not included in the empirical grand averages because of the disagreement of the length-weight relationship in 1935 with that of earlier years (p. 307). The grand average empirical weights for age groups that were represented in the 1935 collection were computed from the grand average empirical lengths (including the 1935 samples) and the grand average value of the coefficient of condition, K, for the collections of 1930, 1931, and 1932 (Table 58).

TABLE 20. *Calculated weight at the end of each year of life, annual increment of growth in weight, and annual percentage increase in weight of the Nebish Lake rock bass. The weights which correspond to the lengths of Table 19 were calculated from the equation,* $\log W = -4.54002175 + 3.003 \log L.$

Males					Females					Ratio of increments of sexes	Difference between increments of sexes
Number of fish	Year of life	Weight in grams	ΔW	$\frac{100\Delta W}{W}$	Number of fish	Year of life	Weight in grams	ΔW	$\frac{100\Delta W}{W}$		
					1	13	189	21	12.5		
					5	12	168	14	9.1		
3	11	204	22	12.1	21	11	154	15	10.8	1.47	7
18	10	182	20	12.3	72	10	139	15	12.1	1.33	5
79	9	162	16	11.0	195	9	124	13	11.7	1.23	3
207	8	146	19	15.0	320	8	111	12	12.1	1.58	7
254	7	127	22	21.0	396	7	99	15	17.9	1.47	7
269	6	105	26	32.9	430	6	84	20	31.2	1.30	6
322	5	79	30	61.2	488	5	64	22	52.4	1.36	8
346	4	49	26	113.0	519	4	42	21	100.0	1.24	5
395	3	23	16	228.6	586	3	21	14	200.0	1.14	2
395	2	7	5.8	483.3	586	2	7	5.9	536.4	0.98	−0.1
395	1	1.2	1.2		586	1	1.1	1.1		1.09	0.1

The superior growth of male rock bass is much more striking with respect to weight than length, although advantages of the males in terms of the number of years required to attain certain weights are of necessity the same as the advantages in the number of years required to reach the corresponding lengths (p. 234).

The years of life in which the males enjoyed the greatest actual and the greatest relative advantage in growth in weight were not the same. The greatest absolute advantage of 8 grams occurred in the fifth year but the greatest relative advantage was in the eighth (weight increment of males 1.58 times that of females). It will be noticed that these maximum advantages of the males with respect to growth in weight occurred one year later than the corresponding greatest advantages with respect to growth in length (fourth and seventh years of life—p. 234). It is true also that the relative advantages of the males were larger for growth in weight than for growth in length (larger ratios of increments in Table 20 than in Table 19). This greater relative advantage of the males in growth in weight accounts
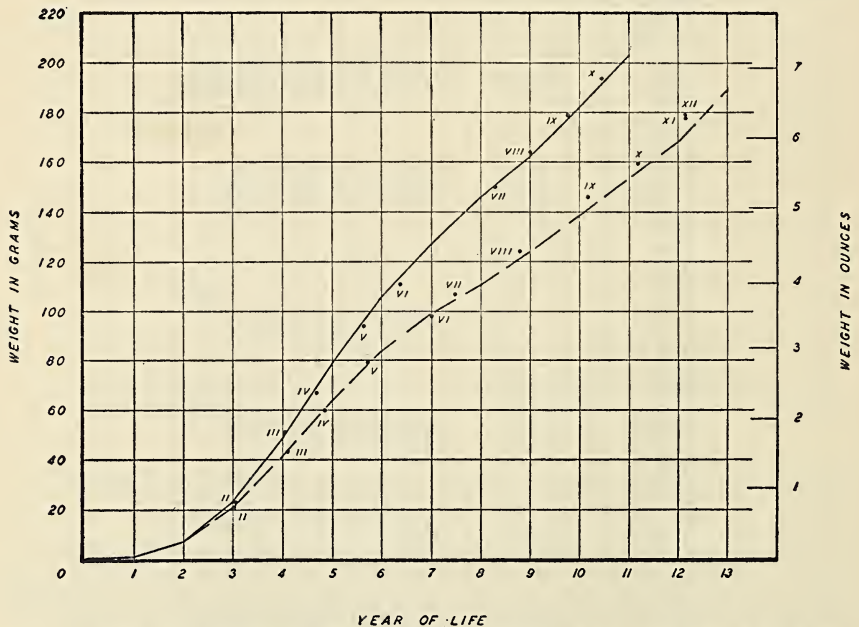

FIGURE 10. Calculated weight of the Nebish Lake rock bass at the end of each year of life. Solid line males, broken line females. The dots show the grand average weights the age-groups at capture.

for the pronounced divergence of the curves for the sexes in Figure 10.

The annual increments of growth in weight (ΔW) of both sexes increased continuously from the first year of life to a maximum in the fifth. The weight increments of the males decreased during the next four years of life but were large in the tenth and eleventh years. The changes in the increments of growth in weight of females beyond the fifth year were irregular. With the exception of the 21-gram growth in the thirteenth year (one fish) the annual weight increments of the females for all years of life later than the sixth fell within the range, 12 to 15 grams.

The percentage growth rate in weight in the second year of life was roughly 500 per cent for both sexes. The growth rate decreased rapidly in later years and did not exceed 20 per cent beyond the sixth year of life of the females or beyond the seventh year of life of the males.

COMPARISON OF THE GROWTH OF THE NEBISH LAKE ROCK BASS WITH THE GROWTH OF THE ROCK BASS IN OTHER LOCALITIES

Growth data based on the examination of scales of rock bass have been published by Wright (1929) for Trout and Muskellunge Lakes in northern Wisconsin and by Hile (1931) for Wawasee and Syracuse Lakes in northern Indiana. Trout Lake lies about 4 kilometers west of Nebish Lake and Muskellunge about 3 kilometers to the southwest.

Neither Wright nor Hile made a division of data according to sex. Hile made no growth calculations from scale measurements. Wright did present growth calculations from scale measurements, but based his calculations on the assumption that the ratio of body length to scale length (radius) is constant beyond the time of formation of the first annulus. Wright's data included no information as to growth in weight.

Because of the defects in the data presented by Wright and Hile, the most valid comparisons of the growth of rock bass in different localities appear to be those based on the average lengths (and weights, when available) of the age groups at capture, with the data for the sexes combined. This type of tabulation of available data on the growth of the rock bass appears in Table 21. The averages for the Trout Lake and Muskellunge

Lake rock bass are the weighted means of the averages given by Wright for his 1927 and 1928 collections separately. The combination of the 1927 and 1928 data from Trout Lake has been made in spite of Wright's expressed belief that the two collections, which were taken at different localities, represent distinct races within the lake. His belief was based on differences in the growth rate of the rock bass in the two collections. However, Wright had no sex records for his specimens; neither was he in position to determine the effect of gear selection on his samples. The relatively rapid growth of the Trout Lake rock bass taken in 1927 as compared to the fish captured in 1928 well may have resulted in a large measure from a great abundance of the more rapidly growing males in the sample and/or on the selective action of the fishing gear. The averages for the Lake Wawasee rock bass are based on the combination of scattered collections made over the 4-year period, 1926 to 1929. The 13 rock bass from Syracuse Lake all were taken during the summer of 1927.

TABLE 21. *Standard lengths (in millimeters) and weights (in grams) of the age groups of rock bass in collections from three northern Wisconsin and two northern Indiana lakes. The data for the sexes are combined. Numbers of individuals are in parentheses.*

Age group	Nebish		Trout	Muskel-lunge	Wawasee		Syracuse	
	Length	Weight	Length	Length	Length	Weight	Length	Weight
VII	161	123	146	139	230	349	..	..
	(123)	(123)	(27)	(57)	(4)	(4)	..	..
VI	152	108	131	125	227	365	..	..
	(49)	(49)	(42)	(74)	(1)	(1)	..	..
V	143	96	114	103	192	255	..	..
	(111)	(111)	(39)	(63)	(5)	(5)	..	..
IV	130	67	..	..	182	199	..	..
	(55)	(55)	..	..	(8)	(8)	..	..
III	117	46	..	..	147	107	129	72
	(116)	(116)	..	..	(10)	(10)	(1)	(1)
II	92	22	..	..	111	46	100	33
	(156)	(156)	..	..	(8)	(8)	(8)	(8)
I	..	..	..	..	55	5	59	6
	..	..	..	..	(20)	(14)	(4)	(4)

The growth of rock bass from northern Indiana is far superior to that of northern Wisconsin rock bass. As an illustration, the III-group rock bass from Lake Wawasee were longer than the V-group fish from Nebish Lake and the VII-group rock bass from Trout and Muskellunge Lakes. Comparisons of Table 21 with the data of Tables 9 and 10 reveal that the size of Wawasee rock bass of age-group V approximated the maximum at-

tained by Nebish Lake fish regardless of age, and that Wawasee rock bass older than age-group V were much larger than the largest fish taken from Nebish Lake. The growth of the rock bass from Syracuse Lake appears to resemble that of the Lake Wawasee population. Age-group I from Syracuse Lake averaged larger and age-group II smaller than Lake Wawasee fish of corresponding age. Only one fish of age-group III was captured in Syracuse Lake.

That relatively good growth may be characteristic of the rock bass in the lakes of northern Indiana is suggested by Evermann and Clark's (1920) observation that in Lake Maxinkuckee the, ". . . . Rock Bass . . . reaches a length of about 12 or 13 inches and a weight of a little less than one pound. The great majority of those caught weigh a half pound or less." In Nebish Lake very few rock bass attain a weight of a half pound.

We can only speculate as to the causes for the superior growth of the rock bass from northern Indiana. Possible contributing factors are higher water temperatures (and in consequence, a probably longer growing season), more abundant food, lesser population densities, and a hereditarily greater capacity for growth.

A comparison of the growth of rock bass in the three northern Wisconsin lakes reveals that the growth of the Nebish Lake stock is superior to that of rock bass in the two neighboring lakes, Trout and Muskellunge. In the age groups for which comparisons are available the advantage of the Nebish Lake fish amounts to roughly two years of growth.

The rock bass is the third species from the lakes of northeastern Wisconsin in which the best growth has been found to occur in a lake with a relatively low productive capacity as estimated from the concentration of bound CO_2 in its waters. A summary of the relationship between the growth rates of the yellow perch, the cisco, and the rock bass in certain northeastern Wisconsin lakes and the average concentration of bound CO_2 in the surface waters is given in Table 22. The growth of the yellow perch was studied by Schneberger (1935) and that of the cisco by Hile (1936a).

In general, the growth rates (in length) of the different stocks of the three species tend to vary inversely with the esti-

TABLE 22. *Relationship between the rate of growth (in length) of three species of fish and the concentration of bound CO_2 (average surface conditions) in parts per million in certain lakes of the northeastern highlands, Wisconsin. In the order of growth rate the stock with the slowest growth has been assigned the value 1.*

Lake	Concentration of bound CO_2 in p.p.m.	Rate of growth		
		Perch	[2]Cisco	Rock bass
Weber	[1]1.2	2	..	..
Clear	[1]2.2	..	4	..
Nebish	4.0	3	..	3
Muskellunge	10.0	..	3-2	1
Silver	15.0	1	2-3	..
Trout	18.5	..	1	2

[1] These values apply to the lakes at the time of the collection of material for the study of the rate of growth. Since the addition of lime in 1933 and 1934 the concentration of bound CO_2 in Weber Lake has stood at 2.0 p.p.m. Since 1935 the average value for Clear Lake has been 2.5 p.p.m.

[2] The positions of the Muskellunge Lake cisco and the Silver Lake cisco, respectively, were 2 and 3 with respect to growth in weight and 3 and 2 with respect to growth in length.

mated productive capacities of the lakes they inhabit. In the cisco the inverse relationship holds without exception. The order of the four lakes with respect to the rate of growth in length of their cisco populations (from the most rapidly to the most slowly growing) is precisely the reverse of their order with respect to the concentration of bound CO_2 in the surface waters. The relationship is not so clear-cut for the perch and rock bass. The best growth of perch does not occur in the lake with the lowest concentration of bound CO_2, but the poorest growth is to be found in the lake that is richest in bound CO_2 (Silver Lake). With reference to the rock bass, the lake with the lowest concentration of bound CO_2 (Nebish Lake) does contain the most rapidly growing population but the poorest growth does not occur in the lake with the highest estimated productive capacity (Trout Lake). However, neither the perch nor the rock bass enjoyed its best growth in the lake with highest estimated productive capacity or its poorest growth in the lake with the lowest estimated productive capacity. It is significant that the three species that show a correlation of good growth with a low concentration of bound CO_2 represent three different families— Percidae, Coregonidae, and Centrarchidae.

Schneberger and Hile were able to demonstrate also a correlation between the growth rates and population densities of the

perch and cisco, respectively. The general relationship was such that lakes with high concentrations of bound CO_2 had dense populations with a poor rate of growth, whereas the population was sparse and the growth rate good in lakes with low concentrations of bound CO_2. Schneberger made no definite statement as to the probable manner in which the population density may affect the growth rate of perch. Hile suggested that the correlation between population density and the rate of growth in the cisco ". . . may depend on differences in the severity of the competition for food, or upon the operation of a 'space-factor', whereby crowding impedes growth independently of the abundance of food."

There are at present no data available for the detection of a possible correlation between the growth rates and population densities of rock bass in the three northern Wisconsin lakes. In a later section of this paper (p. 275), however, evidence will be presented for a possible correlation between annual fluctuations in the growth rate and the population density of the Nebish Lake rock bass stock.

Fluctuations in the Abundance of Year Classes and in Growth Rate

Abundance of Age Groups and Year Classes

A tabulation of the age and year-class composition of each year's collection of the Nebish Lake rock bass appears in Table 23. At the bottom of the table may be seen the numerical and percentage representations of the different year classes for all collections combined. In order to keep the large 1931 and 1932 collections comparable, the samples taken by hook and line, which method tended to capture only the larger and older fish, were excluded from the compilations of data for those years. The specimens taken by hook and line were retained, however, in the compilation of the 1930 data since it was believed that their inclusion would compensate the small amount of fishing with large-mesh gill nets (p. 194) and thus make the 1930 data more nearly comparable with those of later years. No rock bass were taken by hook and line in 1935. Since the percentage occurrence of the age groups and year classes of the males and

TABLE 23. *Numerical and percentage representation of the year classes of the Nebish Lake rock bass in the different years' collections and in all collections combined.*

Year of Capture	Item	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	Total
1930	Age group	…	X	IX	VIII	VII	VI	V	IV	III	II	…	…	…	…	…
	Number of males	…	…	2	3	15	3	9	9	…	…	…	…	…	…	41
	Number of females	…	1	2	8	43	6	6	9	…	…	…	…	…	…	75
	Number, sexes combined	…	1	4	11	58	9	15	24	9	21	…	…	…	…	152
	Percentage	…	0.7	2.6	7.2	38.2	5.9	9.9	15.8	5.9	13.8	…	…	…	…	…
1931	Age group	XII	XI	X	IX	VIII	VII	VI	V	IV	III	II	…	…	…	…
	Number of males	…	…	4	18	115	27	5	8	3	6	10	…	…	…	196
	Number of females	1	2	17	47	99	24	11	7	5	7	9	…	…	…	229
	Number, sexes combined	1	2	21	65	214	51	16	15	8	14	60	…	…	…	467
	Percentage	0.2	0.4	4.5	13.9	45.8	10.9	3.5	3.2	1.7	3.0	12.9	…	…	…	…
1932	Age group	XIII	XII	XI	X	IX	VIII	VII	VI	V	IV	III	II	…	…	…
	Number of males	…	…	3	10	40	7	3	3	8	7	41	78	…	…	200
	Number of females	1	3	13	33	68	9	6	6	2	9	59	59	…	…	268
	Number, sexes combined	1	3	16	43	108	16	9	9	10	16	100	137	…	…	468
	Percentage	0.2	0.7	3.4	9.2	23.1	3.4	1.9	1.9	2.1	3.4	21.4	29.3	…	…	…
1935	Age group	…	…	…	…	…	XI	X	…	VIII	…	VI	V	IV	III	…
	Number of males	…	…	…	…	…	…	1	…	…	…	4	28	5	…	38
	Number of females	…	…	…	…	…	1	…	…	1	…	9	43	8	1	63
	Number, sexes combined	…	…	…	…	.	1	1	…	1	…	13	71	13	1	101
	Percentage	…	…	…	…	…	1.0	1.0	…	1.0	…	12.9	70.2	12.9	1.0	…
All collections	Males, all age groups	…	…	9	31	170	37	18	20	11	13	55	106	5	…	475
	Females, all age groups	2	6	32	88	210	40	23	22	8	16	77	102	8	1	635
	Sexes combined, all age groups	2	6	41	119	380	77	41	48	28	51	173	208	13	1	1,188
	Percentage	0.2	0.5	3.4	10.0	32.0	6.5	3.4	4.0	2.4	4.3	14.6	17.5	1.1	0.1	…

females were similar the data for the sexes were combined for the computation of the percentages.

In all years' collections the representations of the different age groups were decidedly unequal. In 1930, 58 or 38.2 per cent of the total collection of 152 rock bass were in the eighth year of life (age-group VII). No other age group, older or younger, contained even half as many fish. Still more striking was the dominance of the 1931 VIII-group which made up 45.8 per cent of the entire collection and contained more than three times as many fish as the next strongest age group (age-group IX). There was a less pronounced dominance in 1932. The dominant II-group (29.3 per cent of the total) was only slightly stronger than age-groups IX and III (23.1 and 21.4 per cent respectively, of the total collection). The 1935 collection contains the outstanding example of overwhelming dominance of a single age group. In this year 70.2 per cent of the rock bass were in the sixth year of life (age-group V).

On the whole, 1930-1932 collections were characterized by an abundance of old fish (age-group VII and older) and a scarcity of fish of medium age (age-group IV to age-group VI). Age-group II was fairly well represented (12.9 to 29.3 per cent) in all years but only the 1932 material contained a large number of III-group rock bass. Exceptions to the above general statement are offered by the weak VII- and VIII-groups of 1932 and the relatively strong 1930 IV-group. The distribution of ages in 1935 was precisely the reverse of conditions in 1930 to 1932. In 1935, 96.0 per cent of the rock bass belonged to age-groups IV, V, and VI.

The examination of the percentage distributions of the age groups in relation to their year of origin suggests that the unequal representations of the different age groups may be in large measure due to the varying degrees of success of natural reproduction in different calendar years. For example, the 1923 year class which was dominant in 1930 (age-group VII) and 1931 (age-group VIII) and was still strong as the 1932 IX-group must have been very abundant. The 1930 year class also appears to have been strong in numbers. This year class provided the dominant II-group of 1932 and accounted for 70.2 per cent of the 1935 collection. The 1927 year class on the other hand must

have been relatively weak since it was poorly represented in all years' collections.

Although the data of Table 23 point rather conclusively to the presence of relatively rich and poor year classes in the Nebish Lake rock bass population, they do not provide an exact measure of the true relative strength of the year classes. The most important difficulties in the interpretation of the material are related to the disturbing effect of the age at which the year classes appeared in the collections and to gear selectivity. As an illustration of the significance of age it may be pointed out that the 16 XI-group rock bass of the 1932 collection indicate a far greater original abundance for the 1921 year class than the 16 IV-group fish indicate for the 1928 year class. The two year classes were represented by equal numbers of fish in the collection, but at the time of sampling the 1921 year class had been subjected to 7 more years of natural mortality, not to mention the greater exposure to fishing. Consequently the 1921 year class safely can be held to have been originally much the stronger. The percentage representation of the two year classes in all collections combined (1921—3.4 per cent; 1928—4.3 per cent) gives no cause to doubt the above conclusion. Assuming that the samples are adequate, it is true generally that a strong representation of an old age group indicates a much richer year class than does an equally large number of fish several years younger. On the other hand, a scarcity of old fish may be merely the result of natural mortality over a long period of years, whereas a scarcity of fish in a young age group is definitely suggestive of a poor year class.

The effect of gear selection also has an important bearing on the interpretation of the data of Table 23. It has been stated already (p. 197) that the smaller II-group fish are not taken readily by gill nets. As a result the II-group samples all probably contained too few fish. Furthermore, the failure of the gear to take any I-group and 0-group fish caused certain year classes to be totally absent in some years' collections. The 1929 and 1930 year classes were not represented in the 1930 material, and the members of the latter year class were lacking also in 1931. The 1931 and 1932 year classes either were not yet hatched or were too small to be captured at the time of all but the 1935 col-

lections. The effect of gear selection was doubtless much less severe among the older fish, although there is reason to believe that the addition of a mesh size larger than those employed would have led to the capture of more old fish, especially in 1932 (p. 197).

Despite the obvious defects in the data the differences in the representation of the several year classes are so great that a number of them can be classified reasonably safely by such terms as strong, weak, or of moderate strength. The following estimate of the relative abundance of the year classes was based on the careful examination of their representation in the different years' collections with allowance made for age at capture and the probable effect of gear selection. The year classes have been arranged in their estimated order of abundance from the strongest to the weakest.

Exceptionally strong year classes

1923 year class—was dominant as the 1930 VII-group (38.2 per cent) and as the 1931 VIII-group (45.8 per cent) and was very strong as the IX-group of 1932 (23.1 per cent). The great abundance of the year class at such high ages marks it as one of unusual strength.

1930 year class—was dominant in the 1932 collection (29.3 per cent) and made up 70.2 per cent of the 1935 collection. Although there are no gear records for the 1935 material, the statement by the collectors that nets of several sizes of mesh were fished (p. 194) and the excessive abundance of the V-group leave little doubt as to the great strength of the 1930 year class.

Moderately strong to normal year classes

1922 year class—in spite of its advanced age at capture (VIII to X), had a representation of 7.2 to 13.9 per cent in the 1930-1932 collections and made up 10.0 per cent of all collections combined.

1921 year class—was not very strongly represented (2.6 to 4.5 per cent) in the 1930-1932 collections but even this small representation at ages from IX to XI marks the year class as fairly strong. The 1921 year class was probably consider-

ably weaker than the 1922 year class.

Normal to moderately weak year classes

1929 year class—contributed the strongest III-group (21.4 per cent in 1932) but was not exceptionally abundant as the 1931 II-group (12.9 per cent) and the 1935 VI-group (12.9 per cent).

1924 year class—had a fair representation as the 1931 VII-group (10.9 per cent) but was relatively weak as the 1930 VI-group and as the 1932 VIII-group (5.9 and 3.4 per cent, respectively).

Exceptionally weak year classes

1926 year class—was moderately abundant as the 1930 IV-group (15.8 per cent), but this good representation was counterbalanced by the low percentages in 1931 and 1932 (3.2 and 1.9 per cent, respectively).

1925 year class—was fairly strong as the 1930 V-group (9.9 per cent) but was weak in 1931 and 1932 (3.5 and 1.9 per cent, respectively).

1928 year class—as the age-group II made up 13.8 per cent of the 1930 collection but was weak in 1931 and 1932 (3.0 and 3.4 per cent, respectively).

1927 year class—was poorly represented in all collections (from 1.7 to 5.9 per cent over the period, 1930 to 1932) and accounted for only 2.4 per cent of all collections combined.

Year classes of uncertain strength

1919 and 1920 year classes—were represented by such old fish (X to XIII) that it is impossible to judge accurately whether their scarcity is to be attributed to great age or to originally weak year classes.

1931 and 1932 year classes—could not be evaluated satisfactorily since their occurrence was limited to the 1935 collection for which gear records are lacking.

The order of arrangement of the year classes in the preceding outline is to a certain extent a matter of personal judgment, and

may not conform exactly to the true conditions. Decisions concerning the ranking of certain year classes were extremely difficult to make. Nevertheless, the following general summary may be considered valid. Relatively abundant year classes were produced over the period 1921 to 1923; the 1923 year class was phenomenally successful. The 1924 year class was much less abundant than the 1923 year class but was stronger than the exceptionally weak year classes of 1925 to 1928. The 1929 year class was more abundant than those of the four preceding years, and the 1930 year class was again one of exceptional strength. The fluctuations in abundance of the year classes offer a suggestion of a cycle with maxima in 1923 and 1930.

ANNUAL DIFFERENCES IN GROWTH RATE

Materials for the study of annual fluctuations in the growth rate of the Nebish Lake rock bass may be found in Tables 24 and 25. The arrangement of the tables is such that the vertical columns show the (calculated) growth made by fish in different years of life but in the same calendar year, and the horizontal rows offer a comparison of the growth in different calendar years for the same year of life. Each diagonal row gives the growth history of a single year class. For example, the males of the 1921 year class grew 38 millimeters in the first year of life (1921), 32 millimeters in the second (1922), 31 millimeters in the third (1923) . . . .

The plus and minus signs which have been introduced to facilitate the examination of the data indicate whether a particular growth increment is greater or less than the corresponding growth increment for the preceding calendar year. As an illustration, the 31-millimeter growth made by males in the second year of life in 1923 was less than the 32-millimeter growth made by fish of the same age in 1922. Consequently the 31 has been followed by a minus sign. Similarly the 26-millimeter increment of the second-year fish in 1924 represents a further decrease. The growth of the second-year rock bass improved, however, in 1925, and the 30 was followed by a plus sign. Where there was no change the sign was omitted.

The annual fluctuations in the growth of the first year of life are so obviously independent of those of later years that in the

TABLE 24. *Annual increments of growth in length (in millimeters) of the males of the various year classes of the Nebish Lake rock bass.*

Year of life	Increment of growth in calendar years											Unweighted mean
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	
11											7	7
10										6	7+	6
9									6	6	8+	7
8								6-	6	8+	7-	7
7							10+	8-	10+	10	15+	11
6						12-	15-	13-	13	17+	19+	15
5					19-	21+	20+	20	23+	22-	28+	22
4				24-	23+	27+	27	24-	30+	28	33+	27
3			31-	28-	30+	30	26-	23-	29+	32+	34+	29
2		32+	31-	26-	30-	23-	22-	22	27-	31+	28-	27
1	38	39+	37-	40+	33	30-	29-	31+	29-	31+	29-	33
Number of fish taken in year 1930	2	3	15	3	9	9						41
1931	4	18	117	27	5	8	3	6				188
1932	3	10	41	8	5	3	8	7	43			128
1935					1				4	28	5	38
Total	9	31	173	38	20	20	11	13	47	28	5	395

TABLE 25. *Annual increments of growth in length (in millimeters) of the females of the various year classes of the Nebish Lake rock bass.*

Year of life	Increment of growth in calendar years												Unweighted mean
	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	
12												7+	7
11											4	8+	6
10										4−	4	7+	5
9									7	5	5+	8+	6
8								6+	6	6	7+	7	6
7							6	8+	8	8	8	12+	8
6						9	11+	11−	11	12+	14+	20+	13
5					15	15	18+	17−	17	19+	21+	21	18
4				28−	22−	21−	23+	22−	22	25+	26+	30−	24
3			31	30−	28−	28	27−	24−	20−	24+	31+	30−	27
2		28+	32+	32	26−	30+	24−	23−	21−	24−	30+	28−	27
1	32	36+	36	36	36	35−	30−	30	30	29−	29	28	32
Number of fish taken in year 1930	1	2	8	43	6	6	9	5	7				75
1931		17	47	99	24	11	7	2	9	59			219
1932	3	13	33	74	17	9	8	1		9			227
1935					1						43	8	62
Total	6	32	88	216	48	26	24	8	16	68	43	8	583

discussions of changes in growth rate the first-year growth and
that of the second and later years of life have been treated sep-
arately.   The growth beyond the first year will be considered
first.

Growth in the Second and Later Years of Life

The increments of Tables 24 and 25 demonstrate that the
amount of growth made by fish in a particular year of life is
subject to a wide variation from year to year.   The second-year
growth of the males varied from 22 millimeters in 1927 and 1928
to 32 in 1922; that of the females ranged from 21 millimeters
in 1928 to 32 in 1922 and 1923.   Similar fluctuations occurred in
the growth increments of both sexes in later years of life.

It may be seen also that in some calendar years the growth
increments tended to increase or decrease consistently in com-
parison with corresponding increments of the preceding year
and, further, that in certain years the amount of growth made
by rock bass at all ages (exclusive of the first year) tended con-
sistently to be relatively high or low.   Six comparisons are pos-
sible between the growth of male rock bass in 1927 and 1928
(Table 24).   In four years of life (third, fourth, sixth, and sev-
enth) the 1928 growth was below that of 1927.   The remaining
two comparisons (second and fifth years) showed no differences.
Furthermore, the 1928 growth increments were generally lower
than those for fish of the same age in other calendar years.   The
1929 growth, on the other hand, showed improvement in five of
the seven comparisons with 1928.   Growth in 1929 can not be
described, however, as outstandingly good.   The most consist-
ently large growth increments occurred in 1931.   The data for
some years contain certain inconsistencies.   The comparison of
the growth increments of 1924 and 1925, for example, shows
one decrease (fourth year) and two increases (second and third
years) in 1925.   Similarly, two of the 1926 growth increments
were greater than those of 1925, one increment was less, and one
was the same.

The fluctuations in the growth of the females (Table 25)
bear a general resemblance to those of the males.   As was true
for the males, the growth of the females in 1928 was generally
poor, although the decrease in comparison with 1927 was not as

great as for the males; improvement in growth was general in 1929; the 1931 growth increments were exceptionally large; and the data for certain years (as 1925 and 1926) did not give consistent indication of improvement or decline in growth.

Certain generalizations concerning growth in the second and later years of life can be drawn safely from the data of Tables 24 and 25. The growth of both males and females was fairly good in 1922 and 1923. The year 1924 saw the beginning of an irregular but definite downward trend in growth that culminated in the very poor growth of 1927 and 1928. A sharp upturn in growth rate occurred in 1929. This improvement continued through 1931 in which year the growth was exceptionally good.

The description in the preceding paragraph, although valid, does not provide a very precise measure of annual fluctuations in the growth of the rock bass. Consequently, a detailed analysis was made of the growth data in order to determine more exactly the extent to which growth rate varied from year to year. The procedure consisted of the determination of the percentage change in the growth in each year in comparison with the growth of fish in corresponding years of life in the preceding year. Details of the method will be explained in the following paragraphs.

Table 24 shows that comparisons of the growth of males beyond the first year of life in 1922 and 1923 must be limited to the second-year increments of 32 millimeters and 31 millimeters respectively. These increments have been listed in Table 26 under the headings, "Growth in earlier year", and "Growth in later year". The mean of the increments is 31.5 millimeters, and the decrease of 1 millimeter in 1923 represents a change of —3.2 per cent from this mean.[23] The increments of growth for both

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[23] The desirability of computing the percentage change in growth from the mean growth of the two years that are being compared rather than from the growth in the earlier of the two years may be seen from the following example. Let it be assumed that the growth increments of three consecutive years are 10, 8, and 10 millimeters. Growth in the second of the three years declined 20 per cent from growth in the first, and growth in the third year improved 25 per cent with respect to growth in the second. The successive addition of the percentages to determine the position of each year as to the quality of growth gives the following rankings for the three years: 0.0; —20.0; 5.0. Growth in the third year appears to have been better than that in the first. When the mean growth of the years that are being compared is employed for the computation of the percentage change in growth, the percentages for the three years are: 0.0; —22.2; 0.0.

the second and third years of life are available for the determination of the change in growth in 1924 as compared to 1923. In 1923 the combined second- and third-year growth increments of the male rock bass (31 and 31) gave a "total" growth of 62 millimeters. The 1924 growth was 26 millimeters for the second-year rock bass and 28 millimeters for the third-year fish. The "total" growth was 54 millimeters, a decrease of 8 millimeters. This difference was —13.8 per cent of the 1923-1924 mean "total" growth of 58 millimeters. The determination of the change in growth in each of the later years with respect to the growth of the year immediately preceding was made by a continuation of the above process. Each increase or decrease in "total" growth was expressed as a percentage of the mean total growth. The more recent the year under consideration the greater was the number of years of life involved in the determination.

TABLE 26. *Tabulation of data employed in the determination of annual fluctuations in the growth of male Nebish Lake rock bass. For explanation see text.*

Years involved in the comparison	Growth in earlier year	Growth in later year	Mean	Change in growth	Percentage change in growth
1922 and 1923	32	31	31.5	—1	—3.2
1923 and 1924	62	54	58.0	—8	—13.8
1924 and 1925	78	83	80.5	5	6.2
1925 and 1926	102	101	101.5	—1	—1.0
1926 and 1927	113	110	111.5	—3	—2.7
1927 and 1928	120	110	115.0	—10	—8.7
1928 and 1929	116	138	127.0	22	17.3
1929 and 1930	144	154	149.0	10	6.7
1930 and 1931	160	179	169.5	19	11.2

The percentage changes in growth in Table 26 were employed first to fix the position of each year with reference to "goodness of growth" in 1922. The 1923 growth was 0.0 — 3.2 = —3.2 per cent below the 1922 level; the 1924 growth was 0.0 — 3.2 — 13.8 = —17.0 per cent below that of 1922; the 1925 growth was 0.0 — 3.2 — 13.8 + 6.2 = —10.8 per cent below the 1922 growth; . . . However, the 1922-1931 mean of the percentages determined in this manner was —7.4, and the growth of the male rock bass in 1922 must have been 7.4 per cent above the 10-year average and not exactly average (0.0) as assumed originally. The deviation of each year's growth from the 1922 growth was

TABLE 27. *Deviation of the growth of the Nebish Lake rock bass in different calendar years from the average for the 10-year period, 1922-1931. (First-year growth was excluded from the computations).*

Sex	Percentage deviation from average growth in calendar year									
	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931
Male	7.4	4.2	—9.6	—3.4	—4.4	—7.1	—15.8	1.5	8.2	19.4
Female	9.9	8.3	—8.6	—5.4	—5.4	—9.1	—14.7	—5.3	8.6	21.7
Average	8.6	6.2	—9.1	—4.4	—4.9	—8.1	—15.2	—1.9	8.4	20.6

converted, therefore, to a deviation from the 1922-1931 average growth by the addition of 7.4 per cent. These deviations from average growth are listed in Table 27. The procedure for the computation of the annual deviations of the growth of female rock bass from the average (listed in the same table) was identical with that just outlined for the males. The annual percentage deviations of the growth of both sexes from the 1922-1931 average are presented graphically in Figure 11.

The annual deviations of the growth of male and female rock bass from the 1922-1931 average agreed remarkably well. The close correspondence speaks well for the reliability of the original data and of the method employed, since the two sets of percentages were derived independently and from groups of fish with basically different rates of growth. (The males grow more rapidly than do the females.) The means of the percentage deviations of the sexes from the average growth (bottom of 27) may be used to describe the annual fluctuations in the growth of the Nebish Lake rock bass.

FIGURE 11. Annual percentage deviation of the growth of the Nebish Lake rock bass (in the second and later years of life) from the average for the period, 1922-1931. Solid line males, broken line females.

The growth of these rock bass stood at 8.6 per cent above average in 1922.   A slight decline in 1923 was followed by a sharp drop to 9.1 per cent below average in 1924.   Growth improved somewhat in 1925, although it was still below average, and remained at approximately the 1925 level in 1926.   New declines in 1927 and 1928 reduced the growth to 15.2 per cent below average in the latter year.   The next three years saw a rapid and consistent improvement which carried the growth to a point 20.6 per cent above average in 1931.

Possibly the most striking feature of the data on annual fluctuations in the growth of the Nebish Lake rock bass is the rapid improvement in growth from 15.2 per cent below average in 1928 to 20.6 per cent above average in 1931—a total change of 35.8 per cent of the average.   Extensive changes in the growth rates of fish populations have been reported frequently, but these changes usually have been associated with disturbances within the population contingent upon the intensification or relaxation of fishing activities.   The fluctuations in the growth of the Nebish Lake rock bass, on the contrary, may be considered representative of changes that occur under natural conditions, since there is no commercial fishery in the lake and the number of fish removed by anglers, prior to 1934 at least, was negligible. (The formerly rough and narrow road leading to Nebish Lake was improved in that year.)

Data that cover only a 10-year period are not adequate to demonstrate the presence or absence of cycles in the rate of growth.   It should be mentioned, however, that 2 years of growth above average at the beginning of the period were followed by a period of 5 or 6 years of "subnormal" growth (the classification of 1929 must be held questionable), and that these poor-growth years were succeeded in turn by 2 or 3 years in which growth was again near or above average.

Only scattered data are available on annual fluctuations in growth outside the period, 1922 to 1931.   An estimate of the growth in 1921 may be had from the second-year growth of females (Table 25).   From the 1921 and 1922 increments of 28 and 32 millimeters respectively it may be computed that 1921 growth was 13.3 per cent below 1922 growth or 3.4 per cent below the 1922-1931 average.

The growth history of the abundant 1930 year class, as represented in the 1935 collection (age-group V) provides some information as to growth in the three years, 1932 to 1934. This same collection contained small representations of other year classes, but the lack of gear records in 1935 and the consequent lack of information concerning the probable selective action of the nets make it advisable to confine the analyses of the 1932-1934 growth to the data of the single well represented group.

The orientation of the growth of the 1930 year class in different calendar years with respect to the 1922-1931 average has been based on comparisons of the growth increments of the year class with the growth increments of fish in corresponding years of life over the period, 1925 to 1931. This period is the longest for which growth data are available for both sexes for all years of life involved (third, fourth, and fifth—see Tables 24 and 25). As an illustration of the procedure, in 1932 the males of the 1930 year class, then in their third year of life, grew 30.3 millimeters as compared with the 1925-1931 average of 29.1 millimeters for fish in their third year (Table 28). The deviation of the growth of the 1930 year class from the 1925-1931 growth was 4.0 per cent, but since the mean deviation of the 1925-1931 growth of male rock bass from the 1922-1931 average was —0.2 per cent (as determined from Table 27), the deviation of the 1930 year-class growth from the same 10-year average was 4.0 — 0.2 or 3.8 per cent. Similarly the growth of the 1930 year-class males in their fourth year of life in 1933 had a deviation of 3.6 per cent from the average 1925-1931 growth for the same year of life and therefore of 3.4 per cent from the 1922-1931 average.

By the same procedure the 1932 growth of the females was found to deviate 7.3 per cent from the average 1925-1931 growth of female rock bass in their third year of life. The percentages of Table 27, however, showed that the 1925-1931 growth of female rock bass was 1.4 per cent below the 1922-1931 average. Therefore the percentage deviation of the growth of the 1930 year class in 1932 from the 1922-1931 average was 7.3 — 1.4 = 5.9.

The agreement between the sexes with respect to the percentage departure from average growth over the period, 1932 to 1934, was only fair. The greatest discrepancy occurred in 1934

TABLE 28. *Growth increments (millimeters) of the 1930 year-class rock bass, in the years, 1932-1934, compared with average growth of fish in corresponding years of life, 1925-1931, together with estimates of the percentage deviation of the growth of 1930 year-class fish in different calendar years from the 1922-1931 average. The calendar years of the heading apply to the 1930 year class only.*

Item	Year of life and/or Calendar year		
	3	4	5
	1932	1933	1934
Growth of 1930 year-class males	30.3	28.4	19.3
Growth of males (1925-1931) in corresponding year of life	29.1	27.4	21.9
Deviation of 1930 year-class growth from 1922-1931 average	3.8	3.4	—12.8
Growth of 1930 year-class females	28.3	25.6	17.3
Growth of females (1925-1931) in corresponding year of life ..	26.3	24.1	18.3
Deviation of 1930 year-class growth from 1922-1931 average ..	5.9	4.6	—7.0
Deviation of 1930 year-class growth (average for sexes)	4.8	4.0	—9.9

in which year the percentages were —12.8 for the males and —7.0 for the females. The trends were the same, however, for both sexes. It appears valid, therefore, to conclude that the peak growth of 1931 was followed by a 3-year period of decline in growth rate.

Fluctuations in First-Year Growth

On p. 249 it was stated without explanatory discussion that the first-year growth of the Nebish Lake rock bass was "obviously independent" of growth in the second and later years of life. The examination of Tables 24 and 25 will reveal that the chief disagreement between the annual variations of first-year and later growth lay in the failure of the young of the year to share the general improvement in growth in the years, 1929 to 1931. It is true also that first-year growth was good in 1924 and 1925—years in which the growth of older fish was below average.

Details concerning annual variation in the first-year growth of Nebish Lake rock bass are presented in Table 29. The percentage deviations have been calculated with reference to the average first-year growth for the 10 years, 1922 to 1931.[24] The use of this period makes the percentages directly comparable with those for growth in the later years of life (Table 27).

[24] The averages were 32.8 millimeters for the males and 31.9 millimeters for the females.

TABLE 29. *Percentage deviations of first-year growth of the Nebish Lake rock bass in different calendar years from the 1922-1931 average.*

Sex	Percentage deviation from average growth in calendar year											
	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931
Male	..	15.9	18.9	12.8	22.0	0.6	—8.5	—11.6	—5.5	—11.6	—5.5	—11.6
Female	0.3	12.9	12.9	12.9	12.9	9.7	—6.0	—6.0	—6.0	—9.1	—9.1	—12.2
Average	0.3	14.4	15.9	12.8	17.4	5.2	—7.2	—8.8	—5.8	—10.4	—7.3	—11.9

Although the percentages for the sexes in Table 29 do not agree in detail, the general trends in the annual variation in first-year growth are similar. It appears to be justifiable to describe the yearly changes in first-year growth from the average percentages for the sexes. The growth of the first-summer rock bass was approximately at the 1922-1931 average in 1920. Growth improved in 1921 and 1922, fell back a little in 1923, and reached a maximum in 1924 (17.4 per cent above average). Two successive years of sharp decline reduced first-year growth from the 1924 peak to a point 7.2 per cent below average in 1926. Beyond this year the variations were irregular but growth was consistently below average. The poorest first-year growth of the 12-year period was made in 1931, the year in which older fish enjoyed their best growth. The comparison of the percentages of Table 29 with those of Table 27 substantiates fully the earlier contention that the annual fluctuations in first-year and later growth are independent.

At one time the possibility was considered that the disagreement between the annual fluctuations of first-year and later growth may have originated, in part at least, in some defect in the method of growth calculation. Since all collections were made in 1930 to 1932 and in 1935, it follows that in general, the more recent the calendar year for which growth was computed, the lower was the average age of the fish on which the calculations of first-year growth were based. Now if the method of growth calculation contained a defect whereby the older fish tended to have the larger calculated lengths at the ends of the first year, the consistently poor first-year growth in the more recent calendar years could be explained as apparent rather than real. To test this possibility a series of comparisons has been made between calculated lengths at the end of the first year

of life and the corresponding measurements of the anterior radius of the scale to the first annulus (Table 30).

TABLE 30. *Comparison of the average calculated lengths of rock bass of several age groups at the end of the first year of life with the body lengths corresponding to the average lengths of the anterior radii of key scales to the first annulus. The scales were measured at the magnification, X 40.5.*

Sex	Age group	Number of fish	Scale radius in millimeters to first annulus	Calculated length at end of first year of life	Length of fish corresponding to scale measurement
Male	IX	8	12.5	36	33.9
	III	15	10.3	28	29.6
	II	18	12.3	34	33.5
Female	IX	17	13.7	36	36.2
	IV	6	10.2	28	29.4
	III	13	10.0	28	29.0
	II	10	12.0	34	32.9

The data of Table 30 were based entirely on measurements of "key" scales[25] (see p. 209) and hence are free from the distortion that might result from selection of scales by size on the part of the technician who prepared the slides. It may be seen at once that the variations in l_1 are reflected in similar variations in the length of the anterior radius of the scale within the first annulus. The average calculated lengths are not in full agreement with the fish lengths corresponding to the actual scale measurements, but the discrepancies show no definite correlation with age. The length of fish (33.9 millimeters) corresponding to the average scale length (12.5 millimeters) was below the average calculated length (36 millimeters) in the IX-group males, but was equal to or possibly higher in the IX-group females (36.2 as compared to 36). Among the younger fish the average calculated lengths were too low in both III-groups and in the IV-group females, but were too high in both II-groups. The distribution of the discrepancies marks them as the result of random sampling rather than of errors introduced by the method of growth calculation and correlated with age. The observed annual fluctuations in first-year growth described in

[25] Only the best represented age groups of the key-scale collection were included in Table 30.

the table therefore may be considered real.   Further observations on the discrepancies between annual fluctuations in growth in the first and in later years of life may be found on page 275.

PROBABLE CAUSES OF FLUCTUATIONS IN THE ABUNDANCE OF YEAR CLASSES AND IN GROWTH RATE

The obvious correlation between fluctuations in the strength of year classes and annual variations in growth rate of the Nebish Lake rock bass suggests the possibility that the two may have a common cause or may be to a certain extent interdependent. It may be seen from the data of the preceding sections that the 5-year period, 1924 to 1928, was one both of poor growth (in the second and later years of life[26]) and of weak year classes. The remaining years for which data were available were by comparison years of relatively good growth and strong year classes. The extent of the correlation can be brought out better by the ordinal arrangement of the different calendar years with respect to the strength of year classes and growth rate.

Since the data on growth rate given in Table 27 covered the 10-year period, 1922 to 1931, and those on the abundance of year classes included the 10 years, 1921 to 1930, a comparison of annual variations will be assisted greatly if rough estimates are made of the quality of growth in 1921 and of the strength of the 1931 year class. The single comparison between growth in 1921 and 1922 (growth of females in the second year of life, Table 25) yielded the estimate that 1921 growth was 13.3 per cent below 1922 growth and hence 3.4 per cent below the 1922-1931 average. (See p. 257.) In the 11-year period, 1921 to 1931, the growth in 1921 therefore occupies sixth position. The estimate of the strength of the 1931 year class must be based entirely on its representation in the 1935 collection. From Table 23 it may be seen that the 1931 year class made up 12.9 per cent of the 1935 collection and had a representation exactly equal to that of the 1929 year class. The 1929 year class previously was given a ranking of 5 in a 10-year period (p. 248). If some allowance is made for the greater age of the 1929 year class as compared with the 1931 year class at the time of capture in 1935, the 1931 year class should be recognized to be somewhat the weaker. A

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[26] Discussions of first-year growth may be found on p. 259.

ranking of 6 for the 1931 year class in an 11-year period possibly does not do serious violence to the truth.

If the above estimates of the growth in 1921 and the strength of the 1931 year class are accepted, the following ordinal positions of the calendar years are obtained with respect to strength of year class and growth rate. The position, 1, refers to the best growth and the strongest year class.

Position with respect to:

Year	Strength of year class	Growth rate
1923	1	4
1930	2	3
1922	3	2
1921	4	6
1929	5	5
1931	6	1
1924	7	10
1926	8	8
1925	9	7
1928	10	11
1927	11	9

The above arrangement substantiates the previous assertion that the period, 1924 to 1928, was one of poor growth and weak year classes. By comparison, growth was better and year classes were stronger in the years, 1921 to 1923 and 1929 to 1931.

Meteorological conditions may be expected to occupy an important position among the factors that contributed to the observed annual fluctuations in growth rate and the strength of year classes. Detailed tabulations were prepared of weather conditions in Vilas County[27] in regard to temperature, precipitation, and the percentage of possible sunshine in the six months, May to October, over the period, 1921 to 1934. Preliminary examinations revealed no correlation between annual fluctua-

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[27] Records of the U. S. Weather Bureau (Climatological Data for the United States by Sections, Vols. VIII–XXI) were consulted for stations at Rest Lake about 14 miles (22 kilometers) to the northwest of Nebish Lake and at Big St. Germain Dam, about 10 miles (16 kilometers) to the southeast. Tabulations were based on the averages for the two stations. Occasionally defective records or a lack of records for one of the stations made it necessary to employ data from a single locality. These gaps do not affect seriously the validity of the data since the agreement between the stations ordinarily was close.

TABLE 31. *Average air temperatures in °F. at two weather stations near Nebish Lake in each of 6 months over the period, 1921-1934, and the deviation of each month's temperature from the 1921-1931 average for that month.*

Month	Average air temperature (°F.) in calendar year														Average for 1921-1931
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	
May	54.8	59.0	51.6	43.5	48.5	54.6	49.5	53.4	48.5	52.9	49.4	50.6	53.8	58.0	51.4
June	67.4	61.2	66.2	58.0	62.6	57.2	58.2	56.1	59.3	62.6	62.9	63.5	67.9	65.6	61.1
July	71.5	62.8	68.2	61.5	64.5	65.1	62.4	65.8	65.4	65.6	67.0	65.2	68.0	67.7	65.4
August	63.6	63.8	59.9	61.2	66.6	63.4	58.6	63.2	62.3	65.2	61.2	63.8	60.6	61.0	62.6
September	58.4	58.6	57.0	52.6	59.3	53.2	59.8	51.6	53.8	55.8	60.2	50.2	59.7	55.0	56.4
October	46.6	47.1	43.6	51.2	35.2	41.8	46.6	44.0	44.0	43.8	47.5	39.4	40.1	47.6	44.7

Month	Departure of temperature from 1921-1931 mean in calendar year														Average for 1921-1931[1]
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	
May	3.4	7.6	0.2	-7.9	-2.9	3.2	-1.9	2.0	-2.9	1.5	-2.0	-0.8	2.4	6.6	3.2
June	6.3	0.1	5.1	-3.1	1.5	-3.9	-2.9	-5.0	-1.8	1.5	1.8	2.4	6.8	4.5	3.0
July	6.1	-2.6	2.8	-3.9	-0.9	-0.3	-3.0	0.4	0.0	0.2	1.6	-0.2	2.6	2.3	2.0
August	1.0	1.2	-2.7	-1.4	4.0	0.8	-4.0	0.6	-0.3	2.6	-1.4	1.2	-2.0	-1.6	1.8
September	2.0	2.2	0.6	-3.8	2.9	-3.2	3.4	-4.8	-2.6	-0.6	3.8	-6.2	3.3	-1.4	2.7
October	1.9	2.4	-1.1	6.5	-9.5	-2.9	1.9	-0.7	-0.7	-0.9	2.8	-5.3	-4.6	2.9	2.8

[1] Mean of the absolute values.

TABLE 32. *Average precipitation in inches at two weather stations near Nebish Lake in each of 6 months over the period, 1921-1934, the deviation of each month's precipitation from the 1921-1931 average for that month, and the maximum 24-hour precipitation in each month.*

Total precipitation in calendar year

Month	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	Average for 1921-1931
May	2.80	3.98	2.64	3.10	1.27	2.60	3.56	2.08	1.96	4.28	1.48	3.46	3.10	2.03	2.70
June	1.00	5.86	7.16	3.76	4.26	4.10	2.92	5.40	4.98	7.13	6.22	2.54	3.36	3.66	4.80
July	6.23	3.24	6.14	3.05	2.78	3.74	5.70	4.08	4.99	2.35	3.22	2.57	2.02	2.06	4.14
August	3.86	2.57	2.46	5.17	3.43	4.80	1.96	5.74	1.91	0.34	3.70	5.82	1.33	3.18	3.27
September	4.36	5.76	2.22	2.82	4.68	6.66	2.94	5.30	4.25	3.20	6.52	1.79	3.12	10.02	4.43
October	1.23	1.31	1.74	0.88	1.90	2.78	2.31	3.71	2.73	2.90	2.93	1.20	2.73	3.28	2.22

Departure of precipitation from the 1921-1931 mean in calendar year

Month	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	Average for 1921-1931[1]
May	0.10	1.28	−0.06	0.40	−1.43	−0.10	0.86	−0.62	−0.74	1.58	−1.22	0.76	0.40	−0.67	0.76
June	−3.80	1.06	2.36	−1.04	−0.54	−0.70	−1.88	0.60	0.18	2.33	1.42	−2.26	−1.44	−1.14	1.45
July	2.09	−0.90	2.00	−1.09	−1.36	−0.40	1.56	−0.06	0.85	−1.79	−0.92	−1.57	−2.12	−2.08	1.18
August	0.59	−0.70	−0.81	1.90	0.16	1.53	−1.31	2.47	−1.36	−2.93	0.43	2.55	−1.94	−0.09	1.29
September	−0.07	1.33	−2.21	−1.61	0.25	2.23	−1.49	0.87	−0.18	−1.23	2.09	−2.64	−1.31	5.59	1.23
October	−0.99	−0.91	−0.48	−1.34	−0.32	0.56	0.09	1.49	0.51	0.68	0.71	−1.02	0.51	1.06	0.73

Maximum precipitation in 24 hours in calendar year

Month	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	Average for 1921-1931
May	1.06	1.32	0.80	1.08	0.41	0.76	0.89	0.98	0.82	1.24	0.44	0.89	1.16	0.55	0.89
June	0.52	1.98	2.43	0.75	0.87	1.37	1.29	0.80	2.20	2.40	1.32	0.70	0.97	1.08	1.45
July	2.20	1.02	1.15	0.70	0.96	0.70	1.40	1.57	1.80	0.80	0.85	0.95	1.29	0.76	1.20
August	1.10	1.12	0.88	2.30	1.85	1.85	0.94	1.42	0.62	0.30	1.40	2.98	0.70	1.05	1.25
September	2.23	2.17	0.88	1.12	1.60	1.96	0.95	2.47	1.60	1.08	1.30	0.50	1.02	2.41	1.58
October	0.60	0.68	0.80	0.31	0.80	1.16	1.20	1.00	1.20	1.30	0.60	0.42	0.73	1.50	0.88

[1] Mean of the absolute values.

tions in the percentage of possible sunshine and growth or the strength of year classes; consequently no data on sunshine are presented here. Tables 31 and 32 contain records of temperature and rainfall.

It is realized that records of fluctuations in air temperature do not by any means provide a precise measure of fluctuations in water temperature. Nevertheless, water temperatures of a small, relatively shallow lake may be expected to vary in the same direction as air temperatures.

The examination of Table 31 reveals that in general the years in which growth was good and strong year classes were produced tended to have temperature above the average. On the other hand the total precipitation for the 6-month period (Table 32) does not appear to be correlated with either growth or the strength of the year classes. The data for the individual months, however, show that the early-season (May, June, and July) rainfall tended to be above average in the years of good growth and strong year classes. It is particularly noteworthy that the two years with exceptionally rich year classes (1923 and 1930) had especially heavy rainfall in June. Precipitation was above average also in July, 1923, and in May, 1930. The temperature deviations for the early season, especially for June, indicate that the correlation between high temperatures in the season as a whole and growth and the strength of year classes may result largely from the high temperatures in the early part of the summer. It appears valid to conclude, therefore, that the Nebish Lake rock bass tended to grow more rapidly and produce stronger year classes in those years in which the early season had heavy rainfall and temperatures above the average.

There are, to be sure, certain exceptions to the trends outlined in the preceding paragraph. For example, 1921, a year in which growth was only slightly below average and which was estimated to have given rise to a fairly strong year class, nevertheless had such a deficiency of rainfall in June that the early season must be characterized as dry. However, the exceptions that occur do not appear to invalidate the belief that good growth and strong year classes were associated with high temperatures and heavy precipitation in the early season.

In an attempt to obtain more complete information on possible relationships between meteorological conditions and fluctuations in growth and the strength of year classes, a series of computations was made of coefficients of correlation based on annual deviations of growth, abundance, temperature, and rainfall from the mean for the 11 years, 1921 to 1931. With the year classes, the ordinal arrangement of the years (p. 263) was taken as representative of relative abundance. Admittedly a more precise evaluation of the strength of the year classes would have been desirable. It was not believed, however, that the original data were sufficiently reliable to make the (necessarily) arbitrary assignment of weights valid.

Table 33 shows the coefficients of correlation between growth and the strength of year classes of Nebish Lake rock bass and meteorological conditions (deviations from average temperature and rainfall) over the period, 1921 to 1931, for each of six months and for certain groupings of months. (The data for the Muskellunge Lake rock bass will be discussed on p. 276.) If a probability of 0.95 or greater that a correlation exists is accepted as indicative of significance, the smallest significant (absolute) value of the coefficient is 0.60.[28]

The coefficients of correlation of Table 33 support the earlier statement that good growth and strong year classes are associated with high temperatures and heavy rainfall in early season. With a single exception (the correlation between July precipitation and growth) the coefficients were all positive for the first three months. However, only 1 of the 12 coefficients had a value in excess of 0.60 (correlation between June temperature and the strength of the year classes). In the late-season data none of the coefficients exceeded the absolute value of 0.60. The strongest indicated correlations were the positive correlation ($r =$ 0.55) between September temperature and growth and the negative correlations between August precipitation and growth ($r =$ —0.48) and the strength of year classes ($r =$ —0.50).

The general failure of meteorological conditions in the indi-

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[28] If the value of t corresponding to a probability of 0.05, when the number of degrees of freedom (n) is 9, is substituted in the formula, $t = \dfrac{r\sqrt{n}}{\sqrt{1-r^2}}$, the value of r is 0.602. See Goulden (1939) or other of the recent textbooks on statistical methods.

TABLE 33. *Coefficients of correlation (r) between the annual fluctuations in the growth and in the strength of the year classes of the rock bass of Nebish and Muskellunge lakes and the annual fluctuations in temperature or precipitation in certain months and combinations of months.*

| Month or months | Nebish Lake | | | | Muskellunge Lake | | | |
| | Growth | | Strength of year class | | Growth | | Strength of year class | |
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
May	0.20	0.05	0.33	0.36	0.32	0.14	0.30	0.25
June	0.54	0.56	0.69	0.45	0.75	-0.06	0.32	0.17
July	0.24	-0.22	0.43	0.08	0.47	0.29	0.38	0.30
August	-0.01	-0.48	0.10	-0.50	0.12	-0.18	0.13	0.05
September	0.55	0.21	0.12	-0.24	0.31	-0.11	-0.31	-0.35
October	0.12	-0.01	0.17	-0.31	0.23	-0.66	0.06	-0.21
All six months	0.56	0.12	0.62	-0.05	0.74	-0.23	0.33	0.13
May and June	0.47	0.51	0.64	0.56	0.67	0.01	0.46	0.27
June and July	0.44	0.40	0.62	0.52	0.68	0.16	0.37	0.41
May, June, and July	0.43	0.37	0.62	0.62	0.66	0.20	0.47	0.47
July and August	0.17	-0.52	0.37	-0.34	0.42	0.06	0.36	0.24
June and September	0.61	0.57	0.47	0.20	0.61	-0.12	0.03	-0.09
May, June, July, and September	0.53	0.55	0.55	0.47	0.65	0.13	0.29	0.22
August, September, and October	0.53	-0.16	0.31	-0.48	0.53	-0.35	-0.11	-0.22

vidual months to exhibit definitely significant correlations with annual fluctuations in growth and the strength of year classes should not be taken as proof that temperature and rainfall did not have a significant effect on these two phases of the life history of the Nebish Lake rock bass. It is possible—indeed, reasonably may be expected—that growth and the abundance of year classes may be affected more by conditions over a period of 2 or more months than by conditions in any single month. To test this possibility coefficients of correlation were computed between growth and abundance and weather conditions in eight groups of months (see lower part of Table 33). The coefficients for these combinations of months provide much stronger evidence that weather conditions in certain limited periods may have an important effect on annual fluctuations in growth and abundance.

The coefficient of correlation between temperature and growth did not exceed 0.60 for any single month and was below this value for all but one of the groups of months. The total temperature deviation for June and September did, however, exhibit a significant correlation with growth ($r = 0.61$). This apparent effect of temperature fluctuations on annual differences in growth rate may depend on a control of the length of the growing season. In the light of the observations on the course of growth during the season (p. 290), it is not unreasonable to expect that cold weather in June and September may cause the period of active growth to be shorter than usual, and that warm weather in these two months may lead to a relatively long growing season.

The cofficient of correlation between growth and precipitation did not exceed 0.60 for any of the groupings of months but the values were consistently positive for those groups of months that included June. The oligotrophic nature of Nebish Lake gives good cause to expect beneficial effects from heavy early-season rainfall. Where the natural supply of organic materials and nutrient salts is so scanty, the quantity of materials washed in during the course of a heavy downpour[29] well may bring abont

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[29] Comparisons of total precipitation and the maximum precipitation in a 24-hour period (Table 32) reveal that ordinarily the months with a high total precipitation also experienced heavy falls of rain within short periods.

a significant enrichment of the lake. Materials added in early season should be more completely available for utilization than substances washed in during the later months. It is true that the coefficient of correlation between growth and precipitation in June and September was fairly high ($r = 0.57$). However, the correlation with precipitation in June alone was almost equally strong ($r = 0.56$) whereas the correlation between growth and precipitation in September alone was weak ($r = 0.21$). A negative correlation existed between growth and rainfall for the two periods, July and August, and August, September, and October. The absolute values of the coefficients were both less than 0.60. For further discussion of these negative coefficients see p. 273.

High temperatures, especially in early season, show a decidedly positive correlation with the strength of the year classes. The coefficients of correlation were greater than 0.60 for June and for four of the eight groupings of months. No month or combination of months showed a negative correlation between temperature and the strength of year classes. High temperatures possibly may improve food conditions for and thus promote a greater survival of young fish.

The high correlation between June temperatures and the strength of year classes suggests the possibility that the relative abundance of year classes of the Nebish Lake rock bass may be determined by the rate of survival very early in the life of the individuals. The exact time of spawning and hatching of the Nebish Lake rock bass is not known, but the absence of any maturing or ripe fish in a collection taken July 5 and 6, 1930, provides evidence that most if not all of the eggs are deposited and that at least part of the development of the eggs occurs during June.[30]

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[30] A deposition of the eggs much earlier than June is most unlikely, since the ice does not disappear from the lakes until "about the first of May" (Juday and Birge, 1930). In Lake Maxinkuckee (northern Indiana) where the ice usually disappears in the latter part of March the rock bass begin to spawn "about the middle of May and are usually done by June 15" (Evermann and Clark, 1920). In northern New York, where climatic conditions are more nearly comparable with those in northeastern Wisconsin, Greeley (1930) found two nests containing eggs in the Big Chazy River (Champlain watershed) on July 9. However, the eggs already had hatched on July 2 in a nest located in a tributary of this same stream. Greeley and Greene (1931) found a "nest with eggs and a male on guard" on Tibbits Creek (St. Lawrence watershed) on June 5.

Although the coefficients of correlation between precipitation and the strength of the year classes were positive for May and June and for all groupings that included these months, only one coefficient exceeded 0.60 (correlation between strength of year class and precipitation in May, June, and July; $r = 0.62$). This value constitutes evidence for a beneficial effect of heavy early-season rainfall on the survival of young. The most logical explanation of such a' relationship appears to lie in the assumption that materials washed in during the early season bring about an improvement in feeding conditions for and consequently a greater survival of the young fish.

The coefficients of correlation between late-season precipitation and the strength of year classes were all negative but had (absolute) values less than 0.60. Two of the eight groupings also had negative coefficients.

Attention should be called to the existence of a factor that complicates the interpretation of the data of Table 33, namely, the apparent correlation of growth and the abundance of year classes with both temperature and precipitation. For example, there is evidence that growth is correlated positively with June temperature and precipitation. Now if June temperature and precipitation are correlated negatively or vary independently the values of r in Table 33 are too low. If, on the other hand, June temperature and precipitation have a strong positive correlation the values of r in Table 33 may be held to represent, to a certain extent, the combined effects of the two phases of the weather and are therefore too high. The actual computation of the correlation between June temperature and rainfall yielded a value of $r = 0.01$. If partial coefficients of correlation are computed, the following results are obtained: The correlation between June temperature and growth, with rainfall held constant is 0.64; the correlation between June rainfall and growth, with temperature held constant is 0.65. Both of these values are slightly above the lowest significant value, 0.63.[31]

Table 34 shows partial coefficients of correlation computed from the above and from several other combinations of data. The partial coefficients of correlation of growth and meteorologi-

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[31] The computation of the partial coefficient of correlation involves the loss of one degree of freedom; consequently a higher value of r is necessary to obtain a value of t corresponding to a probability of 0.05.

TABLE 34. *Partial coefficients of correlation between the annual fluctuations in growth and in the strength of the year classes of the Nebish Lake rock bass and the annual fluctuations in weather conditions in certain months and combinations of months.*

Biological variable	Variable meteorological factor	Meteorological factor held constant	r
Growth	Temperature (June)	Precipitation (June)	0.64
do.	Precipitation (June)	Temperature (June)	0.65
do.	Temperature (June and September)	Precipitation (June)	0.76
do.	Precipitation (June)	Temperature (June and September)	0.73
do.	Temperature (June and September)	Precipitation (August)	0.50
do.	Precipitation (August)	Temperature (June and September)	—0.29
Abundance	Temperature (June)	Precipitation (June)	0.76
do.	Precipitation (June)	Temperature (June)	0.60
do.	Temperature (June)	Precipitation (May, June, and July)	0.72
do.	Precipitation (May, June, and July)	Temperature (June)	0.66
do.	Precipitation (August, September, and October)	Precipitation (May, June, and July)	0.50
do.	Temperature (June)	Precipitation (August, September, and October)	—0.26
do.	Precipitation (August, September, and October)	Temperature (June)	0.61
do.	Precipitation (August, September, and October)		—0.26

cal conditions based on June precipitation and temperatures in June and September are considerably higher than those based on June weather alone. With June rainfall held constant, the coefficient of correlation between growth and temperature in June and September is 0.76. When the temperature in these two months is held constant the coefficient of correlation of growth with June precipitation is 0.73. The value, —0.29, for the coefficient of correlation between August precipitation and growth, with the June and September temperature held constant gives evidence that the greater negative simple coefficient (—0.48) between August precipitation and growth depended in large measure on the fact that the years with high June and September temperatures had a deficiency in rainfall in August. On purely mathematical grounds it might be argued, of course, that the high simple correlation between growth and June and September temperature ($r = 0.61$) depended in part on the deficiency in August rainfall in the years with high temperatures in these two months. However, it is difficult to conceive in what manner heavy August rainfall might impede the growth of the rock bass in Nebish Lake. In some lakes the increased turbidity that follows heavy rainfall may bring about a reduction in the growth of plankton. Nebish Lake, however, is not subject to high turbidity resulting from heavy precipitation. The soil of the surrounding land is sandy and is covered by a relatively dense growth of vegetation. On the other hand a connection between growth and June and September temperature has a sound biological explanation (p. 269).

Significant partial coefficients of correlation between the strength of year classes and June temperatures were obtained with precipitation held constant in June ($r = 0.76$) and in May, June, and July ($r = 0.72$). The coefficient of correlation between the abundance of year classes and precipitation in May, June, and July, with June temperature held constant ($r = 0.66$) also was above 0.63. None of the remaining partial coefficients had significant values. The partial coefficients of correlation between the strength of year classes and late-season (August, September, and October) precipitation, with early-season (May, June, and July) precipitation held constant, ($r = -0.26$) and with June temperature held constant ($r = -0.26$) have consid-

erably smaller negative values than the simple correlation be-
tween late-season rainfall and abundance ($r = -0.48$). It is
believed that the negative correlation between late-season pre-
cipitation and abundance is the result of a late-season deficiency
in rainfall in those years in which early-season conditions were
conducive to the production of strong year classes.

The data that have been presented and discussed in the pre-
ceding pages appear to make valid the conclusion that annual
fluctuations in both the growth and the strength of the year
classes of the Nebish Lake rock bass are correlated significantly
with annual variations in temperature and rainfall. Growth is
correlated more closely with temperature in June and September
and rainfall in June than with conditions in other months. The
strength of the year classes seems to be correlated most closely
with early-season (May, June, and July) temperature and rain-
fall, with June conditions more important than those for other
months.

The small amount of information on the growth of the Ne-
bish Lake rock bass beyond 1931 (Table 28) makes it possible
to form some judgment as to whether the relationships observed
for the 11 years, 1921 to 1931, hold for growth in later years.
From Table 31 it may be seen that early-season (particularly
June) temperatures were not greatly different in 1931 and 1932.
September temperatures, however, were lower by 10.0° F. in the
latter year. Comparisons of rainfall (Table 32) show 1932 to
have had a drier early season than 1931. On the basis of the
low temperatures in September and the early-season deficiency
in rainfall, growth in 1932 would be expected to be poorer than
growth in 1931. This expectation is in agreement with the
facts; growth declined from 20.6 per cent above the 1922-1931
average in 1931 to 4.8 per cent above average in 1932.

The deficiency in precipitation that characterized the early
season of 1932 continued through 1933 and 1934. However, the
data on temperature fluctuations in June and September give
cause to expect an improvement in growth in 1933, followed by
a decline in 1934. The improvement did not occur in 1933; on
the contrary the deviation from average growth declined slightly
(from 4.8 per cent in 1932 to 4.0 per cent in 1933). The ex-
pected decline did occur in 1934 (from 4.0 per cent in 1933 to

—9.9 per cent in 1934). The relationship between growth and weather conditions in the years, 1932 to 1934, cannot be said to lend strong support to or to be seriously incompatible with the belief that high June and September temperature and heavy early-season precipitation are conducive to good growth. Predictions based on the examination of meteorological data were accurate for two of the three years.

The preceding discussion has been concerned with the effects of only two factors, temperature and precipitation, on annual fluctuations in the growth and the strength of the year classes of the Nebish Lake rock bass. Recognition must be given also to certain biological factors of possibly great importance. In late summer at least, the Nebish Lake rock bass lives in rather close association with perch and smallmouth black bass. Since the three species are to a large degree competitors for food in Nebish Lake (Couey, 1935) large fluctuations in the abundance of any one species probably affect the abundance and growth of the other two species.

Fluctuations in the strength of year classes of the rock bass itself possibly may be reflected in the survival of young and in the growth rate in later years. For example, the great abundance of rock bass that must have existed for several years following the production of the extremely rich 1923 year class may well have contributed to the slow growth and poor survival of young during the period, 1924 to 1928. Furthermore, it is readily conceivable that five consecutive years of poor survival may have reduced the population density sufficiently to permit the observed improvements in survival and growth rate following 1928. Finally, the production of a second exceptionally strong year class in 1930 was followed by a decline in growth rate that began in 1932 and continued at least 2 more years. These considerations seem to throw a justifiable doubt on the biological significance of the statistically significant correlation between meteorological conditions and the fluctuations in the growth and the strength of the year classes of the Nebish Lake rock bass.

Mention should be made also of the fact that first-year growth does not appear to be correlated with either temperature or precipitation. Obviously, the conditions that control the rate of growth in the first year and in the later years of life are not

the same. The first-year rock bass failed entirely to share the improvement in the growth of older fish over the period, 1929 to 1931. In 1931 when the growth of fish in the second and later years of life was at the maximum the young of the year grew more slowly than in any other year of the period, 1920 to 1931 (Tables 27 and 29). Furthermore, the growth of first-year fish reached a maximum in 1924 when the growth of older fish was unusually slow.

The discussion of this section has placed emphasis on the correlation between fluctuations in the strength of year classes and in growth in the second and later years of life. It would be more logical to expect a correlation between first-year growth and survival of young fish. However, such a correlation does not exist. It is true that first-year growth was above average in 1923 when a phenomenally strong year class was produced. On the other hand, members of the strong 1930 year class grew poorly in their first year. Furthermore, the year of maximum first-year growth (1924) gave rise to a relatively weak year class. The lack of correlation between first-year and later growth may be due to the occupancy of different habitats and the consumption of different foods by young of the year and older fish. The lack of correlation between first-year growth and the survival of young is more difficult to explain. It can be said only that the factors that control these two phases of the early life history of the rock bass appear not to be the same. It can be stated also that the abundance of the young of the year does not seem to affect first-year growth.

Information on the annual fluctuations in growth and the strength of year classes of rock bass in Muskellunge and Silver Lakes makes possible a brief examination of the relationship between meteorological conditions and these two phases of the life history of the rock bass in two additional populations.[32] Attention will be given first to the data for the rock bass of Muskellunge Lake.

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[32] The information that will be presented here on the growth and the strength of the year classes of the rock bass of Muskellunge and Silver Lakes has not been based on all available collections. However, the date of completion of the age and growth studies of these two rock bass populations is most indefinite; consequently it has been considered desirable to make use of those portions of the data that are applicable to problems considered in this paper.

TABLE 35. *Annual increments of growth in length (in millimeters) of the males of the various year classes of the Muskellunge Lake rock bass.*

Year of life	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	Unweighted mean
11											6	6
10										7	7	7
9									8	11	13	11
8								9	12	16	15	13
7							14	14	20	19	[1]	17
6						17	17	16	20	18	15	17
5					35	19	18	17	24	17	18	21
4				20	23	19	18	15	21	18	21	19
3			23	19	15	18	17	20	20	15	22	19
2		21	20	17	16	18	17	20	21	17		19
1	37	34	34	35	33	30	30	31	32			33
Number of fish taken in year 1930		9	18	6	3							36
1931	3	20	53	16	18	18	4					132
1932	2	3	9	3	1	4	3	14	12			51
Total	5	32	80	25	22	22	7	14	12			219

[1] Represented by only one fish.

TABLE 36. *Annual increments of growth in length (in millimeters) of the females of the various year classes of the Muskellunge Lake rock bass.*

Year of life	Calendar year											Unweighted mean
	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	
10										9	9	9
9									10	10	9	10
8								9	11	14	12	12
7							10	12	18	18	13	14
6						15	17	14	18	18	18[1]	17
5					19	18	15	16	22	16		18
4				21	21	18	19	15	19	17	20	19
3			22	18	16	16	15	19	20	19	20	18
2		21	19	17	17	16	17	22	21			19
1	35	34	33	32	33	30	28	30	30			32
Number of fish taken in year 1930	7	16	27	21	14							85
1931	18	27	68	6	20	13	8					160
1932		4	10	9	4	4	1	20	13			65
Total	25	47	105	36	38	17	9	20	13			310

[1] Represented by only one fish.

Tables 35 and 36 show the growth increments of the Muskellunge Lake rock bass according to calendar year and year of life. These data were analyzed by the same methods described for the Nebish Lake material. The annual fluctuations in growth are recorded in Table 37. In the Muskellunge Lake data as in the Nebish Lake data the indicated deviation of the 1921 growth (Table 39) from the 1922-1931 average must be considered a rough estimate.[33]

TABLE 37. *Deviation of the growth of the Muskellunge Lake rock bass in different calendar years from the average for the 10-year period, 1922 to 1931. (First-year growth was excluded from the computations.)*

Sex	Percentage deviation from average growth in calendar year									
	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931
Male	24.8	19.9	7.2	3.6	—14.8	—19.3	—18.3	3.4	—7.4	1.1
Female	22.5	12.5	—3.3	—6.9	—14.0	—14.0	—8.8	9.8	1.6	0.6
Average	23.6	16.2	2.0	—1.6	—14.4	—16.6	—13.4	6.6	—2.9	0.8

The age and year-class composition of the rock bass collected from Muskellunge Lake in six calendar years may be seen in Table 38. The records for 1927 and 1928 were taken from Wright's (1929) paper (Wright's method of designating age has been modified to conform with the method used in this paper). The remaining data are presented here for the first time.

The estimate of the ordinal ranking of the calendar years as to strength of the year classes of the Muskellunge Lake rock bass given in Table 39 (the rating, 1, designates the strongest year class) was made from the examination of Table 38. The basis for the rankings will be discussed only briefly and for only a few year classes. The 1923 year class was considered the strongest in the 11-year period because of its dominance as age-groups V, VII, and VIII, and its strength as age-group IX. No significance can be attached to the scarcity of the 1923 year class as age-group IV in the 1927 collections. Although Wright (1929) gave

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[33] Since only three specimens were available, the data on the growth of the 1920 year class of the Muskellunge Lake rock bass were not employed in the computation of fluctuations in growth over the period, 1922 to 1931, and hence were omitted from Tables 35 and 36. The single male specimen had a second-year growth (in 1921) that was 25 per cent above the 1923 level. The 1921 growth of the two females was 4.9 per cent below 1922 growth. The (weighted) mean percentage was 5.1 and hence the 1921 growth was 5.1 per cent above 1922 growth or 5.1 + 23.6 = 28.7 per cent above the 1922-1931 level.

TABLE 38. *Numerical and percentage representation of the year classes of the Muskellunge Lake rock bass in the different years' collections and for all collections combined. (Data for 1927 and 1928 taken from the publication by Wright, 1929).*

Year of capture	Item	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	Total
1927	Age group	X	IX	VIII	VII	VI	V	IV										110
	Number of fish	2	6	9	21	45	25	2										
	Percentage	1.8	5.5	8.2	19.1	40.9	22.7	1.8										
1928	Age group			IX	VIII	VII	VI	V		III								129
	Number of fish			3	21	36	29	38		2								
	Percentage			2.3	16.3	27.9	22.5	29.5		1.5								
1930	Age group			XI	X	IX	VIII	VII	VI	V	IV							141
	Number of fish			1	1	7	25	45	27	17	8							
	Percentage			0.7	0.7	5.0	17.7	31.9	19.1	12.1	5.7							
1931	Age group				XI	X	IX	VIII	VII	VI	V	IV	III					403
	Number of fish				2	20	45	120	21	37	29	22	107					
	Percentage				0.5	5.0	11.2	29.8	5.2	9.2	7.2	5.4	26.5					
1932	Age group						X	IX	VIII	VII	VI	V	IV	III				115
	Number of fish						7	19	12	5	8	3	34	25				
	Percentage						6.1	16.5	10.4	4.4	7.0	2.6	29.6	21.7				
1935	Age group						XIII		XI		IX	VIII	VII	VI	V	IV	III	81
	Number of fish						1		1		2	4	31	14	22	3	3	
	Percentage						1.2		1.2		2.5	4.9	38.3	17.3	27.2	3.7	3.7	
All collections	Number of fish	2	6	13	45	110	132	224	61	61	47	39	172	39	22	3	3	979
	Percentage	0.2	0.6	1.3	4.6	11.2	13.5	22.9	6.2	6.2	4.8	4.0	17.6	4.0	2.3	0.3	0.3	

no information as to the mesh sizes he employed, he mentioned that his nets did not take adequate samples of age-group IV and questioned the complete reliability of his V-group samples. The year class of 1928 was considered the second strongest because of its dominance in 1932 as age-group IV and in 1935 as the VII-group and its great strength in 1931 as age-group III. The estimates of the strength of the remaining year classes were based on similar considerations. A specific statement probably should be made of the reason for the assignment of the lowest ranking to the 1931 year class. The estimate of the strength of this year
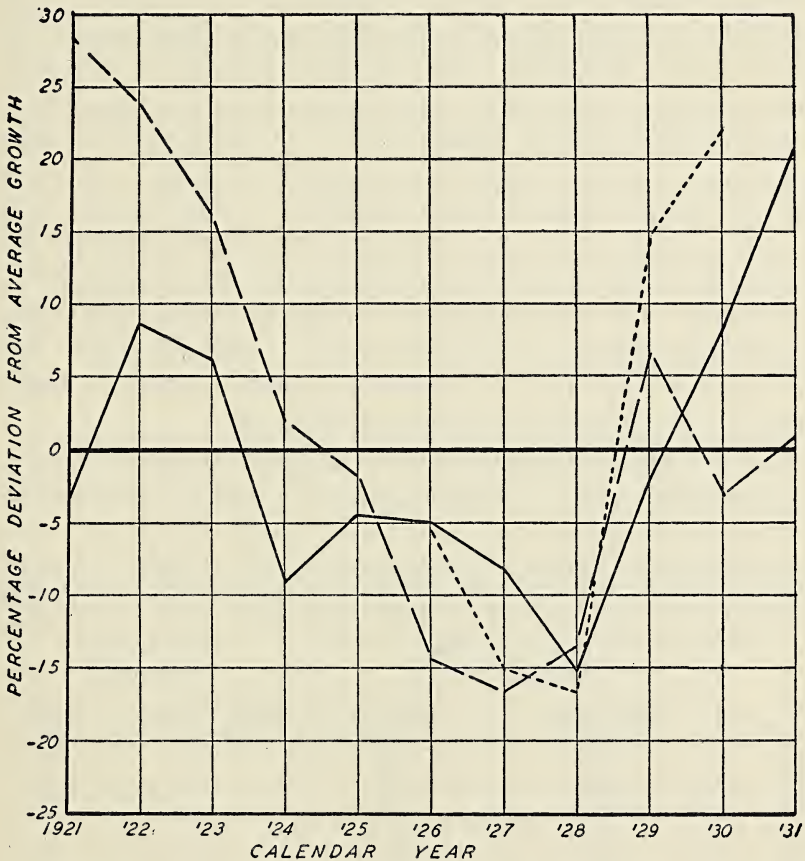
FIGURE 12. Annual percentage deviation of the growth (beyond the first year) of the Nebish Lake and the Muskellunge Lake rock bass from the 1922-1931 average and of the Silver Lake rock bass from the 1926-1930 average. Solid line Nebish Lake, broken line Muskellunge Lake, dotted line Silver Lake. The deviations represent the averages of the values for both sexes.

class of the Nebish Lake rock bass was made difficult by the lack of exact information as to the mesh sizes of the gill nets employed in taking the sample (p. 248). It is known, however, that the gill nets employed for the capture of the 1935 collection from Muskellunge Lake included six different mesh sizes (all of those listed on p. 194 except the 1¼-inch mesh). Nets of all seven mesh sizes were fished in Muskellunge Lake in 1931 but the 1¼-inch mesh net was omitted in 1932 as well as in 1935. The nets fished in 1935, therefore, could have taken greater numbers of IV-group rock bass had they been present in abundance.

Comparisons of the annual fluctuations in growth and the strength of the year classes of the rock bass of Muskellunge and Nebish Lakes (Table 39, Fig. 12) fail to reveal an extremely close agreement between the variations in the two populations. It is true that the data agreed in 7 of 11 years as to whether growth was above or below the 1922-1931 average. Nevertheless, the actual extent of the variations in the several years differed so greatly that the correlation between the annual fluctuations in the growth of the populations was relatively low ($r = 0.38$). The low value of the coefficient may be traced particularly to disagreements as to growth in 1921 and 1931. Had more reliable data been available on growth in 1921, a higher value of r possibly might have been obtained.

The two stocks showed better agreement in the fluctuations in the strength of year classes. The most serious disagreement

TABLE 39. *Comparisons of the annual percentage deviations from 1922 to 1931 average growth and of the strength of the year classes (1 designates the strongest year class) in Muskellunge and Nebish Lakes, 1921 to 1931.*

Year	Deviation from 1922-1931 growth		Strength of year class	
	Muskellunge Lake	Nebish Lake	Muskellunge Lake	Nebish Lake
1921	28.7	—3.4	3	4
1922	23.6	8.6	4	3
1923	16.2	6.2	1	1
1924	2.0	—9.1	6	7
1925	—1.6	—4.4	8	9
1926	—14.4	—4.9	9	8
1927	—16.6	—8.1	10	11
1928	—13.4	—15.2	2	10
1929	6.6	—1.9	7	5
1930	—2.9	8.4	5	2
1931	0.8	20.6	11	6

occurred in 1928 in which year the second strongest year class in 11 years was produced in Muskellunge Lake and the second weakest was produced in Nebish Lake. The correspondence was poor also in 1930 and 1931. The correlation between the rankings in the two stocks was fairly high ($r = 0.56$) but by no means of certain significance.

The annual fluctuations in the growth of the Muskellunge Lake rock bass exhibit a strong positive correlation with fluctuations in temperature (Table 33). The value of the correlation coefficient was high for June ($r = 0.75$) and also was positive for every other month. Furthermore, the value of r exceeded 0.60 for six of the eight groupings of months.

With the exception of the large negative value of the coefficient for October ($r = -0.66$) there is little evidence for a correlation between precipitation and the growth of the Muskellunge Lake rock bass. There is reason to believe, however, that this apparently significant negative correlation between October rainfall and the growth of the Muskellunge Lake rock bass may depend on the circumstance that warm seasons were deficient in October precipitation. The coefficient of correlation between October rainfall and June temperatures was found to be -0.42.

There is no evidence for a significant correlation between the strength of the year classes of the Muskellunge Lake rock bass and annual fluctuations in temperature or precipitation. It is of particular interest that a strong year class was produced in 1928 which year had very low temperatures and only a slight excess of rainfall in June, whereas the extremely weak year class of 1931 was produced in a year in which June temperatures were above average and an excess of rainfall occurred in June.

The failure of precipitation to show significant correlation with either the growth or the strength of the year classes of the Muskellunge Lake rock bass is not surprising. Muskellunge Lake is not only several times larger than Nebish Lake but it is much richer with respect to the organic matter of the plankton and the amount of bound CO_2 in its waters (Table 1). Accordingly, the amounts of nutrient materials washed into Muskellunge Lake during periods of heavy rainfall may be expected to have relatively much less effect.

The agreement between the first-year and later growth of the rock bass was better in Muskellunge Lake than in Nebish Lake (p. 275).   It should be noted, however, that data are lacking on the first-year growth of rock bass in Muskellunge Lake in 1930 and 1931, years in which the Nebish Lake data showed pronounced discrepancies between the growth of the young of the year and older fish.

With the Muskellunge Lake rock bass as with the Nebish Lake rock bass, the possible effects of the occurrence of strong and weak year classes on growth and on the survival of young in later years should not be overlooked.   The production of the three relatively strong year classes of 1921, 1922, and 1923 may have produced a population density that contributed to the declining growth of 1924 and 1925, to the very poor growth of 1926, 1927, and 1928 and to the reduced strength of the 1924 year class and the extreme weakness of the year classes of 1925, 1926, and 1927.   Further evidence that population density may affect the growth of the rock bass may be found in the fact that the changes in the growth of the Muskellunge Lake and Nebish Lake rock bass in 1930 agreed very poorly.   The growth of the Nebish Lake rock bass improved from 1929 to 1930 whereas that of the Muskellunge Lake stock declined.   Possibly this disagreement may be associated with the occurrence of the strong 1928 year class in Muskellunge Lake.   However, the simultaneous occurrence of poor growth and a strong year class in 1928 is hardly compatible with an assumption that periods of poor growth and survival are the result of overpopulation following the occurrence of strong year classes in earlier years.   There appear to be other factors whose effects are independent of the density of the population.

Mention already has been made of the fact that a strong year class of the Muskellunge Lake rock bass was produced in 1928, a year that gave rise to a very weak year class of the Nebish Lake rock bass. The possibility that conditions in Muskellunge Lake in 1928 may have been favorable for the survival of the young of other species as well is suggested by the fact that the 1928 year class of the Muskellunge Lake cisco also was one of unusual strength (Hile, 1936a).   It is of special interest that strong year classes occurred simultaneously in species that

spawn in the autumn[34] (cisco) and early summer (rock bass). Certain other observations on the cisco suggest the existence of unusual conditions in Muskellunge Lake in 1928. The calculated first-year lengths of the 1928 year class of the cisco had a distinctly bimodal distribution (Hile, 1936a), and morphometric studies (Hile, 1936b, 1937) reveal that the 1928 year class of the Muskellunge Lake cisco exhibited pronounced deviations from the normal morphological characteristics of the population. What the unusual conditions were is not known.

There are resemblances between the annual fluctuations in the growth of the rock bass and cisco[35] in Muskellunge lake (Table 40). The growth of both species declined in 1926. In 1927 the growth of the cisco improved slightly but that of the rock bass declined still further. The species agreed, however, in showing improved growth in 1928 and 1929, followed by a new decline in 1930. The decreased growth rate of the Muskellunge Lake rock bass in 1930 was in disagreement with the improvement in the growth of the Nebish Lake rock bass in the same year.

TABLE 40. *Comparison of the annual fluctuations (estimated percentage deviations from average) in the growth of rock bass and ciscoes in Muskellunge Lake.*

Species	Calendar year					
	1925	1926	1927	1928	1929	1930
Rock bass	—1.6	—14.4	—16.6	—13.4	6.6	—2.9
Cisco	10.2	—7.4	—3.2	1.4	9.1	—13.0

The data on the fluctuations of the growth (Tables 41, 42, and 43) and the strength of the year classes (Table 44) of the Silver Lake rock bass are relatively scanty and cover a limited period of years. At best they can be held as only roughly descriptive of the true changes that occurred.[36]

[34] The year classes of the cisco are considered to originate in the year of the spring in which the eggs hatch.

[35] The data on the growth of the cisco have been taken from Hile (1936a). Because of differences in the period of years included in the data for the two species and in the method of computation of the percentages, attention should be given to the direction and relative extent of the changes rather than to the actual values of the percentages.

[36] Nearly all of the Silver Lake specimens were taken by hook and line, a method of collection less satisfactory than the use of gill nets. Small hooks were used in an attempt to minimize selection.

TABLE 41. *Annual increments of growth in length (in millimeters) of the males of four year classes of the Silver Lake rock bass.*

Year of Life	Calendar year						Unweighted mean
	1925	1926	1927	1928	1929	1930	
6	..	..	..	..	..	22	22
5	..	..	..	..	29	33	31
4	..	..	..	19	32	27	26
3	..	..	19	15	20	28	20
2	..	16	16	17	21	..	18
1	32	30	28	29	..	..	30
Number of fish taken in year 1930	25	2	..	..	..	..	27
1931	5	4	2	18	..	..	29
Total	30	6	2	18	..	..	56

TABLE 42. *Annual increments of growth in length (in millimeters) of the females of four year classes of the Silver Lake rock bass.*

Year of life	Calendar year						Unweighted mean
	1925	1926	1927	1928	1929	1930	
6	..	..	..	..	..	20	20
5	..	..	..	..	28	25	26
4	..	..	..	17	26	28	24
3	..	..	18	16	20	26	20
2	..	17	14	18	21	..	18
1	31	31	26	29	..	..	29
Number of fish taken in year 1930	29	3	..	..	..	..	32
1931	21	9	13	20	..	..	63
Total	50	12	13	20	..	..	95

The annual fluctuations in the growth of the Silver Lake rock bass (Table 43, Fig. 12) bear a general resemblance to the changes that occurred in the growth of the Nebish Lake rock bass. Both stocks had a decreasing growth rate from 1926 to a minimum in 1928, followed by pronounced improvements in growth in 1929 and 1930. The improvement in growth in 1930 is in disagreement with the change that occurred in the growth of the Muskellunge Lake rock bass.

Data on the first-year growth of the Silver Lake rock bass are available for only four years (1925 to 1928). These data agree with the data on the growth in later years in showing a decline in 1927, but the improvement in first-year growth in 1928 disagrees with the change in growth in the later years of life.

The 1925 year class of the Silver Lake rock bass stands out as exceptionally strong (Table 44). In comparison, the poorly represented year classes of 1924, 1926, and 1927 may be considered relatively weak. The dominance of the 1928 year class

in the 1931 collection suggests that this year class probably was stronger than the year classes of 1926 and 1927. The general scarcity of old fish in the collections points toward the possibility of a relatively short life span for the Silver Lake rock bass and makes impossible an evaluation of the strength of year classes earlier than that of 1924.

The occurrence of a strong year class of the Silver Lake rock bass in 1925 is in disagreement with the data for both Nebish Lake and Muskellunge Lake where the 1925 year classes were relatively weak. The 1928 year class was rich in Muskellunge Lake as well as in Silver Lake but was extremely poor in Nebish Lake. The rock bass stocks of all three lakes had relatively weak year classes in 1926 and 1927. The 1924 year class apparently was weak in Silver Lake and average or slightly below average in the other two lakes.

Contrary to the situation in Muskellunge Lake, there appears to be no correlation between the fluctuations in the strength of the year classes of the rock bass and cisco in Silver Lake. Only the 1926 year class of the cisco was designated as unusually

TABLE 43. *Deviation of the growth of the Silver Lake rock bass in different calendar years from the average for the 5-year period, 1926-1930. (First-year growth was excluded from the computations.)*

Sex	Percentage deviation from average growth in calendar year				
	1926	1927	1928	1929	1930
Male	—10.5	—10.5	—19.5	16.0	24.3
Female	—0.3	—19.7	—13.6	13.5	20.0
Average	—5.4	—15.1	—16.6	14.8	22.2

TABLE 44. *Numerical and percentage representation of the year classes of the Silver Lake rock bass (sexes combined) in the 1930 and 1931 collections.*

Year of capture	Item	Year class								Total
		1921	1922	1923	1924	1925	1926	1927	1928	
1930	Age group	IX	VIII	VII	VI	V	IV	III	..	.
	Number of fish	4	1	6	1	54	6	1	..	73
	Percentage	5.4	1.4	8.2	1.4	74.0	8.2	1.4	..	..
1931	Age group	..	IX	..	..	VI	V	IV	III	—
	Number of fish	..	1	..	..	26	12	5	52	96
	Percentage	..	1.0	..	..	27.1	12.5	5.2	54.2	..
1930 and 1931	Number of fish	4	2	6	1	80	18	6	52	169
	Percentage	2.4	1.2	3.5	0.6	47.3	10.7	3.5	30.8	..

strong (Hile, 1936a). This same year class of the rock bass already has been found to have been weak. The 1929 year class of the Silver Lake cisco was considered weak; no data are available on the strength of the 1929 year class of the rock bass.

The annual fluctuations in the growth of the rock bass and cisco of Silver Lake also exhibit disagreements (Table 45). The growth of the cisco (Hile, 1936a) failed to decline sharply as did that of the rock bass in 1927 and 1928, while in 1930 the growth of the rock bass improved and that of the cisco declined. However, both species had relatively good growth in 1929.

TABLE 45. *Comparison of the annual fluctuations (estimated percentage deviations from average) in the growth of rock bass and ciscoes in Silver Lake.*

| Species | Calendar year | | | | |
	1926	1927	1928	1929	1930
Rock bass	—5.4	—15.1	—16.6	14.8	22.2
Cisco	—0.7	—0.5	—1.7	7.7	—8.0

A limited amount of data on the relative abundance of the year classes is available for one more population of rock bass of the northeastern highland region. According to Wright (1929) the 1923 year class made up 31.6 per cent (30 in a total of 95) of his 1927 collection from Trout Lake and 40.3 per cent (25 in a total of 62) of his 1928 samples. The 1923 year class was therefore one of unusual strength in three of the four lakes for which data are available. The 1923 year class was represented by only six specimens in the Silver Lake collections. However, the possibility that the Silver Lake rock bass may have a short life span (p. 287) renders the significance of this small representation doubtful.

The data that were discussed in the preceding pages contained numerous agreements and also a number of discrepancies. The possible significance of certain of the observations will be summarized briefly. There can be little doubt that meteorological conditions have important effects on the life history of the rock bass in the lakes of northeastern Wisconsin, and presumably on the life histories of other species as well. These effects are at times similar in different lakes. For example, the simultaneous occurrence of an exceptionally strong 1923 year class of

rock bass in three of four lakes for which data are available can hardly be ascribed to mere chance. There must have been a common cause, and the only factor that reasonably can be assumed to have exerted such a powerful influence simultaneously in the three lakes is weather. The strong positive correlation between annual fluctuations in temperature and the growth rate of both the Nebish Lake and the Muskellunge Lake rock bass populations likewise can be interpreted as similar effects of a common cause.

There is evidence, on the other hand, that at times conditions peculiar to individual lakes may cause weather conditions to have dissimilar effects in different bodies of water and/or that strictly local influences may be sufficiently strong to obscure or overshadow the effects of meteorological conditions. For example, the fluctuations in the growth of both the Nebish Lake and the Muskellunge Lake rock bass stocks exhibited strong positive correlation with temperature fluctuations; however, the growth fluctuations of the two stocks were correlated weakly with each other. The production in 1928 of a weak year class of the Nebish Lake rock bass and of a strong year class of the Muskellunge Lake rock bass (possibly of the Silver Lake rock bass also) must be interpreted as evidence that, in some years at least, local conditions play a dominant rôle in their effects on the life history of the species. The simultaneous occurrence in 1928 of strong year classes of the Muskellunge Lake rock bass and cisco indicates that conditions within that lake were then conducive to the survival of more than one species. In Silver Lake, however, the years of occurrence of strong year classes of the rock bass and the cisco were not the same.

In Nebish Lake the annual fluctuations in first-year growth showed little correlation with the fluctuations in growth in the later years of life. The less extensive data for the rock bass of Muskellunge Lake suggest that the fluctuations in the first-year growth of the rock bass in that lake agreed somewhat more closely with the fluctuations in the growth of older fish.

A continuation of this discussion would contribute little toward the clarification of the general problem of the causes underlying the observed annual fluctuations in the growth and the strength of the year classes. The problem must be recognized as

exceedingly complex. Continued investigations over a period of years doubtless would contribute much to an improved understanding of certain phases of the problem. To be most effective these studies should be conducted simultaneously on a number of lakes, should give consideration to the biology of all important species in each lake, and should have the support of concurrent intensive limnological investigations.

PERCENTAGE OF THE SEASON'S GROWTH IN LENGTH COMPLETED AT THE TIME OF CAPTURE

The routine of field operations, which involved the collection of a variety of species from a number of lakes, made it impossible to trace the progress of the growth of the Nebish Lake rock bass through the summer by means of collections taken at intervals throughout the growing season. It is possible, however, to estimate the percentage of the total season's growth that fish of certain age groups had completed up to the time of capture. The procedure consists of a comparison of the calculated length increment for that part of the growing season preceding capture with the length increment for the entire season as calculated from samples of the same year class taken in subsequent calendar years.[37] The following examples will illustrate the method.

The calculated growth in 1930 of the VII-group males of the 1930 collection up to the time of capture, August 16 to 21, was 6 millimeters (Table 46). Fish of the same (1923) year class appeared in the 1931 collection as age-group VIII and in the 1932 collection as age-group IX. The total 1930 growth of the 1923 year class was determined as 8 millimeters from each of these later collections. The VII-group males of the 1930 collection therefore had completed 75 per cent of their season's growth at the time they were captured. The female rock bass of the same age grew 4 millimeters in 1930 before capture. The total 1930 growth was determined as 7 millimeters from the 1931 VIII-group and as 6 millimeters from the 1932 IX-group. The percentage of growth completed before capture was $100 \times \frac{4}{6.5}$ or 61.5.

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[37] Comparisons must be based on successive samples of the same year class in order to avoid the possible distorting effects of fluctuations in growth rate in different calendar years.

TABLE 46. *Comparison of the calculated growth in millimeters of five age groups of Nebish Lake rock bass in 1930 up to the time of capture, August 16 to 21, with the growth for the entire season as calculated from 1931 and 1932 collections of the same year classes. Numbers of specimens in parentheses.*

Age in 1930	Males				Females			
	1930 growth up to time of capture	Total 1930 growth computed from 1931 collection	Total 1930 growth computed from 1932 collection	Percentage of year's growth completed at capture	1930 growth up to time of capture	Total 1930 growth computed from 1931 collection	Total 1930 growth computed from 1932 collection	Percentage of year's growth completed at capture
VIII	..	..	..	..	3 (8)	5 (47)	5 (33)	60.0
VII	6 (15)	8 (117)	8 (41)	75.0	4 (43)	7 (99)	6 (74)	61.5
VI	..	..	..	..	6 (6)	9 (24)	6 (17)	80.0
V	15 (9)	17 (5)	18 (5)	85.7	13 (6)	14 (11)	13 (9)	96.3
IV	20 (9)	23 (8)	..	87.0	20 (9)	22 (7)	20 (8)	95.2

The percentages of the season's growth completed before capture varied considerably in the age groups of each year's collection (Tables 46, 47, and 48). Some of the variations, without doubt, are traceable to the small numbers of specimens[38] in certain age groups. Because of the selection of the larger II-group fish by the nets (p. 197) it is possible that the estimated percentage of the season's growth completed by this age group is slightly too high. Other variations appear to represent real differences in the course of the season's growth, correlated with sex and age.

At the time of capture the males had, on the whole, completed a lesser percentage of the total season's growth than the females. In the 11 age groups (all three years) for which data were available for both sexes the average percentages were 74.8 for the males and 81.4 for the females. It follows then that the growth of the males exceeds that of the females in the latter part of the season.

An analysis of the actual growth increments (Table 49) reveals that the greater late-season growth of the males accounts in large measure for the superior growth rate of that sex. At capture, 11 age groups of males had completed 15.36 millimeters of the average total of 19.68 millimeters of growth they would have been expected to make had they survived to the end of the season. The corresponding average "partial" growth of females was 14.82 millimeters as compared with an average total growth of 17.41 millimeters. The advantage of the males' growth for the current seasons was 0.54 millimeter at the time of the collections, but the full-season advantage was 2.27 millimeters. In other words, at the time of collection the males had established less than one-fourth of the full-season advantage over the females although they had completed approximately three-fourths of the season's growth. The remaining three-fourths (1.73 millimeters) of the advantage of the males was established in late season during a period in which the males completed only a quarter of the season's growth.

[38] With the exception of the 1935 III-group, the data for all age groups represented by less than five fish were excluded from Tables 46, 47, and 48. Several age groups included in the tables nevertheless contained too few specimens to give highly reliable averages.

TABLE 47. *Comparison of the calculated growth in millimeters of eight age groups of Nebish Lake rock bass in 1931 up to the time of capture, July 29 to August 6, with the growth for the entire season as calculated from 1932 and 1935 collections of the same year classes. Numbers of specimens in parentheses.*

Age in 1931	Males			Females			
	1931 growth up to time of capture	Total 1931 growth computed from 1932 collection	Percentage of year's growth completed at capture	1931 growth up to time of capture	Total 1931 growth computed from 1932 collection	Total 1931 growth computed from 1935 collection	Percentage of year's growth completed at capture
X	..	..	..	6 (17)	8 (13)	..	75.0
IX	4 (18)	7 (10)	57.1	5 (47)	7 (33)	..	71.4
VIII	5 (117)	8 (41)	62.5	5 (99)	8 (74)	..	62.5
VII	5 (27)	7 (8)	71.4	6 (24)	7 (17)	..	85.7
VI	10 (5)	16 (5)	62.5	9 (11)	12 (9)	..	75.0
V	..	..	..	19 (7)	20 (8)	..	95.0
III	24 (6)	33 (7)	72.7	25 (7)	30 (9)	..	83.3
II	26 (10)	34 (43)	76.5	25 (9)	30 (59)	31 (9)	82.0

TABLE 48. *Comparison of the calculated growth in millimeters of two age groups of Nebish Lake rock bass in 1932 up to the time of capture, August 6 to 11, with the growth for the entire season as calculated from 1935 collections of the same year classes. Numbers of specimens in parentheses.*

Age in 1932	Males			Females		
	1932 growth up to time of capture	Total 1932 growth computed from 1935 collection	Percentage of year's growth completed at capture	1932 growth up to time of capture	Total 1932 growth computed from 1935 collection	Percentage of year's growth completed at capture
III	[1]26 (43)	33 (4)	78.8 ..	25 (59)	27 (9)	92.6 ..
II	28 (78)	30 (28)	93.3 ..	26 (59)	29 (43)	89.7 ..

[1] The inclusion of two fish taken on July 12 has no effect on the determination of the average increment.

Two ready explanations of the observed difference in the growth of the sexes suggest themselves. Male rock bass may continue to grow later in the season than do females. It is readily conceivable also that the growth of both sexes may end at approximately the same date but that the males maintain the higher rate of growth through the latter part of the season. Possibly both factors contribute to the sex difference in growth. The slight advantage of the males at capture may depend on more rapid growth or an earlier beginning of the growing season.

The above explanations are concerned with the manner in which sex differences in growth are established rather than with the underlying causes. Hubbs and Cooper (1935) pointed out that a more rapid growth of the males appears to be characteristic of the centrarchids. This relationship is contrary to the usual one in which, "The growth of the sexes is either very similar, or . . . the females grow faster than the males." Hubbs and

TABLE 49. *Comparison of the average growth in millimeters of male and female rock bass of 11 age groups up to the time of capture with the late-season and full-season growth as determined from collections of the same year classes in later years.*

Item	Growth up to time of capture	Growth in entire season	Growth in late season
Growth of males	15.36	19.68	4.32
Growth of females	14.82	17.41	2.59
Advantage of males	0.54	2.27	1.73

Cooper were inclined toward an explanation on the grounds, "that the increased growth of the males has been of selectional significance, enabling them the better to ward off enemies from the nests which they guard so pugnaciously". They found support for their explanation in the fact that among cyprinids males grow more rapidly than females only in those species with nest-building habits.

An earlier seasonal development of the gonads (preliminary to the next year's spawning) in female rock bass with a resultant earlier retardation of growth might well provide the physiological mechanism for the marked difference in the late-season growth of the sexes.

Age as well as sex affects the progress of the season's growth. Comparisons of average percentages for rock bass of the same sex and captured in the same year demonstrate that in 1930 and 1931 rock bass of age-groups V and younger had completed from 11.2 to 28.6 per cent more of the season's growth at capture than had fish of age-groups VI and older (Table 50). (There is some indication that the excess percentage of growth completed by the younger females may have been greater than that of males.) The difference between the older[39] and younger rock bass is a matter of age rather than maturity or immaturity, since the IV- and V-group fish, almost all of which were mature (p. 317), shared the high percentages of the still younger age groups.

Although confirmatory evidence from Nebish Lake collections is lacking, it is believed that the relatively advanced growth of the younger rock bass at capture depends on an earlier be-

TABLE 50. *Comparison of the average percentage of the season's growth completed by old and young rock bass at the time of capture in 1930 and 1931. In parentheses, the number of age groups on which each average percentage was based.*

Sex	Item	Year of capture	
		1930	1931
Male	Percentage of growth completed by VI-group and older	75.0(1)	63.4(4)
	Percentage of growth completed by V-group and younger	86.4(2)	74.6(2)
	Excess percentage of younger fish	11.4	11.2
Female	Percentage of growth completed by VI-group and older	67.2(3)	73.9(5)
	Percentage of growth completed by V-group and younger	95.8(2)	86.8(3)
	Excess percentage of younger fish	28.6	13.9

[39] The division between older and younger fish is purely arbitrary and was based on the examination of the data of Tables 46 and 47.

ginning of the season's growth. The only information as to the time at which the growth of the Nebish Lake rock bass begins was obtained from a collection of large fish taken by hook and line on July 5 and 6, 1930. Several of these older fish apparently had not yet formed the 1930 annuli on their scales (p. 205). Whether the scales of younger fish taken on the same dates would have exhibited the 1930 annuli is not known. However, direct evidence on the relation between age and the time at which the season's growth begins was obtained from the examination of scales of rock bass taken in Muskellunge Lake, July 1 and 2, 1932. In all of the scales with three or four annuli, the last-formed annulus lay near the edge of the scale. Some of the scales with five clearly defined annuli had a narrow margin of new growth whereas others had a broad margin with an annulus apparently in the process of formation at the extreme edge of the scale. These latter scales were doubtless from VI-group rock bass. Among the older fish the marginal growth of the scale was usually broad; only exceptionally was an annulus forming at the edge. These observations indicate that in Muskellunge Lake the rock bass of age-groups III, IV, and V had grown sufficiently to exhibit clear-cut annuli at a date when annulus formation was still incomplete in fish of greater age. The situation in the Nebish Lake rock bass probably is similar.

GROWTH COMPENSATION

Growth compensation—the tendency for individuals with relatively slow growth in early life to have relatively rapid growth in later years—has been observed in so many species of fish that its occurrence can well be considered general.[40] Ordinarily growth compensation sets in immediately after the first year of life; that is, the large yearling fish grow more slowly in the second and later years of life than do the small yearlings. The resultant progressive decrease in the difference in length that existed between large and small yearlings may continue at least to the end of the seventh year of life (Van Oosten, 1937).

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[40] The literature on growth compensation is probably too well known to warrant a review of the subject in this paper. Van Oosten (1929) cited numerous examples of growth compensation.

However, the large yearlings usually will retain a part of their original size advantage, even late in life.

The analysis by Hubbs and Cooper (1935) of the relationship between first-year and second-year growth of three species of sunfish (long-eared sunfish, common sunfish, and bluegill) and one hybrid form (common sunfish $\times$ bluegill) failed to reveal the presence of growth compensation in any of these fish. On the contrary, the data for 12 of 13 collections investigated gave positive correlations (usually highly significant) between first-year and second-year growth. The single exception, a group of female long-eared sunfish from Tomahawk Lake, Montmorency County, Michigan, had a coefficient of correlation of -0.42 ± 0.16 between first-year and second-year growth. The number of fish in this collection was only 12, and the coefficient of correlation is of doubtful significance. Hubbs and Cooper had no reliable data for the study of the relationship between first-year growth and growth beyond the second year of life.

The Nebish Lake rock bass collections, with their abundance of old fish, provide an excellent opportunity not only to determine whether the relationship observed by Hubbs and Cooper holds for yet another centrarchid species, but also to examine the relationship between growth in a centrarchid fish in different years of life over a considerably greater number of years. Tabulations of the growth histories of different yearling length-groups have been made for age-groups II and III of the 1932 collections and for the 1923 year class,[41] (1931 VIII-group and 1932 IX-group combined). In all tabulations the sexes were treated separately.

The original (first-year difference) of 9 millimeters between the largest (above 35 millimeters) and smallest (below 31 millimeters) yearling groups of the II-group males of the 1932 collection (Table 51) continued without change to the end of the second year of life and into the third summer up to the time of capture, since both groups had identical growth increments after

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[41] Age-group VII of the 1930 collection also was a member of the 1923 year class. However, the growth of this age group disagreed slightly with the growth of fish of the same year class in later collections (Tables 14 and 15). In order to have as completely representative and homogeneous material as possible, age-group VII was excluded from the growth-compensation data for the 1923 year class.

the first year.   The differences among all three groups at capture
were exactly the same as those that had existed at the end of the
first year of life.   In the second year of life the medium-sized
(31 to 35 millimeters) yearlings lost 1 millimeter of their or-
iginal 4-millimeter advantage over the small yearlings, but this
loss was regained before capture in the third summer.

TABLE 51. *Relationship between length at the end of the first year of
life and the growth in length in later years as determined from age-group
II of the 1932 collection of Nebish Lake rock bass.*

Sex	Number of fish	Interval of calculated length in millimeters at end of first year	Calculated length at end of year of life			Calculated increment of length in year of life		
			1	2	3[1]	1	2	3[1]
Male	18	Less than 31	29	61	88	29	32	27
	33	31 to 35	33	64	92	33	31	28
	27	More than 35	38	70	97	38	32	27
	Maximum difference		9	9	9	..	..	..
Female	17	Less than 31	29	62	87	29	33	25
	27	31 to 35	33	64	89	33	31	25
	15	More than 35	37	69	96	37	32	27
	Maximum difference		8	7	9	..	..	..

[1] Incomplete growing season.

The data for the II-group females differ slightly from those
for the males.   The original difference of 8 millimeters between
the small and large yearlings was reduced to 7 at the end of the
second year.   However, this 1-millimeter loss was more than
made up in the third summer (difference of 9 millimeters at
capture).   At capture the medium-sized yearlings had lost 2
millimeters of their original 4-millimeter advantage over the
small yearlings but the large yearlings had added 3 millimeters
to their original 4-millimeter advantage over the medium-sized
group.

The most valid conclusion to be drawn from the data for the
II-group appears to be that individual differences in length in
existence at the end of the first year of life tended to be main-
tained with little or no change up to the time of capture late in
the third summer.   This conclusion is in agreement with Hubbs'
and Cooper's observation that second-year growth does not com-
pensate differences in length at the end of the first year. It dis-
agrees with their observation that differences in length at the
end of the first year are accentuated by the second-year growth.

The large yearlings of both the males and females of the

III-group rock bass of the 1932 collection (Table 52) were able to add to their first-year advantage in length over the small yearlings, but in both sexes a period of compensatory growth followed. In the males the first-year advantage of the large over the small fish (6 millimeters) was unchanged at the end of the second year of life. The third year saw the difference increased to 9 millimeters, but compensatory growth during the fourth summer, prior to capture, reduced the advantage of the large over the small fish to the original 6 millimeters. In the females the increase in the original difference in length (8 millimeters) between the large and small fish occurred in the second rather than in the third year of life. (This change agrees with that described by Hubbs and Cooper.) Growth compensation reduced the difference from 10 millimeters at the end of the second year of life to 6 millimeters (2 millimeters below the original) at the end of the third year and to 4 millimeters at capture in the fourth summer.

TABLE 52. *Relationship between length at the end of the first year of life and the growth in length in later years as determined from age-group III of the 1932 collection of Nebish Lake rock bass.*

Sex	Number of fish	Interval of calculated length in millimeters at end of first year	Calculated length at end of year of life				Calculated increment of length in year of life			
			1	2	3	1[4]	1	2	3	1[4]
Male	13	Less than 28	26	58	89	117	26	32	31	28
	15	28 to 30	29	60	96	123	29	31	36	27
	15	More than 30	32	64	98	123	32	32	34	25
	Maximum difference		6	6	9	6	..	..	..	..
Female	19	Less than 28	26	54	85	111	26	28	31	26
	22	28 to 30	29	59	89	115	29	30	30	26
	18	More than 30	34	64	91	115	34	30	27	24
	Maximum difference		8	10	6	4	..	..	..	..

[1] Incomplete growing season.

A more complete picture of the relationships among the growth increments of fish of different lengths in various years of life may be had from data based on collections of the 1923 year class (Tables 53 and 54). By means of a combination of the 1931 and 1932 collections of this year class[42] it was possible to obtain a reliable history of the growth of different sized year-

[42] The calculated lengths for the ninth year of life were determined by the addition of average annual increments of growth.

lings up to the time of capture late in the tenth growing season.

The three length groups of yearling males of the 1923 year class were separated by successive differences of 5 millimeters (Table 53). The second-year growth in length of the three groups was in the order of their first-year length. The small yearlings (32 millimeters average length) grew 24 millimeters in the second year; the medium-sized yearlings (37 millimeters average length) grew 26 millimeters; and the large first-year fish (42 millimeters average length) had a 27-millimeter growth. The difference between the second-year growth of the large and small yearlings increased the difference in their average size from 10 to 13 millimeters. During the third year the large and small fish had the same increase in length (30 millimeters), and the second-year difference was maintained exactly. The data for the next three years are irregular. The difference in the average length between the extreme yearling size groups dropped to the original 10 millimeters at the end of the fourth year, rose to 12 at the end of the fifth, and was again at the original level at the end of the sixth year. In the later years of life there was a period of clear-cut compensatory growth that began in the sixth year of life and extended to the end of the eighth year. Growth compensation in this period reduced the difference in the average lengths of the large and small fish from 12 to 4 millimeters. The latter difference was maintained through the ninth year and into the tenth up to the time of capture.

TABLE 53. *Relationship between length at the end of the first year of life and the growth in length in later years as determined from the males of the 1923 year class of the Nebish Lake rock bass, 1931 and 1932 collections combined.*

Number of fish	Interval of calculated length in millimeters at end of first year	Calculated length at end of year of life									
		1	2	3	4	5	6	7	8	9	[1]10
40	Less than 35	32	56	86	114	133	147	160	170	178	182
70	35 to 39	37	63	94	121	140	153	164	172	180	183
48	More than 39	42	69	99	124	145	157	166	174	182	186
Maximum difference		10	13	13	10	12	10	6	4	4	4

Number of fish	Interval of calculated length in millimeters at end of first year	Calculated increment of length in year of life									
		1	2	3	4	5	6	7	8	9	[1]10
40	Less than 35	32	24	30	28	19	14	13	10	8	4
70	35 to 39	37	26	31	27	19	13	11	8	8	3
48	More than 39	42	27	30	25	21	12	9	8	8	4

[1] Incomplete growing season

The large yearling females of the 1923 year class (Table 54) increased their initial 10-millimeter advantage over small yearling females by 6 millimeters in the second year of life, and added yet another millimeter in the third. There followed a period of compensatory growth (fourth to eighth year of life) which was broken only by an irregularity in the sixth year. (Note a similar irregularity in the fifth year in the data for the males.) Although the growth compensation brought about a material reduction from the largest maximum difference of 17 millimeters, the smallest maximum difference of 8 millimeters was only 2 below the original 10 millimeters.

TABLE 54. *Relationship between length at the end of the first year of life and the growth in length in later years as determined from the females of the 1923 year class of the Nebish Lake rock bass, 1931 and 1932 collections combined.*

Number of fish	Interval of calculated length in millimeters at end of first year	Calculated length at end of year of life									
		1	2	3	4	5	6	7	8	9	[1]10
57	Less than 35	32	56	83	108	125	136	146	154	162	167
85	35 to 39	37	64	96	114	132	142	151	157	164	168
31	More than 39	42	72	100	121	137	149	155	162	171	175
Maximum difference		10	16	17	13	12	13	9	8	9	8
Number of fish	Interval of calculated length in millimeters at end of first year	Calculated increment of length in year of life									
		1	2	3	4	5	6	7	8	9	[1]10
57	Less than 35	32	24	27	25	17	11	10	8	8	5
85	35 to 39	37	27	32	18	18	10	9	6	7	4
31	More than 39	42	30	28	21	16	12	6	7	9	4

[1] Incomplete growing season.

A comparison of the data for the males and females of the 1923 year class reveals that growth compensation produced the same reduction (9 millimeters) from the greatest maximum difference between large and small yearlings in each sex. In the males the advantage of the large over the small fish dropped from 13 at the end of the third year to 4 at the end of the eighth. The corresponding reduction in the females was from 17 at the end of the third year to 8 at the end of the eighth. The relatively large differences in length that separated the large and small female yearlings in later years are traceable therefore, not to the absence of compensatory growth, but rather to the excessive advantage of the large fish at the end of the third year of life.

If the data just described for age-groups II and III of the 1932 collection and for the 1923 year class can be considered to

be descriptive of the relationship between first-year size of rock bass and subsequent growth, the presence of considerable variation in the relationship must be recognized. Some of the variations can be brought out by the following brief summary. The original difference in length between large and small yearlings of the II-group males persisted at the end of the second year and late in the third summer. The females of the same age group underwent slight growth compensation in the second year, but the advantage of the large yearlings was increased during the third summer. The first-year difference in length between large and small yearling males of the III-group underwent no change in the second year, but in the third year the large fish increased their advantage by 3 millimeters only to lose the increase through compensatory growth during the fourth summer. In the III-group females there was an immediate increase (in the second year) over the first-year advantage of large fish over small ones, followed by rather pronounced compensatory growth. The males and females of the 1923 year class differed chiefly in the actual extent of the second- and third-year increase with respect to the original advantage of large over small yearlings. This increase was so much greater in the females that subsequent growth compensation, equal to that found in the males, failed to reduce the difference in length between the large and small female rock bass substantially below the first-year level.

In spite of the variations that do occur, it can be stated definitely that the relationship between first-year length and subsequent growth in length in the rock bass differs from that ordinarily found in that compensatory growth does not set in immediately after the first year. First-year advantage in size may be retained over one or two additional years, but more probably it will be increased in the second and/or third year (*cf.* Hubbs and Cooper, 1935). In the later years growth compensation does occur, but this compensatory growth may do little more than bring the difference in length between large and small yearlings back to the first-year level (1923 year-class females). Again, the growth compensation may bring about a substantial reduction in later years of the original differences in length between large and small yearlings (1923 year-class males; 1932 III-group females).

The question now arises as to the explanation for the deviation of the growth of the rock bass from the more common relationship between first-year length and later growth. Hubbs and Cooper (1935) offered four possible explanations for the positive correlation between first-year and second-year growth in three species of sunfish and one hybrid: (1) A "competitive advantage" during the second year traceable to the attainment of large size in the first; (2) the selection and occupancy during both years of a particularly favorable or unfavorable "ecological niche"; (3) some physiological effect of the rate of growth in the first year on rate of growth in the second; (4) "genetic differences in growth potential between different individuals." Conceivably any one of the above causes or any combination of them may contribute to the relationship described for the rock bass. There is no direct evidence available on the question. Nevertheless, there is good reason to believe that a fifth possible contributing factor should be considered in the explanation of the observed relationship in the rock bass between first-year length and later growth. This fifth possible explanation holds that the early increase in or maintenance of the first-year advantage in length and the later "compensatory" growth are to a certain extent "apparent" phenomena having their origin in the comparison of fish of different age (hatched at different times in the season).

The concept that an "apparent" growth compensation may result from the comparison of fish with identical growth curves but of different age is by no means new. Hodgson (1929) demonstrated conclusively that the comparison of annual increments of growth from curves that were *identical* in form but which started at different points on the time axis gave clear-cut examples of growth compensation.[43] However, Hodgson was dealing with a form (marine herring) whose annual growth increments decreased continuously, and not with one whose growth curve characteristically contains an inflection.[44] Consequently,

[43] Ford (1933) reviewed Hodgson's observations and added more detailed consideration of certain theoretical aspects of growth compensation.

[44] The statement that the growth curve of the rock bass characteristically contains an inflection is justified in spite of the fact that no inflection occurred in the general growth curve of the females and the inflection in the general growth curve of the males was not pronounced (p. 235). The

he was not confronted with a temporary increase in the original advantage of large yearlings.

The manner in which differences in age (time of hatching in the season) may affect the comparison of the growth increments of fish whose growth curves contain inflections may be seen from the examination of Figure 13. The curves a and b which may be taken as typical of large and small yearlings, respectively, are identical in form but originate at different points on the time axis (at t_a and t_b). Because of this difference in age the fish represented by the curve b were smaller than those represented by the curve a at t_1, the time of the formation of the first annulus (that is, AB < AC); furthermore, the fish of group b had the

FIGURE 13. Diagram to illustrate the effects of differences in age (time of hatching in the growing season) on the determination of the relationship between the length at the end of the first year of life and growth in later years. See text for explanation.

growth curves for individual fish contain inflections that are obscured in the computation of grand averages since the year of life in which these inflections occur varies from one individual to another. Curves for the year classes may or may not have inflections (Tables 17 and 18, Figs. 5 and 6).

smaller growth increment in the second as well as the first year of life (GE < FH). In the later years of life, however, the growth increments of the fish of group *b* exceeded those of the fish of group *a* and growth compensation occurred.

The curves as presented in Figure 13 describe only one particular situation. Only slight modifications of them would be necessary to produce variations similar to those appearing in Tables 51, 52, 53, and 54. As an illustration assume that the second annulus was formed at a point where the difference in length between the fish of groups *a* and *b* = NM, that the first annulus was formed at t_1 and the third at t_2. In this situation CB > NM < HG, and the data would show growth compensation in the second year followed by an increase in the advantage of group *a* in the third (*cf.* II-group females of the 1932 collection, Table 51). Nor would it be difficult to arrange a situation where CB = NM = HG, so that the fish of group *a* would retain a constant advantage over 3 years.

It seems, then, that the relationship between first-year length and later growth in length as observed in the rock bass can be duplicated by the comparisons of individuals with the same (theoretical) growth curves but of different age (hatched at different times in the first growing season). It does not appear unreasonable therefore to hold that the average differences in the growth of small, medium-sized, and large yearling size-groups may depend to an important degree on differences in age.

In spite of the evidence that the observed relationships among the annual growth increments may depend in part on differences in age, it would not be valid to contend that age differences alone are responsible. The explanations offered by Hubbs and Cooper for the positive correlation between first-year and second-year growth in sunfishes are biologically sound and therefore must be given consideration along with any other possible explanation. Furthermore, the thesis that growth compensation as a true rather than an apparent phenomenon does not occur among fishes is untenable in the face of known facts. For example, the well-known fact that salmon with an extended stream life grow more rapidly in the sea than do fish that are in the same year of life but which spent a lesser number of years in the stream can not well be interpreted as other than true growth compensation.

A wealth of experimental evidence supports the view that

among animals in general the inherent capacity for growth is lost chiefly through its exercise, and, conversely, the failure to grow does not entail necessarily the loss of the natural ability to grow. Experiments that involved the complete suppression of growth of the albino rat over periods of more than 408 days led Osborne and Mendel (1915) to conclude that, "The growth impulse or capacity to grow, can be retained and exercised at periods far beyond the age at which growth ordinarily ceases." From similar experiments with the albino mouse Thompson and Mendel (1918)[45] made the following observations on the growth of mice following long periods of growth suppression: "While a few cases of permanent stunting have been observed, the rate of growth, instead of being decreased, proves to be accelerated after suppression."

Observations to the effect that the ability to grow is maintained over long periods of inhibited growth are by no means limited to experiments with mammals. Similar results have been obtained for such widely separated groups as fish (Titcomb *et al.*, 1928), salamanders (Springer, 1909; Morgulis, 1912), and insects (Zabinski, 1929). Of specific application to the problem of growth compensation in fish is the observation of Titcomb *et al.*, that brook trout (*Salvelinus fontinalis*) subjected to continuous stunting for as long as 7 months not only retain the capacity for growth at the optimum rate but, "in some cases show an increased rate above our optimum."

The existence of growth compensation in fish as a true rather than "apparent" phenomenon must be recognized. However, the precise extent to which compensatory growth takes place may be obscured through the simultaneous occurrence of an "apparent" growth compensation traceable to differences in age (time of hatching in the season).

LENGTH-WEIGHT RELATIONSHIP AND CONDITION
ANNUAL AND SEASONAL FLUCTUATIONS IN THE
LENGTH-WEIGHT RELATIONSHIP

Tabulations of the length-weight relationship of the Nebish Lake rock bass were prepared for each collection,[46] sexes sep-

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[45] This publication contains numerous references to the literature on the effects of the suppression of growth on later growth on adequate diets.

[46] The July and August samples of 1930 were treated as separate collections.

arately. The examination of the data failed to reveal any consistent differences among the August, 1930, the 1931, and the 1932 materials. Consequently, these three collections were combined to form a general length-weight table (Table 55). The length-weight relationships as determined for the fish taken in July, 1930, and in 1935 are to be found in Table 56.

In Table 55, whose data may be considered descriptive of the length-weight relationship of the rock bass in late July and early August,[47] tabulations have been made for males and females separately and for the sexes combined. There is detectable a tendency for female rock bass to be slightly heavier than males of the same length. However, the differences are not large; neither are they consistent in their occurrence. A combination of the data for the sexes is therefore justifiable. This combination (at the right of the table) includes the small 1930 and 1931 specimens for which there were no sex records. There has been added also a tabulation of total length in inches[48] and weight in ounces. This general relationship is presented graphically in Figure 14.

It may be seen that the weight of the Nebish Lake rock bass at the minimum legal length of 7 inches is 3.3 ounces. Certainly, the present length limit imposes no hardship on anglers, for few would care to keep fish of less weight. The approximate total lengths at which weights of 4, 6, and 8 ounces are attained are 7.5, 8.5, and 9.5 inches, respectively. Only the largest males (average length, 9.6 inches) had an average weight in excess of a half pound.

The rock bass taken in July, 1930, were lighter, and those captured in August, 1935, were heavier (Table 56) than fish of corresponding lengths collected in August, 1930, and in 1931 and 1932. Since the rock bass of the July, 1930, collection were lighter than fish taken in August of the same year, their relatively low weights may be considered the result of the time of capture in the growing season. The rock bass captured in July,

[47] For dates of collection in each year see Table 2.

[48] Since female rock bass have a relatively shorter tail than males at lengths of 160 millimeters and greater (Table 11) the factor employed for the conversion of standard to total length over the interval, 162 to 191 millimeters, was 0.0477, the mean of the factors for the sexes. At the lengths 196 and 200 millimeters, which were represented by males only, the factor, 0.0479 was used.

TABLE 55. *Length-weight relationship of the Nebish Lake rock bass as determined from the combination of the August, 1930, collection and the complete collections of 1931 and 1932.*

	Males			Females			Sexes combined			
Number of fish	S. L.[1] in millimeters	Weight in grams	Number of fish	S. L. in millimeters	Weight in grams	Number of fish	S. L. in millimeters	Weight in grams	T. L.[1] in inches	Weight in ounces
3	200	251	..	..	...	3	200	251	9.6	8.9
3	196	218	..	..	...	3	196	218	9.4	7.7
13	191	199	5	191	203	18	191	200	9.1	7.1
44	186	185	4	187	191	48	186	185	8.9	6.5
70	182	173	22	181	173	92	182	182	8.7	6.1
62	177	163	62	177	161	124	177	162	8.4	5.7
62	172	154	84	172	152	146	172	153	8.2	5.4
14	166	138	61	167	140	75	167	140	8.0	4.9
12	162	125	74	162	125	86	162	125	7.7	4.4
5	156	112	57	157	113	62	157	113	7.5	4.0
12	152	104	54	152	105	66	152	105	7.3	3.7
9	147	93	28	147	94	37	147	94	7.0	3.3
13	143	81	19	143	86	32	143	84	6.8	3.0
6	137	73	9	138	79	15	138	77	6.6	2.7
8	132	65	8	131	66	16	132	66	6.3	2.3
8	127	58	6	127	61	14	127	59	6.1	2.1
23	121	52	17	121	50	41	121	51	5.8	1.8
10	118	48	28	117	46	43	117	47	5.6	1.7
7	112	40	17	112	40	26	112	40	5.4	1.4
6	106	32	8	107	35	16	107	34	5.1	1.2
14	102	30	12	103	31	27	102	30	4.9	1.1
11	96	25	6	96	26	20	96	25	4.6	0.9
25	91	21	25	91	21	56	91	21	4.4	0.8
30	87	19	25	87	19	74	87	19	4.2	0.7
5	82	16	8	83	18	38	82	17	3.9	0.6
..	..	..	..	..	..	13	78	14	3.8	0.5
1	74	12	..	..	..	3	72	12	3.5	0.4

[1] S. L. = standard length; T. L. = total length
[2] Actual value = 0.741.

TOTAL LENGTH IN INCHES
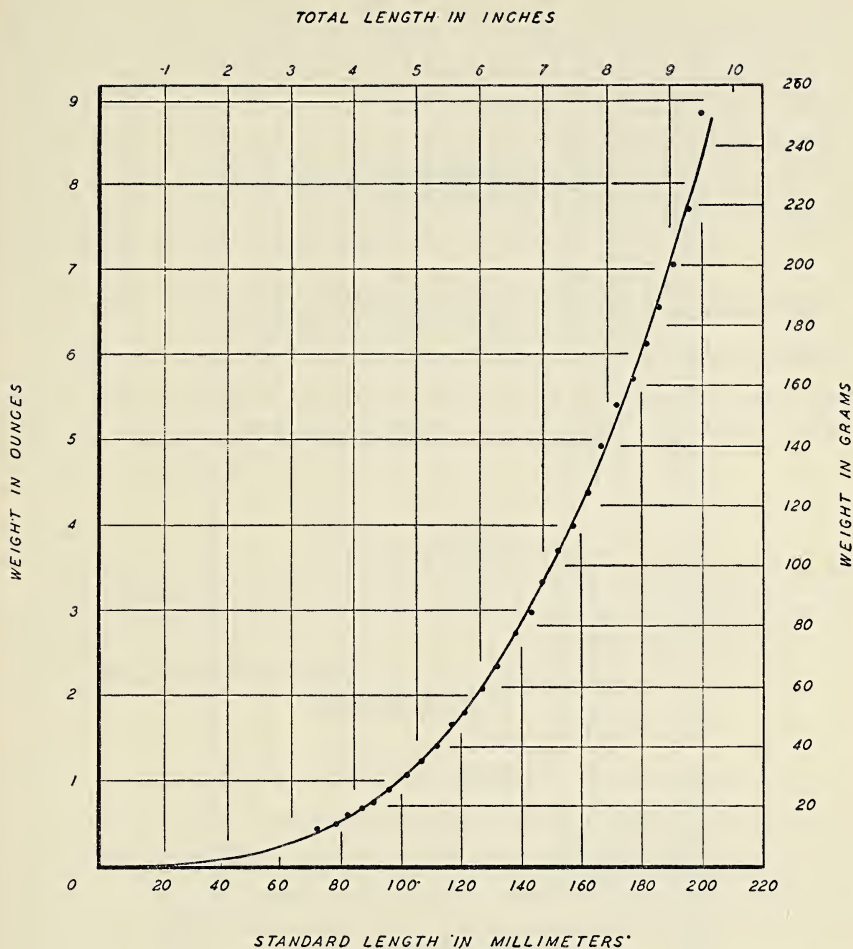
FIGURE 14. Length-weight relationship of the Nebish Lake rock bass (sexes combined) as determined from the combined collections of August 1930, and late July and early August 1931 and 1932. The curve is the graph of the equation fitted to the length-weight data, and the dots represent the empirical averages of length and weight.

1930, differed further from other rock bass taken in the years, 1930 to 1932, in the tendency for females to be lighter, not heavier, than males of the same length.

The time of capture in the growing season possibly may account for the relatively high weights of the rock bass of the 1935 sample. It was pointed out in the preceding paragraph that in 1930 rock bass became relatively heavier between early

TABLE 56. *Length-weight relationship of the Nebish Lake rock bass of the collections of July 5 and 6, 1930, and August 28, 1935. There were no sex differences in the 1935 collection.*

| | July, 1930 | | | | | | 1935 | | |
| | Males | | | Females | | | Sexes combined | | |
Number of fish	S. L.[1] in millimeters	Weight in grams	Number of fish	S. L. in millimeters	Weight in grams	Number of fish	S. L. in millimeters	Weight in grams
2	180	150	..	..	..	..	..	..
11	176	148	3	179	147	1	177	177
24	172	134	6	171	124	3	172	177
22	167	128	2	166	116	1	166	146
18	162	120	17	162	113	4	161	154
10	157	111	17	157	110	10	157	131
1	153	102	12	152	101	16	152	122
1	147	98	1	145	92	17	146	108
..	..	..	3	143	80	16	141	98
1	136	68	1	135	64	14	137	89
..	..	..	..	..	..	13	132	83
..	..	..	..	..	..	5	127	74
..	..	..	..	..	..	4	123	71
..	..	..	..	..	..	1	111	51

[1] S. L. = standard length.

July and early August. If this trend were to continue, the 1935 fish which were captured later in the season than were the rock bass of any previous year (Table 2) might be expected to be heavier than late-July and early-August fish of 1930 to 1932. However, in the absence of comparative material from earlier dates in the 1935 season, the possibility of an explanation on the grounds of an annual fluctuation in the length-weight relationship must not be overlooked.

MATHEMATICAL RELATIONSHIP BETWEEN LENGTH AND WEIGHT

Authors who have investigated the length-weight relationship of fish frequently have mentioned the fact that if form and specific gravity remain constant, this relationship can be expressed in mathematical terms by the equation:
$$W = CL^3,$$
where C = a constant.

Although the cubic parabola does describe the length-weight relationship accurately in some species, exceptions appear to be the rule, and in most forms better results are obtained by the use of the general equation:
$$W = CL^n,$$
where C = a constant,
and n = a constant.

The fitting of a parabola to the length-weight data of Table 55 (sexes combined) revealed that for those collections of the Nebish Lake rock bass the length-weight relationship follows the "cube law" almost exactly. The empirical equation was determined as:
$$W = 2.884 \times 10^{-5} L^{3.003},$$
where W = weight in grams,
and L = length in millimeters.

In logarithmic form the equation may be stated:
$$\log W = -4.54002175 + 3.003 \log L.$$

The comparison of the actual and the theoretical or calculated weights (Table 57) shows that the above equation fits the empirical data reasonably well. The 17-gram discrepancy at an average length of 200 millimeters (only three fish—see Table 55) provides the only large deviation of the calculated from the actual weight. Other deviations of as much as 4 grams occur

TABLE 57. *Comparison of actual and calculated weights of rock bass taken in August, 1930, and in 1931 and 1932, sexes combined.*

Standard length in millimeters	Actual weight in grams	Calculated weight in grams	Standard length in millimeters	Actual weight in grams	Calculated weight in grams	Standard length in millimeters	Actual weight in grams	Calculated weight in grams
200	251	234	157	113	113	112	40	41
196	218	221	152	105	103	107	34	36
191	200	204	147	94	93	102	30	31
186	185	189	143	84	86	96	25	26
182	173	177	138	77	77	91	21	22
177	162	162	132	66	67	87	19	19
172	153	149	127	59	60	82	17	16
167	140	136	121	51	52	78	14	14
162	125	124	117	47	47	72	12	11

among the larger fish, but below the length of 167 millimeters the maximum deviation is 2 grams. For all length groups the mean of the absolute values of the deviations is only a little more than 2 grams.

<p align="center">CONDITION</p>

Further information on the length-weight relationship of the rock bass may be obtained through the study of the coefficient of condition, *K*, whose value is calculated from the equation:

$$K = \frac{W \times 10^5}{L^3},$$

where W = weight in grams,
and L = length in millimeters.

The chief value of the coefficient of condition lies in the fact that *K* is a direct measure of plumpness or relative heaviness. Values of *K* can be compared, therefore, between fish of any size. The coefficient of condition was calculated for every Nebish Lake rock bass whose age was determined.

Table 58 contains a record of the average value of the cofficient of each age group (sexes separately) in each year's collection. The data for the three years, 1930 to 1932, resemble each other rather closely. There are differences, it is true, between the averages of *K* for fish of the same age taken in different years, but these discrepancies are in general not large and are random in their distribution. Females tend to have slightly higher values of *K* than males of the same age. The large values of *K* of the rock bass of the 1935 collection reflect a situation described previously (p. 307).

The changes of condition that accompany increase in age may be described from the averages of *K* for different age groups based on a combination of the 1930-1932 material. The variations of *K* with increase in age are decidedly irregular, but fish of both sexes nevertheless exhibit a tendency to become more plump as they grow older. This tendency is brought out much more clearly by the following tabulation based on combinations of age groups (number of specimens in parentheses) :

TABLE 58. *Coefficient of condition, K, according to sex, age, and year of collection, and K according to age and sex for the 1930, 1931, and 1932 collections combined. Number of specimens in parentheses.*

	Males					Females				
Age group	Year of capture				Average K for 1930, 1931 and 1932	Year of capture				Average K for 1930, 1931 and 1932
	1930[1]	1931	1932	1935		1930[1]	1931	1932	1935	
II	...	2.84 (10)	2.79 (78)	...	2.80 (88)	...	2.95 (9)	2.83 (59)	...	2.85 (68)
III	...	2.80 (6)	2.87 (43)	...	2.86 (49)	...	2.81 (7)	2.88 (59)	3.73 (1)	2.87 (66)
IV	2.87 (9)	2.85 (3)	2.79 (7)	3.44 (5)	2.84 (19)	2.89 (9)	2.95 (5)	2.84 (9)	3.52 (8)	2.88 (23)
V	2.93 (9)	2.97 (8)	2.84 (8)	3.50 (28)	2.91 (25)	3.00 (9)	3.01 (7)	2.86 (2)	3.53 (43)	2.99 (15)
VI	2.85 (3)	2.88 (5)	2.89 (3)	3.64 (4)	2.87 (11)	2.94 (6)	2.87 (10)	2.90 (8)	3.44 (9)	2.90 (24)
VII	2.94 (15)	2.92 (27)	2.90 (5)	...	2.92 (47)	2.91 (43)	2.95 (24)	2.95 (9)	...	2.93 (76)
VIII	2.93 (3)	2.95 (117)	2.83 (8)	...	2.94 (128)	3.02 (8)	2.98 (99)	2.93 (17)	3.54 (1)	2.98 (124)
IX	3.00 (2)	2.98 (18)	2.94 (41)	...	2.95 (61)	3.04 (2)	3.03 (47)	2.96 (74)	...	2.99 (123)
X	...	2.92 (4)	2.93 (10)	3.56 (1)	2.93 (14)	2.90 (1)	2.93 (17)	2.97 (33)	...	2.96 (51)
XI	...	...	3.03 (3)	...	3.03 (3)	...	3.04 (2)	3.07 (13)	3.19 (1)	3.07 (15)
XII	...	...	...	...	...	...	3.06 (1)	3.00 (3)	...	3.02 (4)
XIII	...	...	...	...	...	...	...	3.03 (1)	...	3.03 (1)

[1] August collection only; no age-determinations were made for fish taken in July, 1930.

Age groups	Average K	
	Males	Females
II, III, IV	2.82	2.86
	(156)	(157)
V, VI, VII	2.91	2.93
	(83)	(115)
VIII, IX, X	2.94	2.98
	(203)	(298)
XI, XII, XIII	3.03	3.06
	(3)	(20)

Coefficients of condition were calculated for a small collection of rock bass from Lake Wawasee in northern Indiana by Hile (1931). The collections were made in late June and in July, 1926 to 1928. The average K of the Wawasee rock bass (the range of ages covered was II to VII) was 3.25. A comparison with the Nebish Lake fish shows that the average K of the specimens from Lake Wawasee was intermediate to the averages found for the Nebish Lake stock in 1930 to 1932 and in 1935.

AGE AT MATURITY

All rock bass of age-group V or older were sexually mature.[49] Data on the maturity of the younger age groups (II, III, and IV), in the different years' collections are presented in Table 59. Differences in the nature of the available information for the different collections should be mentioned. In 1930 and 1931 the immature individuals simply were designated as such without record of sex. For these years it has been possible, therefore, to compute the percentage of maturity for the entire age groups but not for the sexes separately. The complete sex records for the 1932 collection have permitted the determination of the percentage of mature fish of each sex in each age group as well as in the age group as a whole. Records of maturity were not made for those 1932 specimens that were preserved for use in the study of the body-scale relationship. Only mature fish were captured in 1935.

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[49] A fish whose state of organs indicated that it would spawn the next season was designated as mature, even when it was relatively certain that it had not spawned during the year it was captured.

TABLE 59. *Maturity and its relation to length in age-groups II, III, and IV of the different years' collections of the Nebish Lake rock bass. All older fish were mature.*

Age group	Maturity	Sex	1930 Number	1930 Percentage	1930 Average length	1931 Number	1931 Percentage	1931 Average length	1932 Number	1932 Percentage	1932 Average length	1935 Number	1935 Percentage	1935 Average length
IV	Mature	Male	9	..	125	3	100	135	6	100	146	5	100	128
		Female	9	..	118	5	100	125	3	100	142	8	100	130
	Immature	Male	6	..	118	0	0	..	0	0	..	0	0	..
		Female		..	..	0	0	..	0	0	..	0	0	..
	Mature / Immature	Both do.	18	75	122	8	100	129	9	100	145	13	100	129
			6	25	118	0	0	..	0	0	..	0	0	..
III	Mature	Male	0	0	..	6	..	116	26	93	122	:	:	:
		Female	0	0	..	7	..	112	46	100	115	1	100	111
	Immature	Male	9	100	99	1	..	118	2	7	103	0	0	..
		Female		100	..		..	..	0	0	..	0	0	..
	Mature / Immature	Both do.	0	0	..	13	93	114	72	97	118	1	100	111
			9	100	99	1	7	118	2	3	103	0	0	..
II	Mature	Male	0	0	..	10	..	89	35	59	95	:	:	.
		Female	0	0	..	9	..	89	22	47	90	:	:	.
	Immature	Male	21	100	80	41	..	85	24	41	87	:	:	:
		Female		100	..		..	..	25	53	88	:	:	:
	Mature / Immature	Both do.	0	0	..	19	32	89	57	54	93	:	:	:
			21	100	80	41	68	85	49	46	88	:	:	:

The time of capture within the season (late July and early August) introduced a degree of uncertainty into the determination of the state of maturity of the smaller fish. The collections were made before the autumnal development of the gonads (preliminary to the next year's spawning) had set in, but at a time when the gonads of fish that had spawned in the year of capture had recovered from the post-spawning condition. Any possible distorting effect of errors in the assessment of the stage of maturity has been reduced greatly by the fact that all determinations were made by the same individual—Dr. Edward Schneberger—and therefore were based on the same criteria.

The youngest age group that contained mature individuals was the II-group. These fish would have spawned the next year at the end of the third full year of life (beginning of the fourth year). It is most unlikely that any of these II-group rock bass had spawned in the year of capture.[50] The oldest age group that contained immature rock bass was the IV-group. These immature fish would not have spawned at the end of the fifth year of life (beginning of the sixth), but the fact that all V-group rock bass were found to be mature indicates that they would have spawned at the end of the sixth year (beginning of seventh). It may be stated, therefore, that the age of the Nebish Lake rock bass at the first spawning, expressed in completed years of life, varies from 3 to 6.

The sexes reach maturity at approximately the same age. In the 1932 collection 59 per cent of the II-group males and 47 per cent of the II-group females were mature. The difference of 12 per cent cannot be considered important. In age-group III all of the 46 females and all but 2 of the 28 males were mature. Here, again, the difference between the sexes is not significant.

There was a general tendency for the percentage of mature fish at a particular age to increase over the 3-year period, 1930 to 1932. Twenty-five per cent of the 1930 IV-group were immature but all fish of this age group were mature in later years.

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[50] Age-group I was not represented in the 1930-1932 or the 1935 collections. However 10 I-group fish, captured (by means of a small-mesh fyke net) and examined in the summer of 1938 by staff members of the Wisconsin Geological and Natural History Survey, were all immature. The ages of these rock bass, whose lengths ranged from 56 to 76 millimeters, were determined by scale examinations.

The percentages of maturity of age-group III increased from 0 in 1930 to 93 in 1931 and to 97 in 1932. For age-group II the corresponding percentages were 0, 32, and 54.

The average length of an age group appears to be related to the percentage of mature individuals. This relationship is brought out sharply by the summary in Table 60 which permits a ready comparison of the annual fluctuations with respect to the average length of the age groups and with respect to the percentage of mature fish. The 1930 IV-group which was the only IV-group that contained immature individuals also had the lowest average length for fish of that age. In age-groups II and III each increase in average length was accompanied by a rise in the percentage of mature fish. (The single III-group rock bass captured in 1935—Table 59—may be disregarded.) The belief that the average size of an age group influences the percentages of maturity finds support in the observation (Table 59) that mature rock bass were consistently longer than immature fish of the same age and captured in the same year. (The 1931 III-group provides an exception, but this age group contained only one immature fish.) The data for 1932 demonstrate that the length advantage of the mature fish holds for the sexes separately as well as combined.

The data of Table 60 give some evidence that slow growth may in itself delay the attainment of maturity. For example, all individuals of the 1930 III-group were immature whereas the II-groups of 1931 and 1932, despite their smaller size, were 32 and 54 per cent, respectively, mature. Similarly the slowly growing 1930 IV-group contained a higher percentage of immature rock bass than did the slightly shorter III-groups of 1931 and 1932. Maturity appears, then, to depend on both size and

TABLE 60. *Relationship between the average length (in millimeters) and the percentage of mature individuals (sexes combined) in three age groups of the 1930-1932 collections of the Nebish Lake rock bass.*

Age group	Item	Year of capture		
		1930	1931	1932
IV	Average length	121	129	145
	Percentage mature	75	100	100
III	Average length	99	114	118
	Percentage mature	0	93	97
II	Average length	80	86	91
	Percentage mature	0	32	54

age. Within an age group the longer fish are the more likely to
be mature, but among fish of similar size, the younger are the
more likely to be mature. In other words, rapid growth seems
to be correlated with an earlier attainment of maturity.[51]

The legal size limit of 7 inches, total length, (146 millimeters,
standard length) is fully adequate for the protection of the
immature Nebish Lake rock bass. The largest immature speci-
men in the collections had a length of only 5.9 inches (123 milli-
meters). In fact, only 11 or 8.5 per cent of 129 immature indi-
viduals exceeded a length of 5 inches (104 millimeters).

SEX RATIO

Among the rock bass for which there were sex records the
females exceeded the males in abundance in each year's collec-
tion (Table 61). Records of sex were complete in 1932 and
1935. The sex was not recorded for the small, immature indi-
viduals in 1930 and 1931. In all collections combined there were
135 females per 100 males.

The incomplete records of 1930 and 1931 make the sex ratios
of the different collections unreliable for comparisons of the rela-
tive abundance of the sexes in the samples taken in different
calendar years. A better measure of fluctuations in the sex
ratio of the different years' samples can be had from the follow-
ing ratios computed from fish of age-group IV and older (prac-
tically all of the fish for which there were no sex records were
members of age-groups II and III):

Year of capture	Number of males	Number of females	Females per 100 males
1930	41	75	183
1931	182	213	117
1932	85	169	199
1935	38	62	163

For rock bass older than the III-group the number of females
per 100 males varied from a minimum of 117 in 1931 to a maxi-
mum of 199 in 1932. It is doubtful whether even these ratios
can be accepted as precise measures of the relative abundance of

[51] This relationship may have its application within a population rather
than between different populations. It is well known that so-called "dwarf"
stocks of several species may mature at an exceptionally small size.

TABLE 61. Numerical representation of the sexes in each age group of each year's collection and for each age group with all collections combined. Below, the sex ratio for each age group of the combined collections.

Year of Capture	Item	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	Total	Females per 100 males
1930	Number of males	..	..	9	9	3	15	3	2	..	..	..	..	41	183
	Number of females	..	..	9	6	6	43	8	2	1	..	..	..	75	
1931	Number of males	10	6	3	8	5	27	117	18	4	..	..	..	198	116
	Number of females	9	7	5	7	11	24	99	47	17	2	1	..	229	
1932	Number of males	78	43	7	8	3	5	8	41	10	3	..	..	206	139
	Number of females	59	59	9	2	8	9	17	74	33	13	3	1	287	
1935	Number of males	..	..	5	28	4	..	1	..	1	..	..	..	38	166
	Number of females	..	1	8	43	9	..	1	..	..	1	..	..	63	
1930 to 1932 and 1935	Number of males	88	49	24	53	15	47	128	61	15	3	..	..	483	..
	Number of females	63	67	31	58	34	76	125	123	51	16	4	1	654	..
	Females per 100 males	77	137	129	109	227	162	98	202	340	533	..	..	135	135

the sexes in the adult population. In one year (1931), at least, gear selection appears to have distorted the ratio (p. 322). It is valid nevertheless to state that a predominance of females is characteristic of the mature fish.

The variation of the sex ratio with age was irregular (Table 61). It is apparent, however, that females were strongly predominant at the higher ages (age-group IX and older). In all collections combined the males exceeded the females in number in only 2 (age-groups II and VIII) of the 12 age groups represented.

In spite of the great irregularity in the relationship between the sex ratio and age, the following tabulation wherein the age groups have been combined three at a time does give some indication of a general trend toward a greater relative abundance of females with increase in age:

Age Groups	Number of males	Number of females	Females per 100 males
II, III, IV	161	167	104
V, VI, VII	115	168	146
VIII, IX, X	204	299	147
XI, XII, XIII	3	21	700

In the combined data of all collections age-group VIII was the only one above age-group II in which the males outnumbered the females. If the 1931 VIII-group were excluded, the combined VIII-groups would contain 11 males and 26 females for a ratio of 236 females per 100 males. Furthermore, the exclusion of the 1931 VIII-group from the combined data for age-groups VIII, IX, and X would increase the sex ratio for those age groups from the listed value of 147 to the much higher figure of 230 females per 100 males.

There is good reason to believe that the sex ratios, 236 females per 100 males for age-group VIII and 230 females per 100 males for age-groups VIII to X, are more descriptive of true conditions than the corresponding values of 98 and 147 calculated from material that included the 1931 VIII-group. The high representation of males in that age group is in disagreement not only with the other VIII-group samples but also with

earlier and later samples of the same (1923) year class—the 1930 VII-group and the 1932 IX-group. An even more convincing argument for the exclusion of the 1931 VIII-group from the sex-ratio data is to be had from direct evidence that the exceptional scarcity of females in the samples of that group can be attributed to the selective action of gill nets.

The investigation of the rôle of gill-net selection on the determination of the sex ratio in the 1931 VIII-group may be confined to a study of the action of the 2½-inch and 3-inch mesh nets since nets of these two mesh sizes accounted for 110 of a total of 115 males and 87 of a total of 99 females of that age group taken in gill nets. The reason for the failure of the 2½-inch and 3-inch mesh gill nets to take a greater number of VIII-group females in 1931 can be brought out by a comparison of the length distributions of the VIII-group rock bass, according to sex, with the length distributions of rock bass that can be taken efficiently by nets of the two sizes of mesh (Table 62). Although nets with both 2½-inch and 3-inch meshes took rock bass over a rather large range of length, the limits within which the two sizes of mesh operated on the Nebish Lake stock with reasonably good efficiency may be set at approximately 145 to 184 millimeters and 165 to 194 millimeters respectively. These "limits of efficiency", which are admittedly arbitrary to a certain extent, have been indicated in Table 62 by horizontal lines.

Differences in the percentages of males and females whose lengths fell within the "limits of efficiency" of the two nets led to differences in the actual fishing intensity to which the sexes were subjected. Eighty-eight per cent of the males were of a length that could be captured by the 2½-inch mesh net and 98 per cent could be taken readily by the 3-inch mesh net (Table 63). All of the females were of a size that could be taken by the 2½-inch mesh net but only 26 per cent were sufficiently long to be taken easily by the 3-inch mesh net. As a result of this situation practically all of the males were subject to capture by either of two nets; the females, on the other hand, were sampled effectively by the 2½-inch mesh net only. The predominance of males in the samples of the 1931 VIII-group may be attributed, therefore, to the greater fishing intensity for fish of that sex.

TABLE 62. *Comparison of length distributions of VIII-group rock bass of 1931 and IX-group rock bass of 1932 with the length distributions of the total catch of 2½-inch and 3-inch mesh gill nets, 1931 and 1932 collections combined. The heavy horizontal lines set off the limits of effectiveness of the two meshes of gill net. Fish taken by hook and line have been omitted from the frequencies for the age groups.*

Length interval in millimeters	1931 VIII-group males	1931 VIII-group females	2½-inch mesh, all ages, 1931-32	3-inch mesh, all ages, 1931-32	1932 IX-group males	1932 IX-group females
200 to 204	..	..	1	1	..	..
195 to 199	1	..	..	3	1	..
190 to 194	..	..	2	13	5	1
185 to 189	13	..	5	40	10	..
180 to 184	34	..	14	69	12	1
175 to 179	28	2	13	100	9	12
170 to 174	30	14	34	85	3	21
165 to 169	8	10	24	30	..	14
160 to 164	..	31	45	5	..	15
155 to 159	..	22	36	2	..	4
150 to 154	1	19	32	..	..	..
145 to 149	..	1	12	1	..	..
140 to 144	..	..	5	..	..	..
135 to 139	..	..	1	..	..	..
Total number	115	99	224	[1]350	40	68

[1] One fish in interval, 115 to 119 millimeters, not shown in table.

The increase in the length of rock bass of the 1923 year class from 1931 to 1932 was sufficient to reduce greatly the distorting effects of gear selection on the determination of the sex ratio. The data of Tables 62 and 63 for the 1932 IX-group indicate a much more nearly equal fishing intensity for the sexes. In a corresponding manner the sex ratios as determined from the combined samples of the 2½-inch and 3-inch mesh nets and from the samples of all gears (including hook and line) were more nearly in conformity with the results for other samples of the older age groups.

TABLE 63. *Effect of the selective action of gill nets on the determination of the sex ratios of the 1931 VIII-group and the 1932 IX-group of the 1923 year class. See text for definition of "range of efficiency".*

Age group	Sex	Item	Gear			¹All gears
			2½-inch mesh gill net	3-inch mesh gill net	2½- and 3-inch meshes	
VIII	Male	Number taken by gear	28	82	110	117
		Percentage within range of efficiency	88	98	..	..
	Female	Number taken by gear	64	23	87	99
		Percentage within range of efficiency	100	26	..	..
		Sex ratio (females per 100 males)	229	28	79	85
IX	Male	Number taken by gear	6	29	35	41
		Percentage within range of efficiency	60	98	..	..
	Female	Number taken by gear	27	22	49	74
		Percentage within range of efficiency	99	72	..	..
		Sex ratio (females per 100 males)	450	76	140	180

¹ Includes rock bass taken by hook and line.

Gill-net selectivity doubtless affected the determination of the sex ratio in other individual age groups, but annual differences in the sizes of gill-net mesh employed and in the length distribution of fish at a particular age may have prevented the distortion of the data for the combined samples of any one age group. (For example, 1931 was the only year in which age-group VIII showed a predominance of males.) The distorted sex ratio of the sample of the 1931 VIII-group was exceptionally damaging to the general data on the relationship between the sex ratio and age because of the much smaller numbers of specimens in the VIII-group samples of other years. The effect of a similar predominance of males in 1931 VII-group[52] was reduced greatly because of the scarcity of males in the 1930 and 1932 samples of the VII-group.

The preceding detailed discussion of the effect of gear selection on the determination of the sex ratio was undertaken primarily to establish the validity of the general conclusion that the relative abundance of females tends to increase with increase in age. The data presented serve further to illustrate the extreme caution that must be observed in the use of gill-net samples for biological studies, and the importance of fishing with a wide variety of mesh sizes. The distortion of the sex-ratio data for the 1931 VIII-group most probably could have been avoided or at least reduced by the use of a 2¾-inch mesh net along with the 2½-inch and 3-inch meshes.

The increase in the relative abundance of the females with an increase in age points toward a differential mortality of the sexes. This differential mortality conceivably may be the result of a greater destruction of the males in the sports fishery or by predators, or it may depend on sex differences in the natural mortality rate; that is, the females may be inherently more viable than the males.

There are strong arguments against an explanation of the changing sex ratio on the basis of either of the first two of the three suggested possible causes listed above. It is true that the

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[52] Gill-net selectivity probably accounts for the abundance of males in the 1931 VII-group as well as in the VIII-group. The males of the two age groups had the same length, and the VII-group females were only 2 millimeters shorter than the VIII-group females.

male rock bass attain legal length approximately a year earlier than do the females (p. 222) and hence are subjected to mortality from fishing at an earlier age. On the other hand, it should be pointed out that the changes in the sex ratio were most pronounced at the later ages when the individuals of both sexes were well above legal size and a differential destruction in the fishery logically could not be expected. It is true also that the mortality from the very limited sport fishery was negligible.[53]

The selective destruction of the sexes by predators should cause the relative abundance of females to decrease rather than to increase with increase in age, since the more rapid growth of the males should carry them first to a size at which they are no longer subject to attack by larger fish. The size at which the Nebish Lake rock bass becomes too large to be attacked by predators is probably small. The only other species taken in abundance by the gill nets were perch and smallmouth black bass (p. 328).

The failure of other possible causes to explain the observed changes in the sex ratio leads to the conclusion that the inherent viability of females is greater than that of males. This conclusion that females enjoy the longer natural life span is in agreement with certain other investigations. Geiser (1923, 1924 a, b) held that a differential mortality of the sexes is general among animals, and that ordinarily the females are more viable than the males.[54] He cited numerous examples from literature to show that the relative mortality of the males is especially high under adverse conditions. Hile (1936a) believed that environmental conditions had an important effect on the sex ratios of the cisco populations of four northeastern Wisconsin lakes. In support of this belief he called attention to the fact that the four stocks followed "the same order with respect to growth in weight

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[53] Prior to 1934, Nebish Lake was very difficult of access. It could be reached only by means of narrow and rough "woods road" that followed the road-bed of a former lumber railway line.

[54] In the 1924b publication Geiser stated that there is "a direct relation demonstrated between the greater longevity (of the sexes) in animals and the possession of a duplex condition of the sex-determining chromosomes." Females would then be expected usually to have the longer lives because of the more common occurrence of the XX, XY type of sex chromosomes. Among the birds whose sex chromosomes are of the WW, WZ type the males live longer than the females.

and the average relative abundance of males", and concluded, "that the less viable males probably suffer greater mortality under adverse conditions that produce slow growth, and hence that the correlation between growth rate and sex ratio may be considered to result from the dependence of these two characteristics on the same environmental factors."

Sex differences in the rate of natural mortality do not provide the explanation for all of the changes of sex ratio with increase in age that have been observed. In the presence of an intensive fishery, sex differences in the age of entry into the fishery may have an important effect on the relationship between the sex ratio and age. Van Oosten (1929) who found that females exceeded the males in number in the younger age groups of the Lake Huron herring but were in the minority at the higher ages, attributed the shifting sex ratio to the earlier attainment of sexual maturity by the females and the consequent tendency for them to appear in and be destroyed by the commercial fishery at an earlier age. The same author (Van Oosten, 1939) believed that the lower age at maturity of the male Lake Huron whitefish led to their destruction in the fishery at an earlier age and thus accounted for the relative scarcity of males in the older age groups. Willer (1925) suggested that the sex ratio of the European lake herring (*Coregonus albula*) may be affected by selective destruction by predators, correlated with sex differences in size.

SPECIES ASSOCIATED WITH THE NEBISH LAKE ROCK BASS

The only species taken with the rock bass in the gill-net collections from Nebish Lake, 1930 to 1932, were the yellow perch, the smallmouth black bass, and the largemouth black bass (Table 64). The hook-and-line catches contained rock bass, perch, and smallmouth black bass but included no largemouth bass.

Over the 3-year period rock bass were approximately twice as abundant in the gill-net catches as perch and seven times as abundant as smallmouth black bass. The number of largemouth black bass was insignificant (only 2 fish in a total of 1,923). It is unlikely that Nebish Lake was supporting a population of largemouth bass at the time of the collections. More probably

the two small specimens taken in 1932 had been introduced. The data of Table 64 give some indication that the proportion of perch in the Nebish Lake fish stock may have been on the increase over the period, 1930 to 1932.

TABLE 64. *Species composition of gill-net catches in Nebish Lake, 1930-1932. In parentheses, catches of species other than rock bass expressed as percentages of the number of rock bass captured in the same year or years.*

Year of capture	Species			
	Rock bass	Yellow perch	Smallmouth black bass	Largemouth black bass
1930	144 ..	348 (33)	8 (6)	.. ..
1931	513 ..	213 (42)	85 (17)	.. ..
1932	492 ..	353 (72)	65 (13)	2 (0)[1]
Total	1,149 ..	614 (53)	158 (14)	2 (0)[1]

[1] Less than 0.5 per cent.

The number of fish in Table 64 should not be taken as indicative of the relative abundance of the species in the lake since the comparative facility with which gill nets capture the three species is unknown. The yellow perch, with its more slender form, might be expected to gill more readily than rock bass. On the other hand, there is reason to believe that smallmouth black bass may avoid gill nets, particularly if the webbing is light-colored. The introduction of more darkly colored nets was found to bring about an immediate increase in the catch of smallmouth bass.

Detailed information concerning the bathymetric distribution of rock bass, perch, and smallmouth black bass in Nebish Lake (presented by Hile and Juday in a paper appearing simultaneously with this report) reveals that to a large extent the three species occupy a common habitat in late July and early August. The only indication of segregation was detected in the tendency for the larger rock bass to occupy slightly deeper water than did perch, smallmouth black bass, and the smaller rock bass.

SUMMARY

1. The investigation of the Nebish Lake rock bass was based on data from 1,453 specimens. Ages were determined and growth histories were calculated for 1,215 individuals.

2. The validity of the annulus on rock bass scales as a true year-mark was established by the following observations:

(a) Fish assigned to the same age group have similar lengths.

(b) There was agreement between the age of small fish as estimated from length-frequency distributions and from scale examinations.

(c) Lengths calculated from scale measurements agreed well with the empirical lengths of younger age groups, including age groups whose ages were established from length-frequency distributions.

(d) Calculated lengths for corresponding years of life agreed well among fish of the same or different ages, but the agreement among different age groups of the same year class was better than among age groups of different year classes.

(e) Calculated growth histories for different age groups and different year classes agreed in showing growth to have been good or poor in certain calendar years.

(f) Certain year classes were persistently abundant or poorly represented in the collections of successive years.

3. Accessory or false annuli were a minor source of difficulty in the determination of age. The erosion of portions of the scale led to the rejection of the scales from a limited number of older rock bass.

4. The mathematical relationship between body length (L) and the length of the anterior radius of the magnified scale (S) was described satisfactorily by the equation:

$$L = 5.84011 \ S^{0.695992}$$

Computations of individual growth histories were made with the assistance of a table of solutions of this equation.

5. The average lengths and weights of the age groups tended to increase from 1930 to 1932. In 1935 most age groups aver-

aged shorter but heavier than the corresponding age groups of the 1932 collection.

6. The length-frequency distributions of the successive age groups ordinarily exhibited large overlap. Fish of the same length interval were represented in as many as six age groups. Only age-group II formed a distinct mode in the frequency distribution for all ages combined.

7. The youngest age groups with grand average lengths above the legal size limit of 7 inches, total length, (146 millimeters, standard length) were age-group V of the males and age-group VI of the females.

8. Where the number of specimens was large the calculated lengths of different age groups of the same year class agreed well. The growth histories of the year classes, however, exhibited rather large variations. These variations were sufficiently great to cause significant changes from one calendar year to another in the relationship of size to age.

9. The general growth curves for the population show that males grow more rapidly than females. The differential growth of the sexes is not distinctly apparent before the fourth year.

10. The rock bass grows more rapidly in Nebish Lake than in two neighboring lakes, Muskellunge Lake and Trout Lake, but much more slowly than in Lake Wawasee and Syracuse Lake in northern Indiana.

11. The growth of the Nebish Lake rock bass is subject to rather large annual fluctuations. The extremes of variation in the growth of rock bass beyond the first year of life occurred in 1931 when growth was 20.6 per cent above the 1922-1931 average and in 1928 when growth was 15.2 per cent below average. Annual fluctuations in first-year growth appear to be independent of fluctuations in the growth of older fish.

12. The strength of year classes also is subject to wide fluctuations. Exceptionally strong year classes were produced in 1923 and 1930. Year classes were very weak in the four years, 1925 to 1928.

13. In general, strong year classes occurred in years of good growth (in the second and later years of life) and weak year classes in years of poor growth. First-year growth, however,

was not correlated with growth in later years or with fluctuations in the strength of year classes.

14. The annual fluctuations in growth in the second and later years of life and the strength of year classes of the Nebish Lake rock bass exhibited correlations with variations in temperature and precipitation.

15. Good growth was correlated positively with high temperatures, especially in June and September. It was suggested that the temperature of these two months may determine annual fluctuations in the length of the growing season. Good growth and heavy precipitation in June also were correlated positively.

16. The occurrence of strong year classes in the rock bass of Nebish Lake was correlated with high temperatures and heavy rainfall in early season (May, June, and July), conditions in June being particularly significant.

17. The correlation between rainfall and the fluctuations in growth and the strength of year classes may depend on the enrichment of this oligotrophic lake by materials washed in during periods of heavy downpour. Temperatures may have a direct effect on the physiological processes of the fish or may affect the abundance of fish food in the lake.

18. Variations from year to year in population density, dependent on fluctuations in the strength of the year classes produced in earlier years, possibly may have an important effect on annual fluctuations in growth and in the survival of young.

19. For comparison, data were presented on the relationship between meteorological conditions and annual fluctuations in the growth and the strength of the year classes of the rock bass populations in the two neighboring lakes, Muskellunge Lake and Silver Lake, and on the strength of the year classes in Trout Lake.

20. The growth of the Muskellunge Lake rock bass was correlated closely with annual fluctuations in temperature. The coefficient of correlation between annual deviations in growth and June temperature was 0.75. No significant correlation could be demonstrated between growth and precipitation or between the strength of year classes and temperature or precipitation.

21. The limited data for the Silver Lake rock bass indicated annual fluctuations in growth rate somewhat similar to those of

the Nebish Lake rock bass. The occurrence of a strong year class in 1925 and possibly in 1928 disagreed with the Nebish Lake data.

22. Agreements such as those indicated by the existence of a positive correlation between temperature and the growth of rock bass in both Nebish Lake and Muskellunge Lake (and probably in Silver Lake also) and by the simultaneous occurrence of strong year classes of rock bass in 1923 in Nebish Lake, Muskellunge Lake, and Trout Lake point toward a common effect of weather conditions on the rock bass populations of the area. Other observations indicate that, in certain years at least, conditions peculiar to the individual lakes may play a dominant rôle. The growth fluctuations of the rock bass in Nebish Lake and Muskellunge Lake both were correlated significantly with temperature but were, themselves, weakly correlated ($r = 0.38$). Furthermore, the 1928 year class was strong in Muskellunge Lake (and probably in Silver Lake) but extremely weak in Nebish Lake, and the 1925 year class was exceptionally rich in Silver Lake but relatively poor in both Nebish Lake and Muskellunge Lake.

23. The greater part of the season's growth had been completed at the time of capture in late July and early August. At capture the older rock bass had completed a lesser percentage of the season's growth than had younger fish, and males had completed a smaller percentage of the season's growth than had females.

24. The superior late-season growth of the males accounts in large measure for the generally more rapid growth of rock bass of that sex.

25. The relationship between the length at the end of the first year of life and growth in later years is subject to considerable variation. First-year advantage in size may be retained over 1 or 2 additional years, but more probably it will be increased in the second and/or third year of life. Compensatory growth occurs in the later years.

26. The observed relationship between first-year length and later growth in length may be to some extent an "apparent" phenomenon traceable to differences in the age (time of hatching in the season of origin) of individuals. Nevertheless there are

also conclusive arguments for the existence of growth compensation as a real as well as an "apparent" phenomenon.

27. Male rock bass were slightly heavier than females of corresponding length in the collection of July 5 and 6, 1930, but females were slightly heavier than males in the combined collections of late July and early August, 1930 to 1932. No sex differences were found in the weights of fish of corresponding length in the collection of August 28, 1935.

28. Rock bass captured in 1935 were much heavier for their length than were fish captured in earlier years. However, the 1935 collection was taken later in the season than were the collections of previous years. Since fish captured earlier in the season (late July and early August) in three consecutive years (1930 to 1932) exhibited only small differences in the length-weight relationship, the high weights of the 1935 specimens may represent a seasonal rather than an annual fluctuation.

29. The mathematical relationship between the standard length in millimeters (L) and the weight in grams (W) of rock bass captured in late July and early August, 1930 to 1932, (sexes combined) was described satisfactorily by the equation:

$$W = 2.884 \times 10^{-5} \, L^{3.003}$$

This equation approximates the cubic parabola very closely.

30. The coefficient of condition, K, increased irregularly with an increase in age. Female rock bass of the 1930-1932 collections tended to have slightly higher values of K than male rock bass of the same age.

31. The first spawning of the rock bass may occur as early as the beginning of the fourth year of life (end of third) or as late as the beginning of the seventh year of life (end of sixth). The age at which a majority was mature varied in the different years' collections. Males and females mature at approximately the same age. The legal size limit of 7 inches affords full protection to immature fish.

32. The rate of growth affects the time of attainment of maturity. An age group that has grown rapidly may contain a higher percentage of mature fish than an older age group in which the fish are of greater average size but have grown slowly.

The mature individuals of an age group ordinarily average longer than immature fish of the same age.

33. Females were more abundant than males in each year's collection. The relative abundance of females increased irregularly with increase in age. The greater relative abundance of females in the older age groups indicates the existence of a differential natural mortality of the sexes.

34. The gill-net collections of 1930 to 1932 included 614 yellow perch, 158 smallmouth black bass, and 2 largemouth black bass in addition to the 1,149 rock bass.

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A CREEL CENSUS ON LAKES WAUBESA AND KEGONSA, WISCONSIN, IN 1939

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INTRODUCTION

Creel censuses have now been conducted on lakes Waubesa and Kegonsa for 4 years, beginning in 1936 (Juday and Vike, 1938; Juday, Livingston, and Pedracine, 1937; Frey, Pedracine, and Vike, 1939). Over this 4 year period there have been significant changes in the relative abundance of the different species of fish, which will be discussed in this paper.

During 1938 an attempt was made to contact all the fishermen using the lakes, but this proved to be impracticable with the help available. In the 1939 season with only the help of Lawrence Vike, a W. P. A. assistant, available on the project, it would have been even more difficult to contact the majority of the fishermen. Consequently, it was decided to confine our efforts to those boat liveries which cooperated best during the 1938 season. Four boat liveries were canvassed on Waubesa and 5 on Kegonsa. Each lake has 10 boat liveries with a total of 119 boats capable of being rented. In addition there were this past season 461 cottages on Waubesa and 416 on Kegonsa, many of which are occupied the year around. In spite of the large number of cottages on the lakes most of the fishing is done through the boat liveries.

Census cards were left with the boat livery operators, who filled out one card for each boat rented from them. Information desired on the cards consisted of number of fishermen, hours fished, and numbers of the various species of fish caught. No attempts were made to solicit more detailed information. The cards were collected once a week by Vike, who also obtained measurements on fish during the season, and performed other

duties pertinent to the census, as obtaining daily records of surface temperature and transparency on Kegonsa.

This census was made possible through Wisconsin Conservation Department and W. P. A. funds. Special thanks are also due the various boat livery operators for the excellent cooperation given during 1939. Each year as the men become better acquainted with the census methods and understand the reasons for conducting a census, the cooperation becomes more willing and more nearly complete.

TREND OF FISHING DURING THE SEASON

More than half of all fish recorded from Waubesa were caught during the first 3 weeks of the fishing season, from May 15 to June 5. During the latter part of June and the first part of July there were scarcely any fish caught. This slump was followed by a period of increased catch during the latter part of July, then a gradual decline for the rest of the season. It is interesting that in 1938 the weekly catch started out poorly, reached a season's maximum during the first part of July, and then declined gradually. Hence, even in the same lake fishing cannot be expected to be equally good at the same time in different years (Fig. 1).

The weekly catch in Kegonsa was uniformly small throughout the season. More fish were taken per week during the last 2 weeks of July than at any other time, coinciding roughly with the period of increased take in Waubesa though somewhat later. In Kegonsa likewise, the curve for 1939 is very different from that for 1938, the latter showing a pronounced peak during the first part of the season, followed by a gradual decline.

QUALITY OF FISHING

On the basis of the census cards completely filled out the catch per hour of effort was 1.53 fish for Waubesa and 0.82 for Kegonsa. For Waubesa 393 cards of 775 turned in contained complete data. Most of the cards classed as incomplete lacked only the number of hours fished. Assuming that the figure for average length of fisherman day for each week is representative of all fishing for that week and recalculating on this basis, the results are 2.25 fish per hour for Waubesa and 1.14 for Kegonsa.

More significant than these statements of average catch per unit effort are the curves showing the seasonal variation in the rate at which the fish were caught (Fig. 2). A comparison of Figures 1 and 2 reveals that the weekly figures for total fish caught and the rate at which they were caught follow each other quite closely, with the best fishing in Waubesa at the opening of the season and again during late July, and the best fishing in Kegonsa during late July and early August. As might be expected a curve for fishing effort plotted as hours fished each week has similar peaks and depressions. Except for the tendency of fishing effort to be greater during the weeks of Memorial Day, July 4th, and Labor Day, all three types of curves are in fairly close agreement. In lakes such as these readily accessible to many fishermen it seems that the total fishing effort and the resulting number of fish caught depend, with the exception of holidays, directly upon the rate at which the fish can be caught. If fishing is good, the word soon gets around, more fishermen use the lake and more fish are caught. As fishing becomes poorer, fewer fishermen use the lake, resulting in fewer fish being caught.

INFLUENCE OF LIMNOLOGICAL CONDITIONS UPON FISHING

As a supplementary project the general limnology of the lakes was investigated during 1939. Vertical series of water samples were analyzed physically, chemically, and biologically at bi-weekly intervals. Vike took daily readings of surface temperature and transparency in Kegonsa, curves for which are shown in Figure 1 to facilitate comparison with the weekly catch. The temperature curve can be regarded as representing conditions in Waubesa as well as Kegonsa, since our vertical series showed that the temperatures at similar depths in the lakes usually differed by not more than 0.1° or 0.2° C. on a given day. The peaks and depressions of the surface temperature curve follow closely the major fluctuations in mean daily air temperature recorded at the Madison station of the United States Weather Bureau.

Transparencies, measured by a Secchi disc, were not identical in the lakes on the same dates. In general, however, transparency in both lakes varied in the same direction, so that the

general fluctuations can be regarded as similar in the lakes. Transparency was usually several tenths of a meter greater in Waubesa than in Kegonsa. This might contribute to better fishing in Waubesa for those species which depend primarily on sight in locating and selecting food.

The low transparency in both lakes during the summer was produced by a heavy bloom of blue-green algae, chiefly *Microcystis*. Growth of algae in these lakes appears to be stimulated by the effluent from the Madison sewage disposal plant, amounting to about 10 million gallons daily (Frey, 1940). This treated effluent enters the river system just above Waubesa, does not reach Kegonsa until after passing through Waubesa and a 4 mile stretch of the Yahara River connecting the lakes. It has been the practice for several years to spray the lakes with a weak solution of copper sulfate in an attempt to control the algae. Both lakes were sprayed lightly in the summer of 1939.

During the last week in June and the first half of July there was a period of warm, calm weather, shown in Figure 1 by the extensive period of warm surface temperature in the lakes. As this occurred during the warming period of the lakes, there developed a resistance to mixing by light winds due to differences in density and viscosity of the surface and bottom water, and the lakes stagnated at the bottom. On July 6 there was no oxygen in the lower waters of either lake, and there was a marked thermal stratification. On July 20, however, following a period of colder, windy weather indicated in Figure 1 by the sharp depression in the temperature curve occurring about July 17, the lakes were disturbed to the bottom; oxygen was renewed at all depths, free carbon dioxide was eliminated from the lower waters, and by wind action the bloom of algae was broken up, causing the transparency to be more than twice as great in each lake as on July 6. There is no way of knowing at present whether these changes were merely coincidental with the period of better fishing occurring at this time, or actually some of the environmental conditions responsible for its production. It seems likely that the fish were stirred to greater activity by the physical and chemical changes.

NUMBERS AND POUNDS OF FISH REMOVED

As stated earlier in the paper it was impossible to obtain complete coverage of all fishing. For this reason all figures for total production are estimates, but estimates made as carefully as possible to make them reliable. The actual returns for each boat livery were raised according to the percent coverage given by that livery. By assuming that each boat from a non-cooperating livery had the same effectiveness in fishing as a boat from a cooperating livery, the total fishing done through the boat liveries was estimated. Finally, as in obtaining the production figures for 1938, it was estimated that 80 per cent of all Waubesa fishing was done through boat liveries, 75 per cent of all Kegonsa fishing.
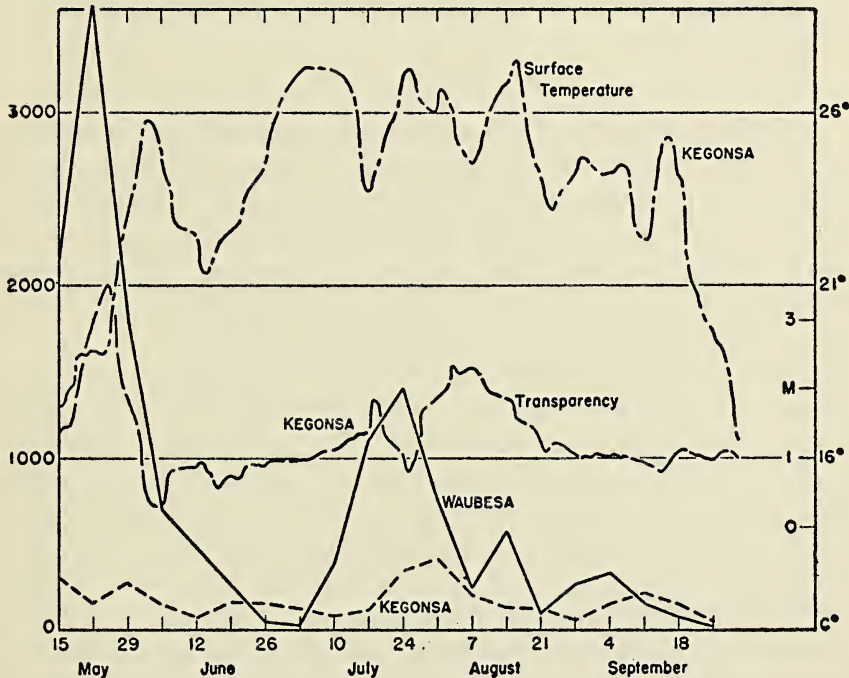
FIGURE 1. Fluctuations in reported weekly catches on Waubesa and Kegonsa during the 1939 fishing season. To facilitate comparisons, curves for surface temperature and transparency of Kegonsa are also shown. Both of the latter curves have been smoothed by a moving average of three and the scales for them are indicated in the right hand margin of the diagram. Transparency is indicated in meters.

TABLE 1. *Actual numbers of fish recorded on the census cards, percentage composition of the catches based on these numbers, and estimated total numbers and pounds caught. The method of obtaining the latter figures is discussed in the text.*

Species	Waubesa				Kegonsa				
	Larson	Hillside	Vingum	Oven	Sunnyside	Blegen	Dibbs	Colladay	Anderson
Bluegill	8.3	11.9	...	5.8	2.4	1.2	6.7	4.7	1.3
Pumpkinseed	...	...	0.1	0.6	...	0.2	...	...	0.3
Black crappie	82.2	81.6	98.5	89.7	46.9	9.4	27.6	26.6	48.8
Rock bass	0.1	...	...	0.1	...	0.1	1.5	0.7	0.2
Perch	3.0	0.7	...	...	6.6	0.7	3.7	17.2	5.0
White bass	3.0	3.8	1.1	1.5	38.9	86.1	42.5	43.8	36.2
Smallmouth bass	0.5	...	...	...	0.4	0.1	...	0.4	0.8
Largemouth bass	0.1	...	...	0.8	...	0.1	...	0.4	0.2
Wall-eyed pike	1.5	0.3	...	0.7	3.0	1.0	3.0	0.7	0.3
Northern pike	1.0	0.4	...	0.4	0.5	0.2	6.0	1.5	1.0
Bullhead	0.3	1.3	0.2	0.4	1.1	0.2	9.0	4.0	3.5
Carp	...	...	...	0.1	0.2	0.8	...	...	2.4
Total fish reported	1362	2174	8743	2257	1098	1281	134	274	621
Estimated percent cooperation	70	96	97	75	45	97	40	75	60
Number of boats	27	11	10	9	21	10	14	7	17
Fish per boat based on total estimate for each livery	72	206	910	334	116	132	24	52	61

Fishing during the 1939 season was decidedly poorer in both lakes than in 1938. In Waubesa half as many fish were caught as in 1938, in Kegonsa only one-fourth as many. Although Kegonsa is half again as large as Waubesa in surface area, there were 3 times as many fish caught in Waubesa. Twenty fish weighing 13½ pounds were caught per acre in Waubesa, and only 4 fish totalling 3 pounds per acre in Kegonsa.

The trends in population shifts observed in former creel censuses on these lakes continued in the directions previously noted (Frey, Pedracine, and Vike, 1939). In Waubesa crappies increased to 93 per cent of the total catch. All other species of fine fish decreased in relative abundance. Game fish (wall-eyed pike, northern pike, largemouth and smallmouth black bass) comprised less than 1 per cent of the total recorded catch. In Kegonsa white bass and crappies continued to increase in relative numbers, the latter more rapidly. All other species of fine fish continued to decline. Three per cent of the fish recorded were game fish.

Although it was assumed in making estimates of the total production that the fishing value of boats in cooperating and non-cooperating liveries is the same, for want of a better ad-

justment standard, it should be pointed out here that such is probably not the case (Table 2). Vingum's boat landing is located only a few hundred feet from one of the best crappie points in Waubesa. Hence, during the periods of good crappie fishing Vingum's boats were used more frequently than those of the other liveries. This helped raise Vingum's average to 910 fish per boat for the season; in contrast Larson's boats averaged only 72 fish. In Kegonsa the 2 boat liveries on the north shore, Sunnyside and Jens Blegen, showed 2 to 5 times as many fish caught per boat over the season as the 3 liveries on the southwest shore.

Table 2 shows likewise that the percentage composition of the catch from different liveries on the same lake is diffeernt. Vingum's and Oven's boat landings are on the steep, rocky east
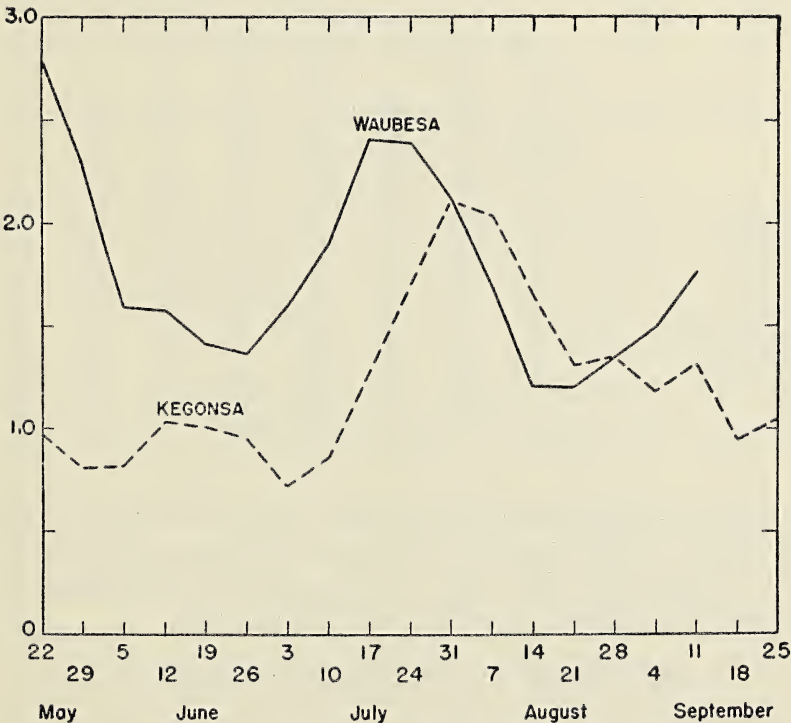
FIGURE 2. Weekly variations in fish caught per angler hour. These curves are based on figures adjusted for all cards having number of fishermen listed, on the assumption that the weekly figures for length of fisherman-day are representative also of the fisherman not reporting hours. Both curves have been smoothed once by a moving average of 3.

shore where the crappies tend to be concentrated. Larson and Hillside are located farther north on the east shore where the slope is more gradual and weeds more abundant. In Kegonsa the high percentage of white bass from Jens Blegen's landing is accounted for mainly by two men, who could catch numbers of white bass almost any time, even when other fishermen had little success. One can see that the records for one livery alone would not constitute an adequate sample of the season's fishing. The records for Oven's landing on Waubesa are the only ones which approximate the season's percentages for the entire lake.

TABLE 2. *Variation among the various boat liveries in amount and intensity of fishing, percentage composition of the catches, and estimated percentage coverage.*

Species	Waubesa				Kegonsa			
	Actual numbers recorded on cards	Percentage composition of catch	Estimated total fish caught	Estimated pounds fish per species	Actual numbers recorded on cards	Percentage composition of catch	Estimated total fish caught	Estimated pounds fish per species
Bluegill	505	3.47	1520	890	72	2.11	290	200
Pumpkinseed	18	.12	60	20	4	.12	10	5
Black crappie	13531	93.09	37550	24810	1048	30.75	4460	2460
Rock bass	4	.03	10	5	6	.18	30	15
Perch	60	.41	200	80	165	4.84	680	270
White bass	256	1.76	730	580	1932	56.69	6280	5390
Smallmouth bass	7	.05	30	70	11	.32	40	90
Largemouth bass	19	.13	60	130	3	.09	10	20
Wall-eyed pike	43	.30	140	230	54	1.58	230	380
Northern pike	32	.22	100	550	27	.79	120	660
Bullhead	56	.39	150	70	59	1.73	250	110
Carp	5	.03	20	50	27	.79	90	220
Totals	14536		40570	27485	3408		12490	9820

In spite of the fluctuations from one livery to another we feel that we have for the present purposes an adequate sample of the fishing from each lake, with possible slight overemphasis on crappies in Waubesa and white bass in Kegonsa.

TOTAL HOURS AND NUMBER OF FISHERMEN

Only half as many fishermen used Waubesa in 1939 as in 1938, one third as many fishermen used Kegonsa as in 1938. The total number of hours fished was correspondingly decreased. Waubesa again was more than twice as heavily fished as Ke-

gonsa. Waubesa fishermen fished ¾ hour less, yet caught 3 fish more per fisherman day than the Kegonsa fishermen (Table 3).

TABLE 3. *Total hours and fishermen, per acre estimates, and per diem estimates for hours and fishermen.* (a). Length of fisherman day was obtained from cards with complete information. (b). Estimated fish caught per fisherman day was obtained by multiplying (a) by the adjusted figure for fish caught per fisherman hour (see text). (c). Estimated total hours fished was obtained by dividing the estimated catch by the adjusted figure for fish per fisherman hour. (d). Estimated total fisherman-days was obtained by dividing (c) by (a).

	Waubesa	Kegonsa
Area in acres	2034	3145
Estimated total fisherman-days	4590	2340
Estimated total hours fished	18030	10960
Estimated fisherman-days per acre	2.3	0.7
Estimated hours fished per acre	8.9	3.5
Estimated fisherman per calendar day	35	18
Estimated hours fished per calendar day	140	80
Length fisherman-day (hours)	3.93	4.69
Estimated fish caught per fisherman day	8.84	5.35
Estimated pounds fish caught per fisherman day	6.0	4.2

SHIFTS IN RELATIVE ABUNDANCE OF SPECIES SINCE 1936 AS SHOWN BY CREEL CENSUS RETURNS

The relative abundance of the various species of game and pan fish in the populations as revealed by creel census data since 1936 has not been static, but has shown definite directional trends for all species except the perch in Kegonsa (Fig. 3). All other fish in the lakes have been either steadily increasing or decreasing in relative abundance during the period covered by census records. Bluegills and game fish (wall-eyed pike, northern pike, largemouth and smallmouth black bass) have been steadily decreasing in relative abundance, as have also perch and white bass in Waubesa. Each year in Waubesa black crappies have been increasing in relative bundance, until during 1939 they comprised 93 per cent of all fish caught by anglers. Both crappies and white bass have been increasing in Kegonsa, but the increase in relative abundance of white bass in 1939 may actually have been less than indicated. From Table 2 it can be seen that if Blegen's boat landing had been omitted from the census, the relative abundance of crappies would have been higher than 31 per cent, but white bass would have been relatively less abundant than in 1938. These data suggest that crappies
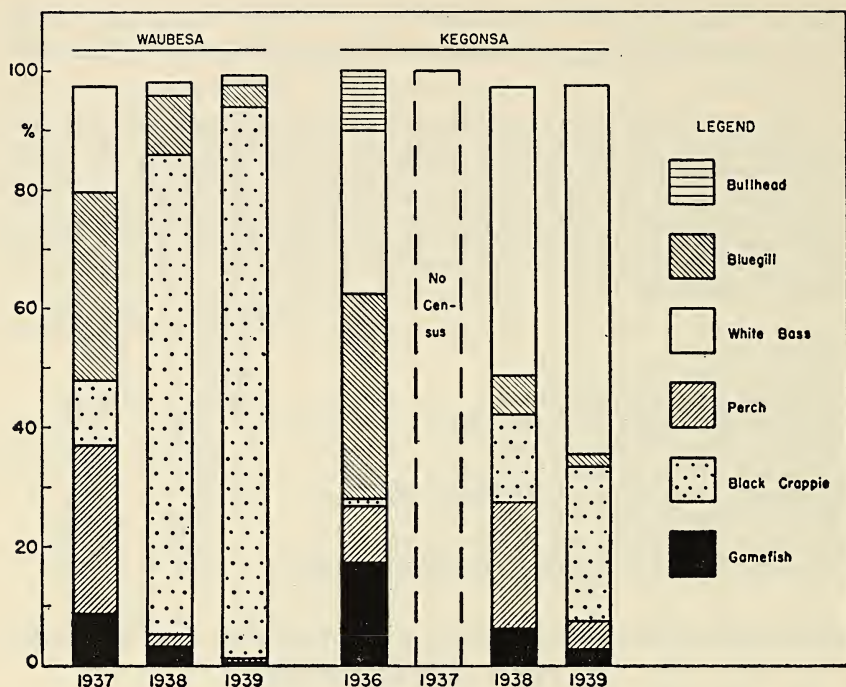
FIGURE 3. Shifts in relative abundance of the major species of game and pan fish in Waubesa and Kegonsa, based on creel census records beginning in 1936. For each figure the difference from 100 per cent is accounted for by several minor species, chiefly bullheads.

in Kegonsa are beginning to gain the upper hand, and soon may be displacing the white bass as the most abundant fine fish.

CORROBORATIVE EVIDENCE FROM CONSERVATION DEPARTMENT RECORDS

Both lakes have a large carp population and both lakes have been heavily seined in an effort to control the carp. Prior to 1936 the seining was carried out by commercial fishermen; but when the big hatch of carp appeared in 1936, the Conservation Department took over the job and has gradually displaced the commercial fishermen from these lakes.

Each time a seine is pulled in the lakes or a trap net lifted, the supervising conservation warden must report to the Conservation Department not only the estimated pounds of each species of rough fish removed, but also the estimated numbers of

each species of game and pan fish in the net. We were very fortunate to gain access to the original records in the Conservation Department files and from them have obtained interesting material substantiating and supplementing the creel census results.

It has been difficult to interpret the data because of the many variables involved. The estimates for each lake have not been made by the same man since 1934 but by at least 10 different men on each lake. Most of the conservation wardens estimated the numbers of fish by simple inspection with no attempt at a definite procedure. Only one warden attempted to arrive at fair
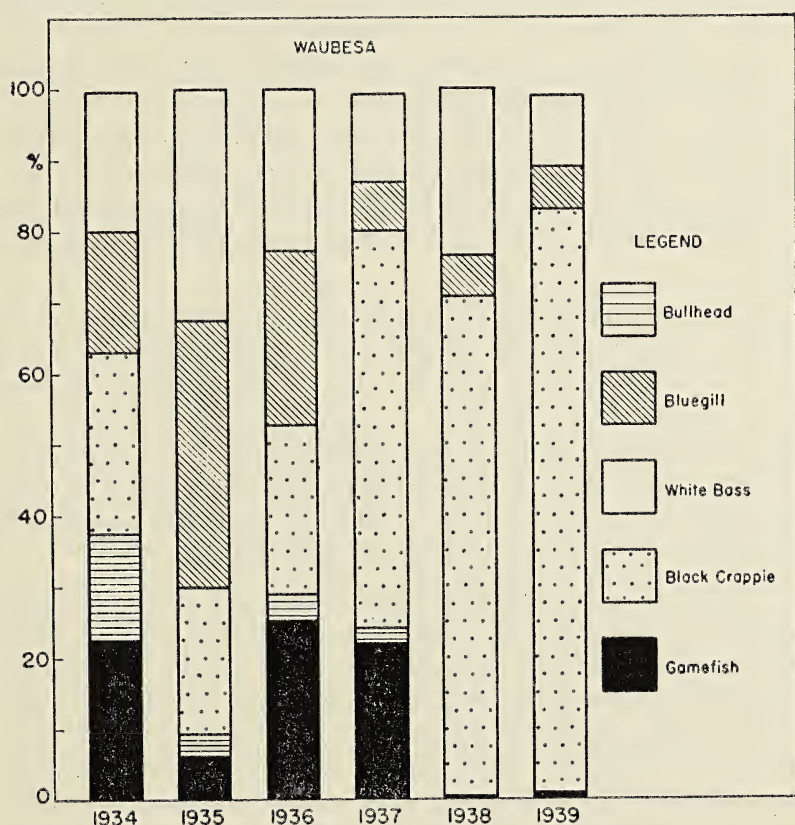
FIGURE 4. Fluctuations in percentage composition of game and pan fish in Waubesa. These percentages are based on estimates of numbers of game and pan fish in seine hauls by rough fish removal crews. For each figure the difference from 100 per cent is accounted for by small numbers of miscellaneous species.

estimates by counting the number of dip nets of fine fish and the average number of fish per net. It has been found that the wardens' estimates of pounds rough fish in a seine haul are seldom in error more than 15 per cent. No attempts have been made by the wardens to determine the magnitude of errors made in estimating numbers of fine fish, but until definite tests are made it may be assumed to be somewhat of the same magnitude as that of the rough fish estimates (Fig. 4 and 5).

Another variable involved is the gear—both length of seine and size of mesh. The length of seines used has varied from 1000 to 7000 feet, with an average of approximately 4500 feet. There was a tendency for the commercial fishermen to use larger size mesh than have the Conservation Department crews. During 1934, 1935, and the spring of 1936 the nets were usually 2-/or 3-inch stretch mesh in the bag to 5-/or 6-inch stretch in the wings. In the fall of 1936 the state crews used long minnow seines of ½ inch mesh to get the small carp. Next year the nets were ⅞- to 2-inch mesh, and in 1938 and 1939 were uniformly 2- to 4-inch stretch, increasing in size as the 1936 carp became larger.

A third variable is the size of the fish caught. In only a few instances was the average length of the various species stated. Hence, it is not known whether the large numbers of some species of pan fish appearing in certain years were all legal length, constituting part of the removable stock, or undersized and unimportant from the fisherman's immediate point of view. This might help explain a few of the discrepancies between the creel census records and the Conservation records.

In spite of these variables, there is a rather close agreement between the two types of records for Waubesa, and an agreement not quite so close for Kegonsa. The notable exception is the perch, which was abundant in the fishermen's catches in 1936 and 1937 but almost lacking in the seine hauls of those years. There are two possible explanations for this; either the perch, being a slender fish, was not held by the size net used, or else the perch, though caught, was not reported on the wardens' sheets, which contained no printed blank for number of perch.

Another discrepancy between the two groups of data is in the case of the wall-eyed pike. During 1938 there were large

numbers of undersize wall-eyes caught by the fishermen in both lakes, yet few were reported in the seine hauls. In 1939 there were fewer undersize pike caught by the anglers, but there was no compensatory increase in numbers reported from the seine hauls, and there was actually a decrease in numbers of legal length wall-eyed pike reported by the fishermen. With the exception of these two slender species, and possibly the northern pike as well, we feel that the seine hauls constitute an adequate sampling of the fish populations in the lakes because of the length of seines used and the sampling of nearly all habitats in the lakes. It would be desirable to establish a definite procedure for estimating numbers of game and pan fish in a seine haul to reduce errors from this source.

For shifts in the other species the two types of records are in rather close agreement. For Waubesa the shifts in relative abundance of the various species have the same general trends as those observed from the creel censuses (Fig. 4), namely; all fine fish have been decreasing in relative abundance except the black crappie, which increased to 82 per cent of the fine fish reported in the hauls in 1939. The sharp decrease of bluegills in 1937 is associated with a sudden rise in crappies. In 1938 game fish, which had remained consistently abundant in the hauls, declined to almost nothing.

Graphs for average numbers of each species per haul show a marked rise of crappies in 1937, a very sharp rise to 4400 per haul in 1938, then a fall in 1939. Game fish decreased in numbers after 1937. Bluegills were fairly constant in numbers except for a slight increase in 1938. During 1934 through 1936 fine fish averaged 600 per haul. In 1937 and 1939 they averaged 1600, and in 1938, 6200. The increase of fine fish per haul beginning in 1937 may be an actual increase in population or only an apparent increase produced by more efficient sampling with the small mesh seines used by the state crews. It is significant that the estimates for 1938, showing such a marked increase in crappies and lesser ones in bluegills and white bass, were made by the only warden who attempted to establish some basis for his estimates. It should be pointed out that the total fishermen's catch in Waubesa was almost twice as great in 1938 as in 1937

or 1939, roughly corresponding to the fluctuations in abundance in the seine hauls.

The records for Kegonsa (Fig. 5) are incomplete for 1936. Yet they also show interesting correlations with the creel census returns. White bass are the dominant fish and have been increasing in relative abundance. Crappies have slowly lost ground after an increase in 1936 or 1937. This observation is in disagreement with the census returns. Bluegills and game fish have declined in relative abundance, game fish quite markedly in 1938. The relative scarcity of game fish and bluegills in 1934 is more apparent than real, being produced by the great abundance of white bass in that year. This abundance does not seem to be
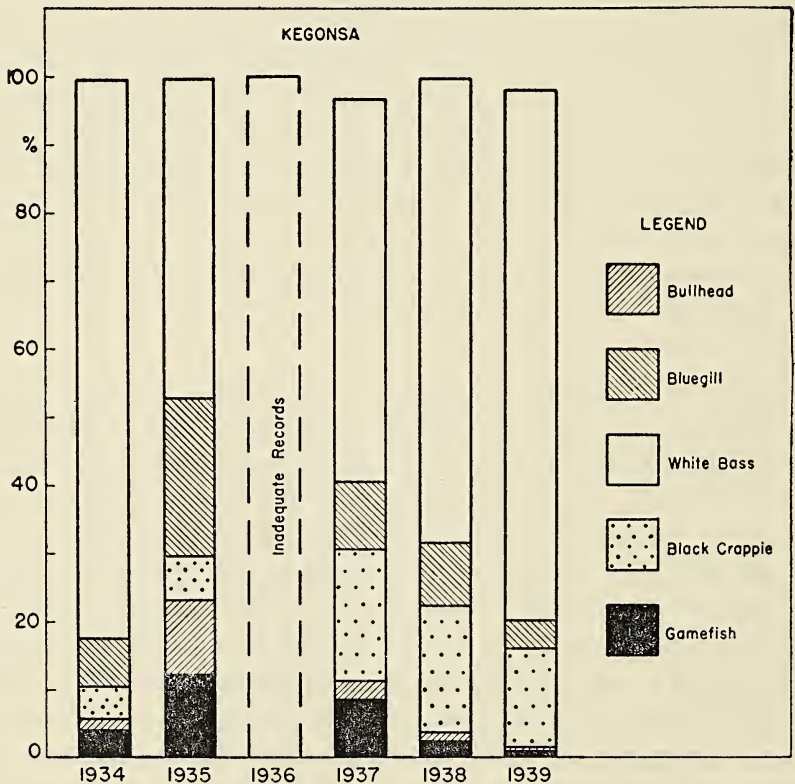
FIGURE 5. Fluctuations in percentage composition of game and pan fish in Kegonsa, based on Conservation Department rough fish removal records. There are no adequate records for 1936. For each figure the difference from 100 per cent is accounted for by small numbers of miscellaneous species. Compare with Fig. 4.

associated with exceptional white bass fishing; fishermen say that white bass fishing was only fair in 1934 through 1936, but was exceptionally good in 1937. The number of fine fish per haul was 200 greater in 1939 than in 1938, yet anglers caught only one-fourth as many fish in 1939 as in the previous season. Bluegills and game fish have decreased in average number per haul, game fish very sharply in 1938. It appears that the number of white bass caught by anglers does not necessarily correspond to the available numbers in the lake, as is evidently the case with the black crappie.

COMPARISON OF STOCKING WITH CENSUS RECORDS

Prior to 1935 the only kinds of fish regularly stocked in the lakes were wall-eyed pike and black bass. Conservation Department records, recently organized with W.P.A. help, show that a total of 46 million wall-eyed pike fry have been planted in Waubesa, 56 million in Kegonsa, usually at the rate of one or more million each year (Table 4). In Waubesa 110 thousand black bass of both species, mostly fingerlings, have been liberated, 163 thousand in Kegonsa. During the period 1886 through 1896, 3947 carp were planted in the waters of Dane County, but unfortunately the localities are recorded only as "Dane County" instead of the specific waters in which they were planted.

Each lake has received white bass plantings on two occasions. Waubesa received small plantings of 1000 fingerlings on August 29, 1919, and 2625 of miscellaneous sizes on September 20, 1927. Kegonsa was stocked with 400,000 white bass of miscellaneous sizes on June 6, 1891, and 2625 on September 20, 1927. The former large planting may well have contributed to the present dominance of white bass in Kegonsa. Beginning in 1935 a more intensive stocking program was begun; instead of stocking only wall-eyed pike and black bass there were also planted northern pike, bluegills, sunfish, black crappies, perch, bullheads, and even sturgeon.

In previous years both Waubesa and Kegonsa, especially the latter, were well known for their excellent wall-eyed pike fishing. Other game fish were also abundant. It could have been argued at that time that stocking was producing desired results, and such may well have been the case; however, even with continued
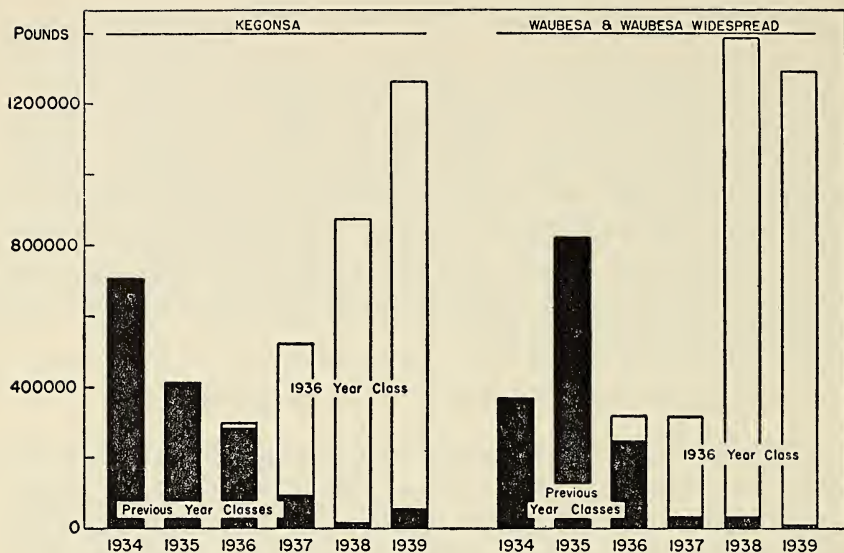
FIGURE 6. Estimated pounds of carp removed each year from Waubesa and Kegonsa during the period 1934 through 1939, based on Wisconsin Conservation Department records. The 1936 year class totals are separate from those of the other year classes to show the increasing dominance of this year class in the carp populations.

large yearly plants of wall-eyed pike fry and black bass fingerlings, the relative and actual abundance of these fish has decreased in the past few years. It is still rather early to decide what the effects are of stocking the pan fish, although the early plants of young bluegills, crappies, and perch would be expected to have yielded dividends in 1939, and the adults would be expected to have an immediate effect on the catch. These results are not evident from the census returns.

DYNAMICS OF THE FISH POPULATIONS

Composition of a fish population cannot always be managed simply by planting in a lake large numbers of immature fish of the species desired. Conditions in the lakes must be biologically favorable for the survival and growth of these fish.

Carp have become very abundant in the Madison lakes. The hatch and survival of carp is not uniform from one year to another, but occurs in peaks of abundance, separated by an interval of a few years. The hatch in 1931 was large, and the hatch in

1936 was truly astonishing. In that year 1¼ million carp fingerlings were seined and trapped in Kegonsa, 5¾ million in Waubesa, and 2 million more from the Yahara River adjacent to Waubesa. The Conservation Department requires its supervising wardens to make estimates of the number of pounds of carp caught in each seine haul by a rough fish crew, separating the total into four different sizes of carp—less than ¾ pound, ¾ to 2 pounds, 2 to 5 pounds, and more than 5 pounds. From Conservation Department records and from intensive studies on the growth rate of the 1936 year class of carp and the age composition of the carp populations since 1936, it has been possible to construct Figure 6 showing the pounds of carp removed each year and the amount of each total contributed by the 1936 year class (Frey, 1940). In the four year period 1936 through 1939 approximately 3 million pounds of 1936 year class carp have been removed from Waubesa and the Waubesa Widespread, 2½ million pounds from Kegonsa. The carp catch in Waubesa in 1939 amounted to 540 pounds per acre.

Abundance of carp fry and fingerlings in 1936 stimulated an increase in the more labile predator populations—white bass in Kegonsa and black crappies in Waubesa. Thompson and Bennett (1938) found in Horseshoe Lake of southern Illinois that the black crappie was more important than any other fish in the lake in eating small forage fish and the young of other game fish. The predacious habits of the white bass are well known. When trapping operations for carp were first begun in July, 1936, the carp fingerlings measured 2500 per quart, a size which could readily be eaten by any of the predacious fishes in the lakes.

During 1938 and 1939 nearly all black crappies caught by the fishermen and most of the white bass were of the 1936 year class (Fig. 7 and 8), the same as the carp. The records for 1936 show that most of the adult white bass in Kegonsa at that time were of the 1931 year class, corresponding to the abundant 1931 year class of carp. Either the same factors are responsible for the relative abundance of year classes of carp and white bass, or, as appears more likely, the survival and abundance of white bass is greatly influenced by the size of the carp hatch. No data were obtained on crappies in 1936 and 1937. It is interesting to suppose that the 1931 year class was abundant in this species also.
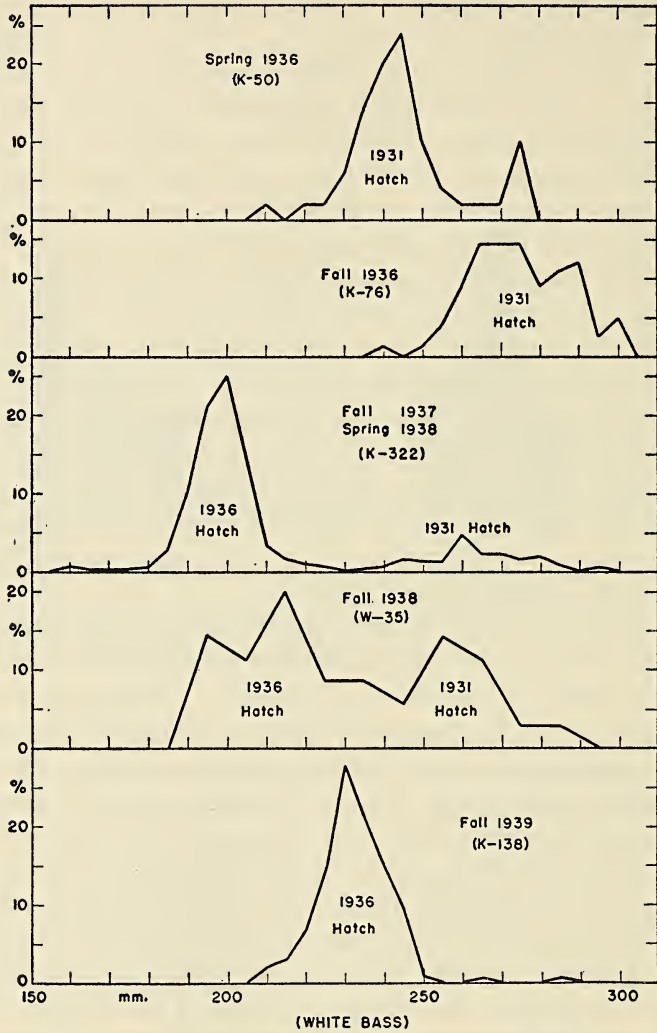
FIGURE 7. Shifts in length-frequency distribution and year class composition of the white bass population in Kegonsa and Waubesa. All curves are based on Kegonsa records except that for the fall of 1938. The height of a curve for any length-class is equal to the per cent of the total number of fish occurring in that length-class. Actual frequencies for each curve are listed in parenthesis. K = Kegonsa, W = Waubesa.

Carp grow so rapidly that only for a short time during the first season are they of a size small enough to be eaten by the lesser predators. Crappies and white bass which hatched in 1936 grew more the first season than did previous year classes,

as would be expected from the abundance of food. After the first season there was increased competition for food and less food to be had. The effects of food competition in the enlarged populations are strikingly shown among the 1931 year class white bass. In 1936 most of the white bass had 4 or 5 annuli on their scales depending on the time caught, placing them in the 1931 year class. No fish were found which could be assigned to the 1932 year class, and only a few belonged to the 1933 year class. Yet in the fall of 1937 the large white bass had 5 annuli
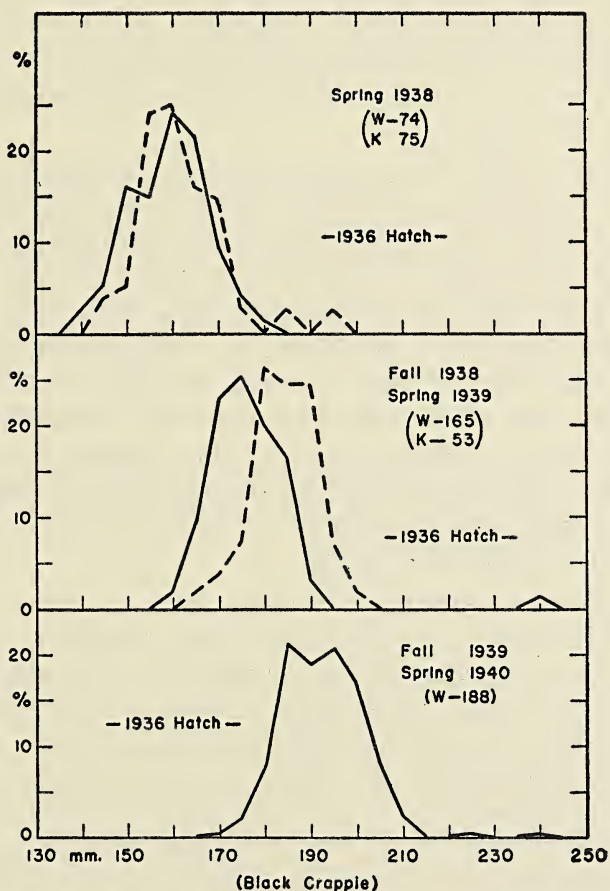
FIGURE 8. Shifts in length-frequency distribution and year-class composition of the black crappie populations in Waubesa and Kegonsa. Curves in solid line are for the Waubesa population, those in broken line for the Kegonsa population. Figures in parentheses are the frequencies on which each curve is based. K = Kegonsa, W = Waubesa. Compare with Fig. 7.

on their scales, placing them in the 1932 year class, and in 1938 there were still 5 annuli, which would ordinarily place these fish in the 1933 year class.   Growth calculations of these white bass showed such close similarity the only possible conclusion was that these fish all belonged to the 1931 year class.   Severe lateral resorption injury of the scales indicated the intense competition for food during 1937 and 1938.   Because of scarcity of food, the 1931 year class did not grow in length during 1937 and 1938 and hence failed to form annuli in these two successive seasons. Lack of growth in a year class might occur more commonly than one would be inclined to believe.   Thompson and Bennett (1938) observed that the 1932 year class of black crappies in Horseshoe Lake did not grow at all in 1936, 1937, and 1938 because of dwindling food supplies.

Although no fish census was conducted on Kegonsa in 1937, fishermen were unanimous in their opinion that this was one of the best years for white bass fishing they could remember. Fewer white bass were caught in 1938 and still fewer in 1939.   During 1937 and 1938, most of the 1931 year class white bass were removed from Kegonsa by the fishermen.   Crappie fishing in Waubesa was very good in 1938, not quite so good in 1937.   In the fall of 1937 most of the 1936 year class had reached legal size. Nearly all large crappies of previous year classes had been removed from Waubesa and Kegonsa by the spring of 1938.   Those white bass and crappies examined in 1938 were feeding largely on Daphnia and dipterous larvae.

It might be expected that a large hatch of carp each year could support large predator populations.   However, the rough fish removal operations of the Conservation Department were so intense that most of the large, mature carp were removed from the lakes.   The meager hatches of carp in 1937 and 1938 were easily controlled by the white bass and crappies, reducing the survival almost to zero.   In 1939 when the 1936 year class female carp spawned for the first time there were large numbers of eggs spawned and hatched in Waubesa and Kegonsa.   On July 11, 1939, there were estimated to be 270 million carp eggs attached to the weeds in Waubesa.   Previously large numbers of eggs had been found in *Cladophora* during late May and early June.   Fertility of the eggs varied from 30 to 95 per cent during

the season. In spite of the rather large hatch there was little survival, indicating the effectiveness of the natural controls. A few 1939 year class carp were caught in a 250,000 pound haul in Waubesa Widespread on April 15, 1940, but this constitutes the only evidence for survival of the 1939 year class.

Apparently the white bass and crappies have been eating all small fish in the lakes. Few forage minnows were found in 1939, although reports of fishermen indicate these fish were formerly abundant. There has been no detectable survival of white bass or crappies hatched since 1936, indicating either that the removal of large fish seriously depleted the spawning populations, or else that the small fry and fingerlings were quickly eaten.

Stocking of game and pan fish fry and fingerlings since 1936 has not resulted in the desired increase of these species, although there has been some survival of bluegill year classes since 1936. The decrease in gamefish, perch, bullheads, and bluegills noted from the fish census records and rough fish removal records has resulted from removal of the large fish by anglers with no effective replacements of small fish, possibly because they were eaten by crappies and white bass.

These disturbances in the fish populations may be expected to continue until a suitable balance is once again established between predators and prey. It is unlikely, however, that the lakes will soon return to the conditions existing before 1936, because of the serious depletion of rooted aquatic plants by the carp (Frey, 1940). In 1939 *Potamogeton pectinatus*, a narrow-leaved species, was the only higher aquatic plant of importance in Waubesa, with the minor exceptions of two small patches of *Potamogeton americanus* and one of *Vallisneria* at the outlet. No weeds of any kind were found at a depth greater than 1.6 meters. Restriction of the weed zone would affect those fishes which breed there or obtain most of their food in the weeds, such as the bluegill, small perch, crappie, largemouth bass, bullhead, etc. (Reighard, 1915). Hence, the decrease in abundance of some species may continue until rooted aquatics once more become plentiful in the lakes.

Conclusions

1. This census is based on returns from certain boat liveries which gave the best cooperation in 1938. Total production has been calculated from carefully considered estimates.

2. Fishing in Waubesa was only half as good in 1939 as in 1938, only one-fourth as good in Kegonsa. As estimated 40 thousand fish were caught in Waubesa, 12 thousand in Kegonsa.

3. Waubesa fishermen fished ¾ hour less, yet caught 3 fish more per fisherman-day than the Kegonsa fishermen.

4. Half of all Waubesa fish recorded were caught during the first 3 weeks of the season from May 15 to June 5.

5. Curves for number of fish caught per fisherman hour, weekly effort, and weekly catches follow one another rather closely, suggesting that in lakes like these near population centers the weekly effort and weekly catch depend directly upon the rate at which the fish can be caught.

6. There is evidence that the mid-season improvement in fishing resulted from a disappearance of stagnation conditions in the lakes following a period of cold, windy weather.

7. Ninety-three per cent of the fish caught in Waubesa were black crappies; 57 per cent of the Kegonsa fish were white bass.

8. In Waubesa crappies continued to increase in relative abundance; all other fine fish continued to decrease. In Kegonsa both white bass and crappies continued to increase at the expense of the other fine fish.

9. The large hatch of carp in 1936 stimulated an increase in the crappie population of Waubesa and the white bass population of Kegonsa.

10. Competition for food among white bass in Kegonsa was so keen after 1936 that the 1931 year class did not grow in length during 1937 and 1938, and hence did not form annuli on their scales.

11. Game fish were formerly more abundant than during the past few years, although intensive stocking of these species has continued unabated. Stocking of pan fish species, while rather recent, likewise does not seem to be producing the desired re-

TABLE 4. *Number and kinds of fish used by the Conservation Department in recent years in stocking lakes Kegonsa and Waubesa.*

Lake	Year	WE-Pike Fry/Ad.	Black Bass Fing.	Black Bass Ad.	Black Bass Misc.	Nor. Pike Fing.	Bluegill Fing.	Bluegill Ad.	Bluegill Misc.	Sun-fish Fing.	Black Crappie Fing.	Black Crappie Ad.	Black Crappie Misc.	Perch Eggs	Perch Fry	Perch Fing.	Perch Ad.	Perch Misc.	Bullhead Fry	Bullhead Fing.	Bullhead Ad.	Sturgeon Ad.
Waubesa	1939	6250000	6400	21			5000				25800	3000		6773760		15000				25000		
	1938	5419704	1000	54			8000									20000				3000		
	1937	5902000	214	65		3750	31000	4000			16000	4000				42000	1700				500	21
	1936	2055000	4860			3820								4410000	3520000	1320						
	1935	3421000	14525		3600	3750																
	1934	987525							6300				2200					4000				
	1933	1312500	1875																			
	1931	486240																				
Kegonsa	1939	6250000	10000				2000			12000	10000	2000		2903040		20000	200		2000			
	1938	5419704	500				25000	2000				5000				12000				22000		
	1937	5975830	2300	30	178	11409	30000	2000							352000	22600	7200				6000	
	1936	2055000	3540			4480										1980						
	1935	3421000	14525		2400	3750			5500				3000					2000				
	1934		1960																			
	1933	1312500	5174																			
	1931	1094040	2500																			
	1930	2463126																				

sults.   White bass and crappies have greatly reduced the effectiveness of propagation of these species, both by natural and artificial means.

12. White bass and crappies have prevented a noticeable survival of the 1937 and 1938 year classes of carp, and have greatly hindered the survival of the 1939 hatch which was considerable.

13. Eating and uprooting of weeds by the carp has reduced the breeding and feeding habitats of such fish as bluegills, crappies, small perch, largemouth bass, etc.   The only weed of importance in Waubesa in 1939 was *Potamogeton pectinatus*.

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THE CHLOROPHYLL CONTENT AND PRODUCTIVITY OF SOME LAKES IN NORTHEASTERN WISCONSIN*

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Introduction

The chlorophyll content of the lakes of northeastern Wisconsin was first studied by Kozminski (1938). In most cases, he made only one series of determinations at various depths for each lake. More recently, Riley (1940) has published the results of several series of chlorophyll determinations in a Connecticut lake (Linsley Pond).

Kozminski found a considerable diversity in the types of vertical distribution of chlorophyll in the various lakes he studied, and proposed a tentative classification of the lakes based on chlorophyll distribution. However, Riley found that the chlorophyll distribution in Linsley Pond during the nine-month period of observation passed through four of the five types which Kozminski described in his classification. Riley concluded that Kozminski's classification, while biologically significant, probably had little or no typological value.

In the present investigation, which was limited to two months, July and August, in the summers of 1938 and 1939, repeated observations were made on the vertical distribution of phytoplankton chlorophyll in several of the lakes studied by Kozminski. In some of the lakes, a considerable variation in distribution was found within this two-month period.

Another phase of this investigation has been the correlation of the chlorophyll observations with measurements of photosynthetic capacity. This phase is important in relation to the problem of lake productivity. If the chlorophyll content of a

sample of lake water may be used as a measure of photosynthetic capacity, it is evident that the determination of chlorophyll affords a convenient method of evaluating the biological productivity, or at least the phytoplankton productivity, of a lake. Riley (1940) found only a slight correlation between chlorophyll content and photosynthetic capacity in Linsley Pond. However, the results given below indicate that in the Wisconsin lakes, with certain limitations, the chlorophyll content of the upper waters of a lake may be used as an approximate index of photosynthetic capacity.

The contribution of higher aquatic plants to photosynthetic productivity has not been studied in this investigation. In most cases, photosynthesis by the higher plants would be a small, though not negligible, fraction of the total photosynthesis in a lake.

<div align="center">METHODS</div>

Chlorophyll determinations.—The method used for determining chlorophyll, except for a few modifications, was essentially that described by Kozminski (1938).

Instead of a pump, used by Kozminski, a sampling bottle of three-liter capacity was used to obtain all sub-surface samples of lake water. Except for its larger size, the sampling bottle was like one previously described (Meloche, Leader, Safranski and Juday, 1938). In all cases, samples were taken near the point of greatest depth for each lake. The deepest sample was usually taken one or two meters above the bottom of each lake. The amount of lake water used for a single determination varied from a half liter, for some of the Scaffold Lake samples, to eight liters for samples from Crystal Lake. The plankton material was concentrated by passing the sample of water through a Foerst centrifuge[1] at a rate of approximately one liter every five minutes. It was found to be necessary to centrifuge each sample from Scaffold Lake three times to obtain approximately complete removal of the chlorophyll-bearing organisms. A single centrifuging was sufficient in all other cases, except for certain samples of water blooms where the results are only indirectly related to the present investigation. Kozminski used a Sharples

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[1] This centrifuge is similar to one previously described (Juday, 1926) but with a three inch bowl and a speed of 50,000 r. p. m.

supercentrifuge in his investigations, but the Foerst centrifuge was found to be as efficient, and more convenient because of the ease with which the residue could be removed from the centrifuge bowl. The Foerst centrifuge was also used in the determination of total particulate organic matter (expressed as the difference between dry weight and ignited weight of the centrifuge residue).[2]

For the chlorophyll determinations, most of the water remaining with the centrifuge residue (usually ten to fifteen ml.) was removed by transferring the residue to a small rotating-arm centrifuge, centrifuging for five to fifteen minutes and then pouring off the supernatant water. Chlorophyll and other pigments were then extracted by adding acetone to the residue in the centrifuge tube. After a brief centrifuging, the acetone extract was poured off into a 25 ml. volumetric flask, and a fresh sample of acetone added to the residue. After two, or occasionally three, treatments with acetone, the extraction was complete. The combined extracts were made up to a volume of 25 ml. with additional acetone, and the chlorophyll then determined with a photoelectric colorimeter, using a red filter to eliminate the effect of carotenoid absorption in the blue and green. In the summer of 1938, a modified Cenco "Photelometer" was used, as described by Kozminski (1938). In the summer of 1939, the procedure was the same except that an Evelyn photoelectric colorimeter was used. The #660 red filter available with this instrument gave greater sensitivity than did the Corning #243 filter which was used with the Cenco colorimeter. For both instruments, a calibration curve was obtained by using a sample of chlorophyll obtained from the American Chlorophyll Company, which presumably consisted of approximately three parts of chlorophyll *a* to one of chlorophyll *b*. Undoubtedly, this ratio varied somewhat in the samples of phytoplankton which were investigated. Since the red absorption band of chlorophyll *b* is weaker than the *a* absorption band, variations in the ratio of the two components result in errors in the determination of total chlorophyll. However, it is probable that chlorophyll *a* was always consider-

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[2] For the most part, data on particulate organic matter were obtained by other investigators. We are indebted to Dr. C. Juday for making these data available for use in the present paper.

ably in excess of chlorophyll *b,* so that the error due to this factor probably did not exceed ten per cent.   Another possible source of error is the ease with which cholorophylls *a* and *b* are decomposed into the corresponding phaeophytins, for which the intensity of red absorption is somewhat different[3].   The absolute magnitude of the error due to this factor cannot be evaluated in the present work, but since the treatment of each residue was very similar, the relative error is probably smaller than the absolute error.

Photosynthetic measurements.—The photosynthetic capacity of water samples, as a function of light intensity, was determined by suspending the material for several hours in clear bottles at different depths in Trout Lake.   The time of exposure was varied between one and nine hours, depending on the approximate phytoplankton content of the sample.   The resulting changes in dissolved oxygen were measured by the Winkler method.   The details of the general procedure have been given previously (Manning, Juday and Wolf, 1938).   Each sample of water was adjusted approximately to the temperature of the upper waters of Trout Lake, and thoroughly aerated before being transferred to the photosynthesis bottles.   During these investigations, the temperature of the Trout Lake water averaged about 22.5° C., with a variation of about 2° C. in either direction.

Light intensity measurements.—The amount of solar radiation incident on the surface of Trout Lake during the photosynthesis experiments was measured with a recording solarimeter; the percentage of transmission by the water was determined with a thermopile or photocell apparatus which could be lowered to any desired depth (Birge and Juday, 1932; Whitney, 1938).

Morphometric data.—The morphometric data used in calculating the total chlorophyll and particulate organic matter content of the various lakes is given elsewhere (Juday and Birge, 1941).

RESULTS

Chlorophyll determinations

Weber Lake.—The results of the chlorophyll and organic matter determinations for Weber Lake are shown in Table I and

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[3] F. P. Zscheile and C. L. Comar, private communication.

TABLE I

Distribution of chlorophyll in Weber Lake.

The upper figures for each date represent chlorophyll concentration in mg/m³; the lower figures, in italics, show the ratio of chlorophyll concentration to the concentration of particulate organic matter. The 1937 results were obtained by Kosminski.

Depth (meters)	7/30/37 7/29/37	7/14/38	7/28/38	8/12/38	8/25/38	7/10/39	7/17/39	7/24/39	7/31/39	8/7/39	8/14/39	8/21/39	8/28/39
0	1.9 / *.0011*	3.2 / *.0027*	5.4 / *.0032*	3.7 / *.0019*	2.4 / *.0019*	8.1 / *.0035*	5.4 / *.0024*	5.0 / *.0031*	3.1 / *.0026*	2.8 / *.0023*	2.4 / *.0030*	2.8 / *.0021*	1.7 / *.0018*
2	3.0 / *.0019*												
3	2.1 / *.0014*		5.6	3.5	2.1	8.8	7.1	4.5	2.9	2.9	2.5	2.1	1.9
4		3.0 / *.0020*											
6	2.3 / *.0027*	4.1 / *.0030*	6.2 / *.0058*	4.6 / *.0041*	2.2 / *.0013*	10.0 / *.0042*	7.6 / *.0047*	5.4 / *.0041*	4.0 / *.0036*	3.4 / *.0035*	2.9 / *.0041*	2.1 / *.0030*	2.1 / *.0034*
7	3.1 / *.0029*												
8	3.5 / *.0036*	5.8	6.0 / *.0039*	5.5 / *.0040*	2.7 / *.0020*	10.0 / *.0035*	10.0 / *.0056*	7.7 / *.0045*	5.1 / *.0050*	2.9 / *.0032*	3.5 / *.0058*	3.5 / *.0019*	2.9 / *.0046*
10			5.6 / *.0050*	4.5 / *.0049*	6.7 / *.0073*	8.9 / *.0043*	7.6 / *.0042*	8.5 / *.0053*	5.1 / *.0050*	3.6 / *.0044*	2.7 / *.0037*	2.7 / *.0054*	3.1 / *.0053*
11	13.6 / *.0120*	3.2											
12		7.2	2.6	15.3	5.4 / *.0040*	4.9 / *.0045*	4.9 / *.0045*	5.5 / *.0046*	8.9 / *.0086*	4.0 / *.0056*	3.8 / *.0024*	2.8 / *.0047*	3.7 / *.0069*
Totals for entire lake: Chlorophyll (kgs.)	3.3	4.3	6.6	4.6	3.8	10.1	8.2	6.3	4.5	3.5	3.2	2.8	2.6
Organic matter (kgs.)	1370	1420	1530	1460	1470	2880	2210	2030	1450	1120	1030	1010	790
Ratio (chl/org mat.)	*.0024*	*.0030*	*.0042*	*.0032*	*.0026*	*.0035*	*.0037*	*.0031*	*.0031*	*.0032*	*.0031*	*.0028*	*.0032*
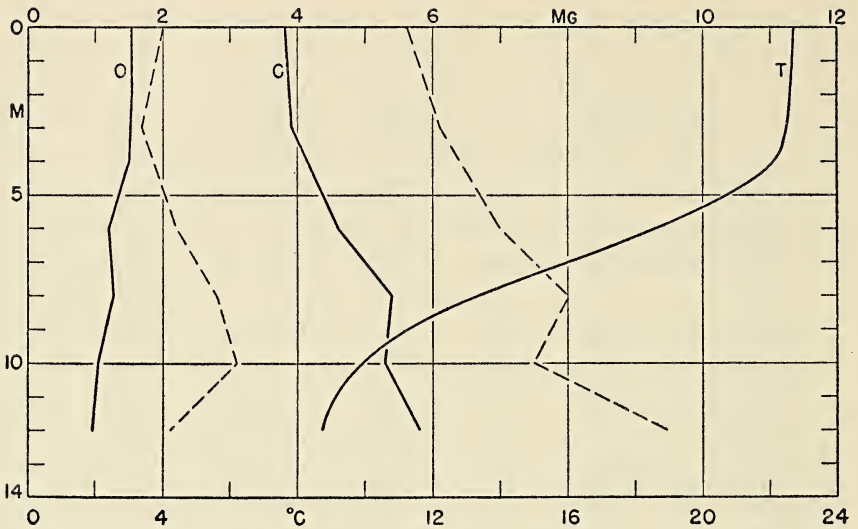
FIGURE 1. Weber Lake, 1938-1939. Average temperature (T), particulate organic matter (O) and chlorophyll concentration (C) during July and August. Ordinate, depth in meters; abscissae, chlorophyll concentration in mg/m^3, particulate organic matter in mg/l, and temperature in degrees centigrade. Each curve represents the mean of twelve determinations, four in 1938 and eight in 1939. The dotted lines on either side of the average chlorophyll curve are drawn at a distance from the latter equivalent to one standard deviation.

Figs. 1, 2 and 3. To facilitate comparison, the results obtained by Kozminski are included in Table I and Figure 2 (curve E). Perhaps the most striking feature of the chlorophyll results is the wide variation, both in total quantity and in depth distribution, shown in Figure 2 (1938) and particularly in Figure 3 (1939). Weber is a soft-water seepage lake, so that heavy rains in the late spring of 1939 resulted in an unusually high water level. It is probable that this was responsible, in part, for the high concentration of chlorophyll and particulate organic matter during July, 1939. The last four or five chlorophyll curves in Figure 3 are probably more nearly representative of the normal condition.

Figure 3 also suggests that the chlorophyll is produced in large part by organisms in the upper water, with a slow sinking process carrying large numbers of chlorophyll-bearing organisms to the deeper levels. Thus, the depth of maximum chlorophyll concentration moved steadily downward from a position
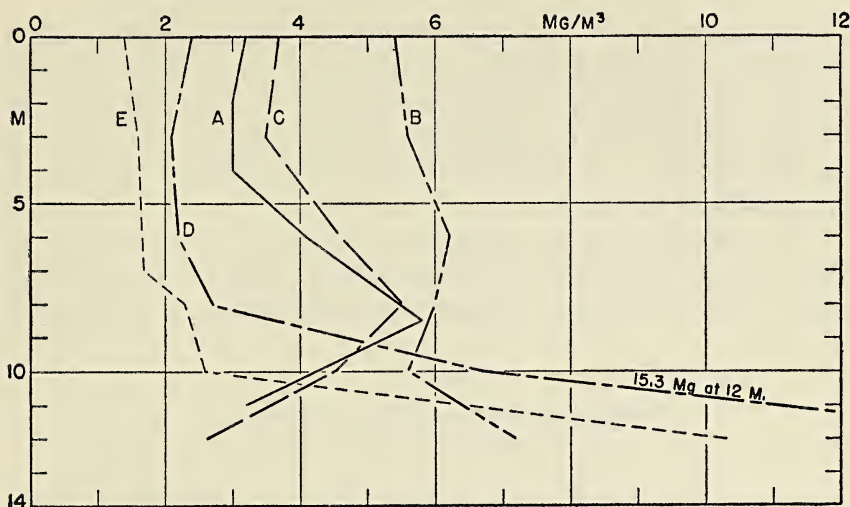
FIGURE 2. Chlorophyll concentrations in Weber Lake, 1938. Ordinate, depth in meters; abscissa, chlorophyll concentration in mg/m³. A, July 14; B, July 28; C, Aug. 12; D, Aug. 25; E, concentrations observed by Kozminski, July 29-30, 1937.
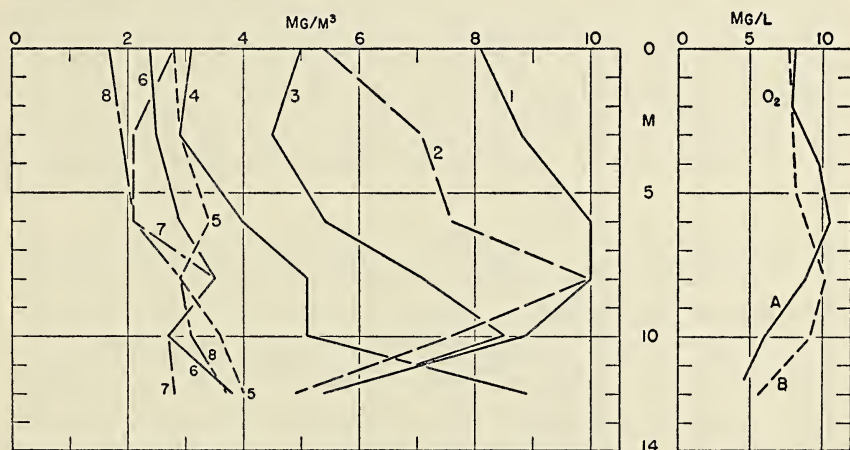
FIGURE 3. Chlorophyll concentration (mg/m³) and dissolved oxygen concentration (mg/l) in Weber Lake, 1939. Chlorophyll: curves 1 to 8, July 10 to Aug. 28 at weekly intervals. Dissolved oxygen: A, July 3; B, July 24.

between six and eight meters on July 10 until it was just above the bottom, at twelve meters, on July 31. By August 7 this sharp maximum had disappeared, presumably into the lake bottom or into the region immediately above the bottom. In the meantime,

the concentration in the upper waters dropped rapidly until a relatively constant level was reached and maintained during August. Evidently Kozminski's observations (E in Fig. 2) were made at a time when the maximum chlorophyll layer was nearing the lake bottom. A similar situation was observed on August 25 in 1938 (D in Fig. 2).

The dissolved oxygen records in Figure 3 are included to show that photosynthesis in Weber Lake at eight, ten and twelve meters was more than sufficient to compensate for respiration

TABLE II

Distribution of chlorophyll in Trout Lake.
For explanatory note, see Table I.

Depth (meters)	7/26/37 7/27/37	8/23/37	7/13/38	7/27/38	8/11/38	8/24/38	7/15/39	8/15/39
0	2.5 .0015	3.5 .0019	2.7	2.1 .0024	2.5 .0021	2.6 .0025	3.0	4.4 .0015
5			4.8	2.2 .0016	2.5 .0020	2.8 .0022	3.2	3.5 .0022
8		3.0 .0016						
9	3.3 .0032							
10		5.4 .0042	4.7	4.0 .0035	5.1 .0046	3.0 .0021	5.6	4.0 .0031
12	3.8 .0045							
15		2.8 .0058	3.1	3.9 .0049	4.2 .0063	4.2 .0053	3.7	2.5 .0032
18	2.8 .0032							
20	2.1 .0030	1.9 .0010	2.9	2.3 .0030	2.3 .0045	1.1 .0011	3.3	2.0 .0069
25	1.5 .0026							
27		1.2 .0015				1.3 .0024		1.3 .0024
28.5							2.0	
33	1.5 .0017	1.4 .0012	1.9	0.9 .0010	2.4 .0031	1.3 .0014		1.4 .0009
Totals for entire lake: Chlorophyll (kgs.)	415	488	558	415	488	399	548	478
Organic matter (kgs.)	1.60 x10^5	2.21 x10^5		1.55 x10^5	1.47 x10^5	1.79 x10^5		2.08 x10^5
Ratio (chl/org mat.)	.0026	.0022		.0027	.0033	.0022		.0023
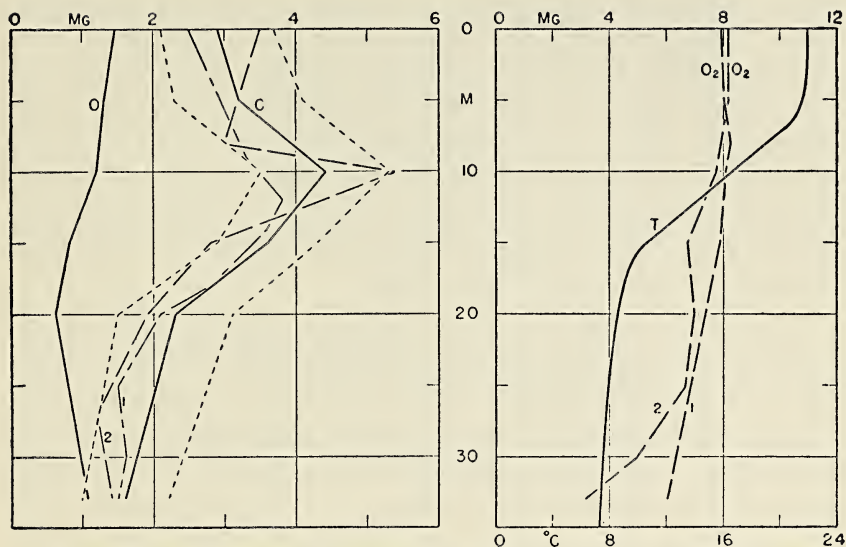
FIGURE 4. Trout Lake, 1938-1939. On the left side are shown the average particulate organic matter (O) in mg/l, and the average chlorophyll concentration (C) in mg/m³ during July and August. Each curve represents the mean of six determinations, four in 1938 and two in 1939. Standard deviation for chlorophyll is indicated as in Figure 1. The broken line curves (1 and 2) represent chlorophyll measurements by Kozminski in July and August, 1937. On the right hand side are shown the average temperature (T) in degrees centigrade (mean of six determinations) and the dissolved oxygen concentration (O₂) in mg/l on July 4, 1939 (1) and July 25, 1939 (2).

between July 3 (A) and July 24 (B), since the dissolved oxygen concentration at those depths increased during that time.

Table I indicates that during the period of observations the total chlorophyll content of Weber Lake varied from 2.6 kilograms to 10.1 kilograms, a factor of approximately four, while the ratio of total chlorophyll to total particulate organic matter varied from 0.0024 to 0.0042, a factor of less than two. During the summer of 1939 the correlation between chlorophyll and total particulate organic matter was quite close; both decreased steadily during the summer.

Trout Lake.—The results of the chlorophyll and organic matter determinations for Trout Lake are summarized in Table II and Figure 4. It appears that the chlorophyll content in Trout Lake is much more stable than in Weber Lake with respect both to distribution and to total amount. This is shown in Figure 4

by the relatively small standard deviation for the chlorophyll values. The curves representing Kozminski's 1937 series are in good agreement with the subsequent results. Most of the individual series show a maximum chlorophyll concentration in the thermocline. This is not surprising since the rate at which water density changes should be an important factor in the stratification of suspended organisms which are incapable of independent locomotion. There is little or no evidence for a similar maximum of total particulate matter.

Nebish Lake.—Table III and Figures 5 and 6 summarize the results of the chlorophyll and particulate organic matter determinations for Nebish Lake. Within the limited period of observation in 1939 (July 27 to Aug. 24), the chlorophyll content and distribution were relatively stable, as indicated by the small standard deviation shown in Figure 5. The high chlorophyll

TABLE *III*

Distribution of chlorophyll in Nebish Lake.

For explanatory note, see Table I.

Depth (meters)	7 /31 /37	7 /27 /39	8 /3 /39	8 /9 /39	8 /17 /39	8 /24 /39
0	2.8 .0018	2.7 .0019	3.3 .0034	5.0 .0032	2.9 .0019	6.8 .0041
3	2.7 .0017	3.6 .0017	4.4 .0054	5.3 .0064	3.2 .0029	5.4 .0056
5	1.9 .0013	4.9 .0027	4.7 .0051	4.6 .0035	5.9 .0052	5.6 .0053
8	14.6 .0106	10.5 .0072	10.0 .0090	8.9 .0086	8.2 .0069	8.5 .0058
10	20.8 .0159	62.8 .0487	44.0 .0250	49.2 .0328	46.0 .0309	44.8 .0147
12	18.7 .0089	17.1 .0118	36.4 .0150	58.0 .0228	44.0 .0113	50.2 .0180
14	20.2 .0105	11.4 .0075	17.0 .0181	27.4 .0139	18.9 .0141	33.2 .0266
Totals for entire lake: Chlorophyll (kgs.)	8.7	13.1	13.0	14.9	12.4	15.9
Organic matter (kgs.)	2970	3560	1920	2620	2520	2590
Ratio (chl/org mat.)	.0029	.0037	.0068	.0057	.0049	.0061
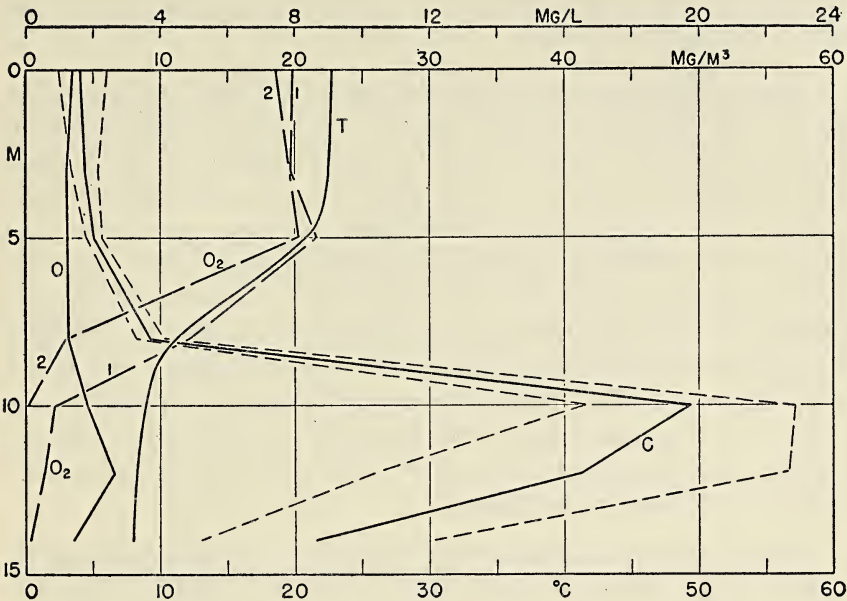
FIGURE 5. Nebish Lake, 1939. Average temperature (T) in degrees centigrade, particulate organic matter (O) in mg/l, and chlorophyll (C) in mg/m³. Standard deviation for chlorophyll is indicated as in Figure 1. Each curve represents the mean of five determinations in late July and August. In addition, the dissolved oxygen concentration (O₂) is shown for July 6 (1) and July 20 (2).

concentrations at ten and twelve meters were due to the presence of large numbers of a small flagellate[4], which so far has not been further indentified. From Table III it may be seen that on July 27, 1939, the chlorophyll content at ten meters was nearly five per cent of the total particulate organic matter. From the results of other investigations (Sargent, 1940; Manning, unpublished results) it is probable that the chlorophyll content of algal cells is seldom much higher than this figure. It is therefore probable that this single organism constituted most of the particulate organic matter at ten meters on this date. The curve for average particulate organic matter (O in Fig. 5) shows a fair correlation with the curve for average chlorophyll (C in Fig. 5),

[4] This statement is based on observations by Dr. Lenore Dunlop on material which had been centrifuged and fixed. The same or a similar organism was observed by Dr. Dunlop in samples from Little Rock and Muskellunge Lakes (see below).

though the maximum appears to occur at a greater depth than the chlorophyll maximum.

Both oxygen records in Figure 5 were obtained in July, 1939, before the first chlorophyll record. However, examination of plankton samples indicated that the concentration of the unidentified flagellate was high in the deeper waters throughout July. Despite the abundance of chlorophyll-bearing organisms, the oxygen concentration decreased, at five meters and below, between July 6 and July 20. In Weber Lake, a much smaller proportion of chlorophyll-bearing organisms was able to increase the oxygen concentration during July at eight meters and below (see above, p. 370). The difference in behavior is probably due to the lower transparency of Nebish Lake; at ten meters, during midday, the intensity in Nebish is of the order of fifteen percent of that at ten meters in Weber.

Figure 6 shows evidence for the kind of sinking process in Nebish Lake which was indicated for Weber Lake in Figure 3. On July 27 (curve A) the chlorophyll concentration at ten meters was much greater than at twelve meters. A week later (curve B), the concentration at ten meters was only slightly greater
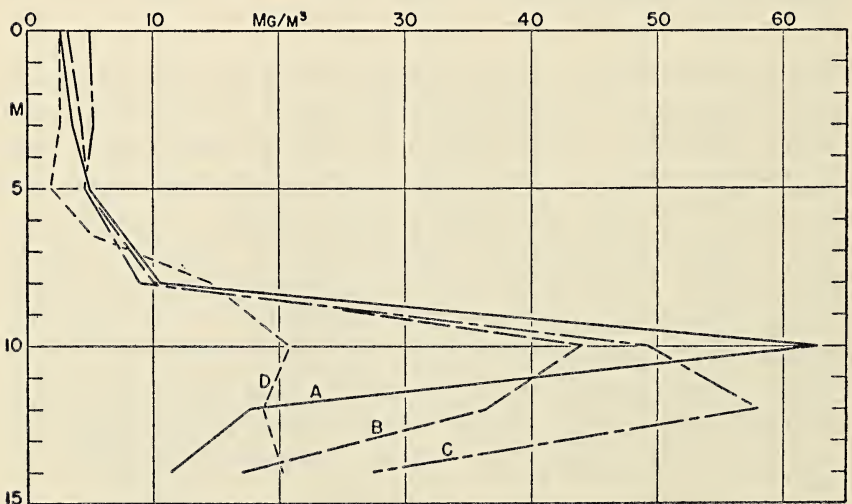
FIGURE 6. Chlorophyll concentrations in Nebish Lake: A, July 27, 1939; B, Aug. 3, 1939; C, Aug. 9, 1939; D, concentrations observed by Kozminski, July 31, 1937.

than at twelve meters, while on Aug. 9 (curve C), the maximum concentration was at twelve meters.

The 1937 determinations by Kozminski (D in Fig. 6) show a high concentration below the thermocline, though the increase is less marked than for 1939.

TABLE IV

Distribution of chlorophyll in Scaffold Lake.
For explanatory note, see Table I.

Depth (meters)	7/22/39		8/5/39	8/11/39	8/18/39	8/25/39
0	60 .0064	40 .0057	19	42 .0102	25	35 .0069
2	50	43	21	44 .0073		37 .0066
4	112 .0109	100 .0105	77	115 .0135	104	82 .0113
6	103 .0108	98 .0119	101	92 .0133	69	68 .0149
8	145 .0121	117 .0136	104	119 .0166	84	98 .0175
10	221 .0115	268 .0161	238	236 .0156	208	204 .0193

Scaffold Lake.—Table IV and Figure 7 summarize the results of chlorophyll and organic matter determinations for Scaffold Lake in 1939. The average curve for three series of dissolved oxygen determinations is also shown in Figure 7. Total yields for the entire lake are not given in Table IV, since the necessary morphometric data were not available.

Generally speaking, the chlorophyll concentration in Scaffold Lake was much greater than for any of the other lakes studied. Practically all of this chlorophyll was contained in a single unidentified species of alga. This alga is a minute, unicellular, rod-shaped organism about two microns in length, apparently surrounded by a gelatinous sheath.[5] The concentration of this organism during July and August was usually great enough to give a yellow-greenish opalescent appearance to the entire lake, though it never appeared as a scum on the lake surface. Speci-

[5] Dr. G. W. Prescott has suggested that this organism may be a member of a group classified by Huber-Pestalozzi (1938) as *Chlorobacteriaceae*).
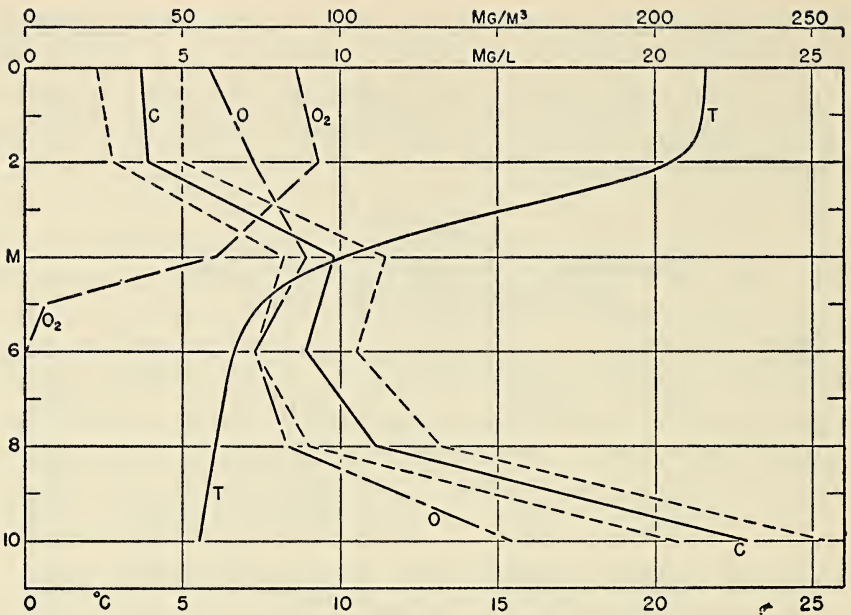
FIGURE 7. Scaffold Lake, 1939. Average temperature (T) in degrees centigrade, particulate organic matter (O) in mg/l, dissolved oxygen (O_2) in mg/l, and chlorophyll (C) in mg/m³. Each curve represents the mean of five, four, three and six series of determinations, respectively, in July and August. Standard deviation for chlorophyll is indicated as in Figure 1.

mens taken from near the surface were yellowish-green in color; those from depths below four meters were more nearly grass-green in color.

It is interesting to note that by far the greatest chlorophyll concentrations in Scaffold Lake occurred where dissolved oxygen was entirely absent. The light intensity below five meters is negligible (less than a hundred-thousandth of noon sunlight at six meters). After being aerated, samples taken from a depth of ten meters were still able to photosynthesize at normal light intensities. Further information regarding photosynthesis in Scaffold Lake water will appear in a subsequent report.

The correlation between particulate organic matter and chlorophyll at different depths is excellent (see Fig. 7). This is probably due to the fact that the unidentified alga constitutes most of the particulate organic matter in Scaffold Lake. The higher ratio of chlorophyll to organic matter in the deep-water

samples (see Table IV) is probably an indication of the general tendency for plants to have a higher chlorophyll content at low light intensities (see Sargent, 1940).

The depth distribution of chlorophyll was fairly constant, as shown in Figure 7 by the comparatively small values for standard deviation.
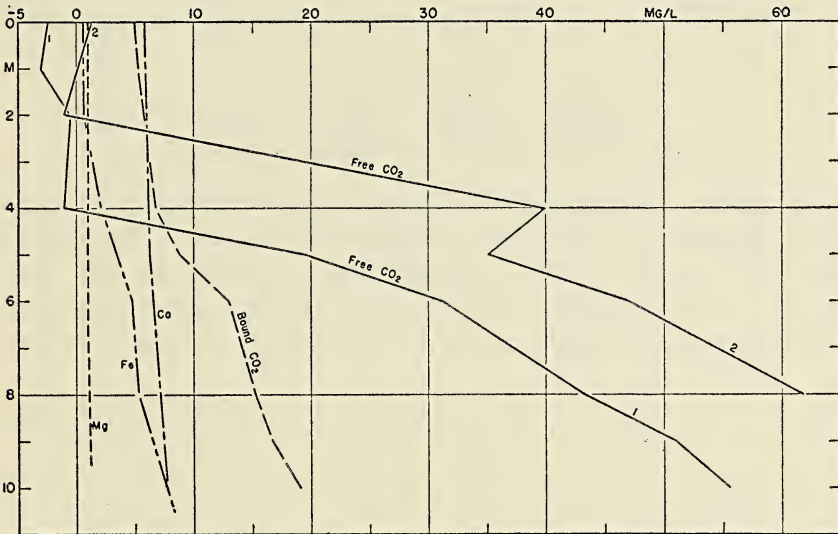
FIGURE 8. Chemical characteristics of Scaffold Lake water, 1939. All concentrations are shown in mg/l. The curves for calcium, bound carbon dioxide and free carbon dioxide (1) were determined on July 7, the curve for magnesium was determined on July 14, while the curves for total iron and free carbon dioxide (2) were determined on August 10.

Figure 8 shows some general chemical characteristics of Scaffold Lake water in 1939.[6] It is remarkable that a relatively deep soft-water lake, such as Scaffold, can maintain for long periods such an enormous phytoplankton population. The increase in free carbon dioxide at six, eight and ten meters in the period between July 7 and August 10 indicates that the organisms at those depths were continuing to metabolize under anaerobic conditions.

Little Rock Lake.—Table V and Figure 9 summarize the results of chlorophyll and organic matter determinations for Little

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[6] The chemical analyses were performed by Mr. B. C. Hafford.

TABLE V

Distribution of chlorophyll in Little Rock Lake.

For explanatory note, see Table I.

Depth (meters)	7 /21 /38	8 /3 /38	8 /17 /38	8 /3 /39	8 /26 /39
0	4.8 .0045	3.8 .0036	10.7 .0078	5.2 .0060	2.2 .0017
2.5	4.5	4.0	14.8	6.1 .0055	2.4
5	9.2	9.8	22.1	10.1 .0070	6.3 .0058
7	13.2 .0127	28.4 .0199	54.4 .0186	33.7 .0591	46.8 .0139

Rock Lake. Total yields for the entire lake could not be calcu-
lated because of insufficient morphometric data. The various
individual series showed considerable variation in the total
amount of chlorophyll, but all agreed in showing a maximum
near the bottom, at seven meters. From Table V, it may be seen
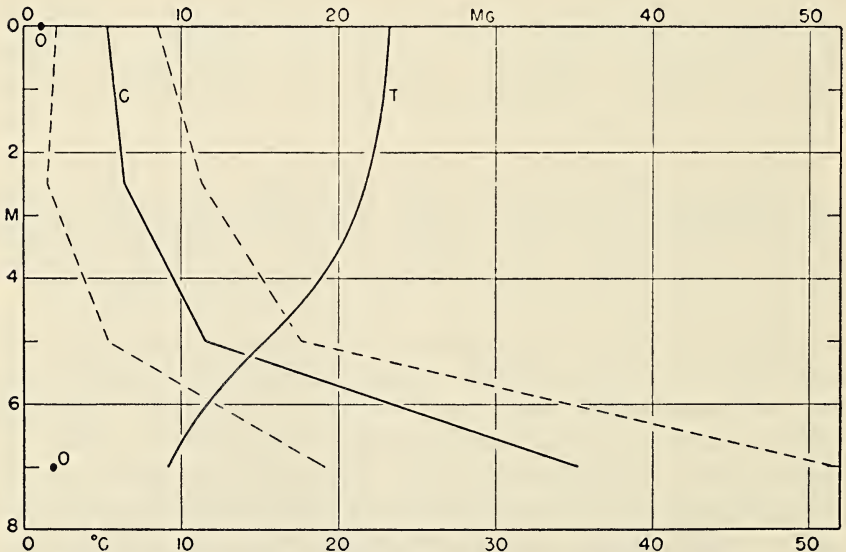
FIGURE 9. Little Rock Lake, 1938-1939. Average temperature (T)
in degrees centigrade, particulate organic matter (O) in mg/l (two depths
only), and chlorophyll (C) in mg/m^3. Standard deviation for chlorophyll
is indicated as in Figure 1. The chlorophyll curve and the plankton points
represent the mean of five series of determinations each, while the tem-
perature curve represents the mean of four series of determinations. All
observations were made during July and August.

that on August 3, 1939, the ratio of chlorophyll to total particulate organic matter at seven meters was nearly six percent. This is the highest ratio found in these investigations. It is probable that the particulate organic matter in this case consisted almost entirely of chlorophyll-bearing phytoplankton. A small flagellate, identical or very similar to that observed in the deep water of Nebish Lake, was fairly abundant at seven meters in Little Rock Lake, though not nearly as abundant as in Nebish Lake.

TABLE VI

Distribution of chlorophyll in Muskellunge Lake.

For explanatory note, see Table I.

Depth (meters)	8/3/37	7/26/39	8/23/39
0	3.1 .0024	2.4 .0015	3.6 .0040
3		3.0 .0025	
5		4.0 .0030	3.5 .0036
7	5.2 .0042		
8	4.8 .0023	5.6 .0038	3.3 .0025
10	11.2 .0048	12.2 .0064	3.5 .0020
12	12.7 .0053		8.4 .0056
14			8.4
15	14.8 .0076	7.7 .0061	
19	30.4 .0133		37.8 .0313
21		8.4	
Totals for entire lake: Chlorophyll (kgs.)	157	131	118
Organic matter (kgs.)	4.00 x10⁴	3.70 x10⁴	3.00 x10⁴
Ratio (chl/org mat.)	.0039	.0035	.0039
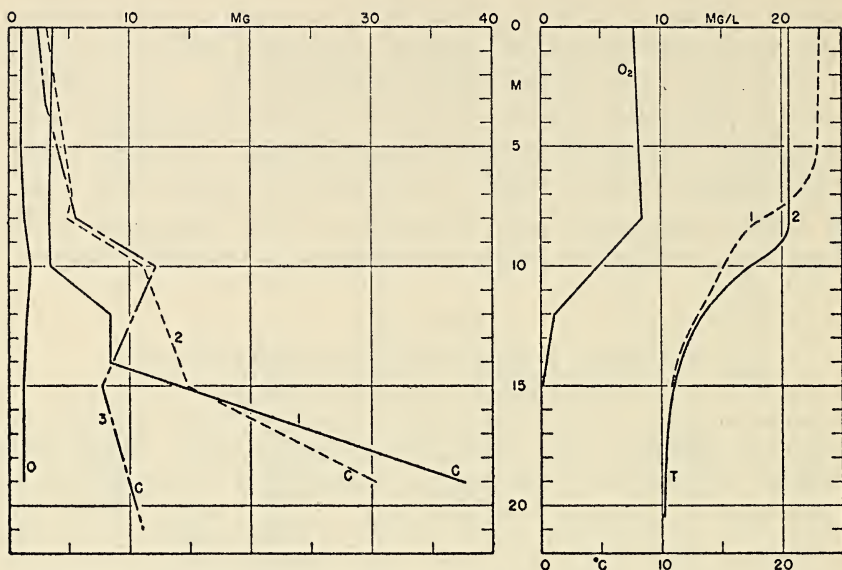
FIGURE 10. Muskellunge Lake, 1937-1939. Chlorophyll concentrations (C) in mg/m³, particulate organic matter (O) in mg/l, dissolved oxygen (O₂) in mg/l, and temperature (T) in degrees centigrade. Chlorophyll curves: (1) Aug. 23, 1939; (2) observations by Kozminski, Aug. 3, 1937; (3) July 26, 1939. The curve for organic matter represents the mean of two series, one July 26, 1939, the other August 23, 1939. The dissolved oxygen curve is for July 26, 1939. The temperature curves are for July 26, 1939 (1) and for August 23, 1939 (2).

Muskellunge Lake.—Table VI and Figure 10 show the results of the few observations which were made on Muskellunge Lake. It is possible that the chlorophyll curve for July 26, 1939 (3 in Fig. 10) would have been more like the others if the deepest sample had been taken at nineteen meters instead of at twenty-one meters. Large numbers of a flagellate, similar or identical to that found in the deeper waters of Nebish and Little Rock lakes, were observed in the nineteen meter samples taken from Muskellunge Lake on August 23, 1939. Note the absence of oxygen below fifteen meters.

Crystal Lake and Helmet Lake.—One series of chlorophyll determinations in Crystal Lake and one in Helmet Lake were made in the summer of 1939. In both cases the distribution was similar to that found in 1937 by Kozminski, as shown in Figure 11. Crystal Lake water is the clearest and least colored of those
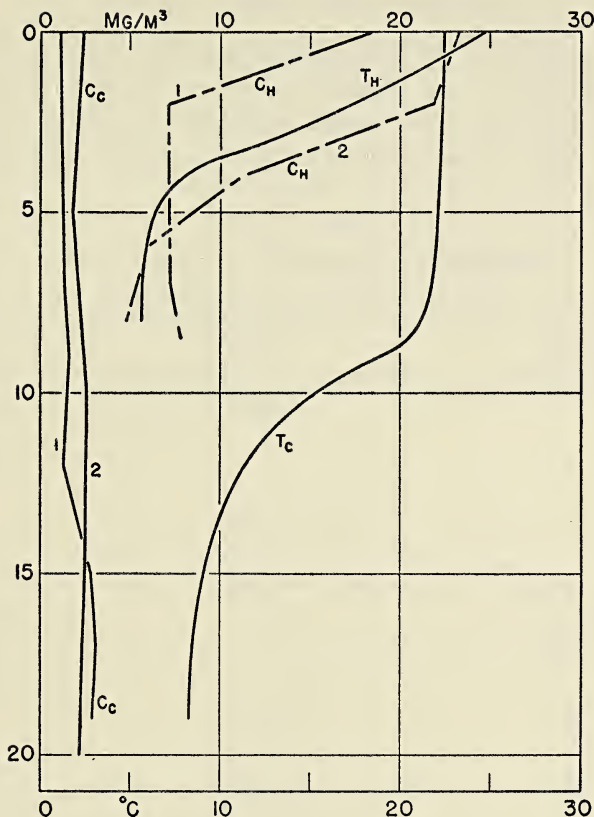
FIGURE 11. Crystal Lake and Helmet Lake, 1937-1939. Chlorophyll concentrations (C) in mg/m³, and temperatures (T) in degrees centigrade. Chlorophyll in Crystal Lake (C$_c$): (1) observations by Kozminski, August 11, 1937; (2) August 19, 1939. Chlorophyll in Helmet Lake (C): (1) observations by Kozminski, August 5, 1937; (2) July 19, 1939. Temperatures: (T) Crystal Lake, August 19, 1939; (T) Helmet Lake, July 19, 1939.

studied, with a color of zero or near zero on the platinum-cobalt scale, while Helmet Lake water is the most highly colored, with the surface water frequently having a color of greater than 250 on the same scale.

The amount and distribution of organic matter, as well as of chlorophyll, in Crystal Lake is shown in Table VII. The data for particulate organic matter in Helmet was not reliable because of large quantities of fine silt suspended in the water.

Photosynthesis measurements

From results of photosynthesis measurements at different light intensities, it was usually possible to determine the maximum rate, and the approximate intensity required to give the maximum rate. This maximum, with certain limitations, can

TABLE VII

Distribution of chlorophyll in Crystal Lake

For explanatory note, see Table I.

Depth (meters)	8/11/37	8/19/39
0	1.1 .0009	2.4 .0021
5		1.8 .0014
7	1.3 .0011	
9	1.6 .0020	
10		2.6 .0028
12	1.3 .0011	
15	2.8 .0031	2.5 .0026
17	3.1 .0054	
19	2.9 .0042	
20		2.2
Totals for entire lake: Chlorophyll (kgs.)	4.32	6.64
Organic matter (kgs.)	3320	3640
Ratio (chl/org mat.)	.0013	.0018

be used as a measure of the photosynthetic capacity of a sample of lake water.

Table VIII shows the results of a number of experiments of this type. The maximum rate is expressed in terms of the milligrams of oxygen evolved per milligram of chlorophyll per hour.

A respiration correction was made in every case. The results of a large number of experiments were omitted from Table VIII, for one or more of the following reasons:

(1) Because of insufficient accuracy, no result was included if the maximum reaction was less than 0.25 mg/l of oxygen. This would appear to result in a selection favoring the more efficient samples, but the effect cannot be great, since the average for eight series showing a detectable reaction, but of less than 0.25 mg/l, is 7.7 mg O_2/mg chl/hour, a figure actually higher than the average for Table VIII.

(2) No result was included if the light intensity was too low to produce the maximum reaction.

TABLE VIII

Maximum rate of photosynthesis of epilimnion waters
as a function of the chlorophyll content.

Lake	Date	Maximum rate (mg O_2/mg chl/hr)
Big	Aug. 21, 1937	8.2
Little Rock	Aug. 4, 1939	5.8
Lost	July 18, 1938	6.5
Midge	Aug. 23, 1937	7.7
Nebish	July 28, 1939	13.7
	Aug. 3, 1939	10.3
	Aug. 24, 1939	5.7
Scaffold	July 7, 1939	2.4
	July 14, 1939	6.3
	July 22, 1939	3.1
	July 29, 1939	6.0
	Aug. 11, 1939	5.1
	Aug. 18, 1939	8.1
	Aug. 25, 1939	6.0
Stella	July 18, 1938	6.1
Weber	July 11, 1939	6.1
	July 18, 1939	8.3
	July 25, 1939	6.2
Wildcat	Aug. 17, 1937	6.6

Average maximum ($\pm$ standard error) = 6.7 $\pm$ 0.6.

(3) No result was included if the sample consisted predominantly of a "bloom", since the maximum rate per milligram of chlorophyll in such cases was usually found to be very low, indicating probable deterioration of the phytoplankton material constituting the bloom.   The average maximum for thirty-five series of this type was 3.2 mg O_2/mg chl/hour.   Only three of these thirty-five series showed maximum rates as high as the average for Table VIII.   For the same reason, results of measurements with samples taken from deep water, i. e., below the thermocline, are not included in Table VIII. Though these samples frequently contained large concentrations of chlorophyll, the maximum reaction was small.   In no case did the maximum rate per milligram of chlorophyll for such samples exceed one-third of the average for Table VIII, and usually it was less than twenty percent of this average.

Considerable variation is shown in the nineteen results given in Table VIII.   However, if the two highest and the two lowest values are omitted, the remainder show a much smaller variation, indicating that within the limitations given above, chlorophyll may usually be used as a fairly good index of photosynthetic capacity.

All of the results shown in Table VIII were obtained from photosynthesis experiments lasting from five to nine hours. These long exposures were necessary to give a measurable reaction.   As a result, a single bottle was exposed to a considerable range of light intensities.   A bottle showing maximum reaction may actually have spent some time at intensities above and below the optimum.   However, at light intensities near the optimal value, photosynthetic rate changes only slightly with change in light intensity.   Rough calculations showed that on the average, an observed maximum should be increased by four or five per cent to compensate for time spent at other than optimal intensities.   For this reason, the value of 7.0 may be considered as a more correct mean value for maximum rate in Table VIII than the observed mean of 6.7.   A rate of 7.0 milligrams of oxygen per milligram of chlorophyll per hour corresponds to a reduction of one carbon dioxide molecule by one chlorophyll molecule in approximately eighteen seconds.   This is in approximate agreement with the results of others (Gaffron and Wohl, 1936).

Calculation of lake productivities

Shortcomings of chlorophyll as an index of photosynthetic capacity.—The following are probably some of the factors responsible for variations in the photosynthetic capacity of a given quantity of chlorophyll:

(1) Other pigments may contribute to photosynthesis. Recent work (Dutton and Manning, 1941) shows that light absorbed by carotenoids is utilized for photosynthesis in the marine diatom *Nitzschia closterium*. It is probable that carotenoid pigments function similarly in some other organisms. The carotenoid-chlorophyll ratio is not constant in different species of algae, nor in the same species under different conditions.

(2) Chlorophyll *a* and chlorophyll *b* may not be equally effective.

(3) Chlorophyll may be present in senescent or otherwise inactive plant material.

(4) Even aside from the foregoing factors, a strict proportionality between photosynthetic rate and chlorophyll content would be expected only at low light intensities, because of the varying capacity for the enzyme (Blackman) reaction in different species, and in the same species under different conditions of growth (Emerson, Green and Webb, 1940; Sargent, 1940). In a lake, with normal chlorophyll distribution, all but a relatively small fraction of photosynthesis is produced by light of high enough intensity to result in at least partial limitation by the Blackman reaction.

(5) The temperature in Trout Lake was only approximately constant during the summer period of observation. Change in temperature causes a change in maximum photosynthetic rate.

In view of the factors just discussed, it is perhaps surprising that the results shown in Table VIII are as consistent as they are.

Productivity calculations.—In determining productivity, Riley (1940) and Winberg (1937) used the straight-forward procedure of taking water samples at a series of depths, and resus-

pending the samples in clear and in black bottles at the same depths. After a period of several days, the amount of photosynthesis and respiration was determined by measuring the change in dissolved oxygen.

The chief objection to this type of procedure is that enclosure in bottles results in greatly increased bacterial activity (Stark, Stadler, and McCoy, 1938). Over a period of a week, as used by Riley, increased bacterial development would influence the concentration of dissolved oxygen, and perhaps also the condition of the phytoplankton. In all of the Wisconsin lakes studied in the present work, except for Scaffold, long exposure would have been necessary to obtain a reasonable reaction.

A second objection to this method is that it must be repeated in full at frequent intervals to evaluate productivity as influenced by light intensity, plankton concentration, temperature or other uncontrollable factors.

When the necessary equipment is available, a series of chlorophyll determinations may be made much more easily and quickly than a series of photosynthesis measurements such as described above, particularly when the phytoplankton concentration is low.
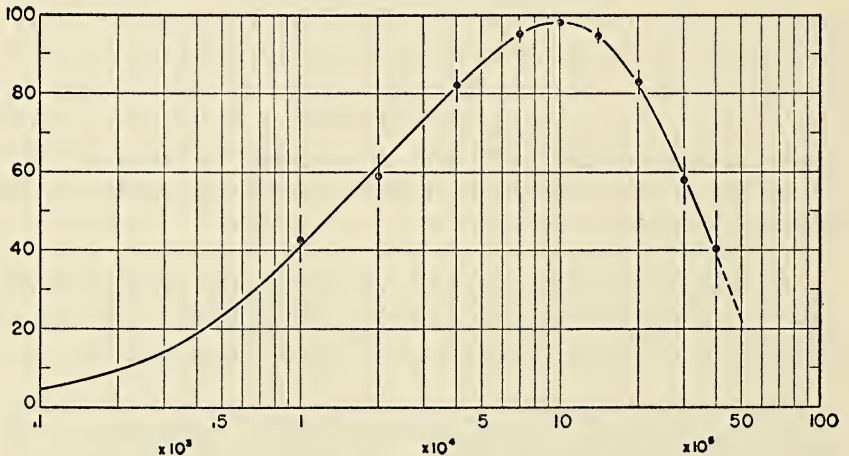

FIGURE 12. Average curve for the rate of phytoplankton photosynthesis as a function of light intensity (mean of twelve series of determinations). The light intensity scale is logarithmic. The average rate is shown as a percentage of the maximum rate. The standard error at different intensities is given by half the length of the vertical line drawn through each point.

Therefore, in view of the degree of consistency shown by the results in Table VIII, it appears worthwhile to give the results of productivity calculations based on the measurements of chlorophyll concentration described above.

For these calculations, in addition to knowing the maximum rate possible for a given amount of chlorophyll, it is necessary to know the variation of rate with light intensity. Figure 12 shows an average curve for rate of phytoplankton photosynthesis as a function of light intensity (mean of thirteen individual series). All available series were used for which the ~~ount of reaction and the number of experimental points \ ~re great enough to give an accurate curve for rate versus intensity. The rates for the different series were made comparable by giving a value of 100 to the maximum rate and expressing rates at other intensities as a percentage of this maximum. The average maximum shown in Figure 12 occurs at an intensity of 10^5/ergs/cm^2/-sec, and is only two per cent below the limiting value. All of the individual series were at or close to their maximum at this intensity. Infra-red radiation is not included in the intensities shown in Figure 12. The dotted-line portion between 4×10^5 and 5×10^5 ergs/cm^2/sec represents an extrapolation. The portion below 10^4 ergs/cm^2/sec is also extrapolated, but extrapolation in this region should be quite accurate, since the rate of photosynthesis is known to be nearly proportional to light intensity in this range.

For numerical calculation, the value of 7.0 (mg O_2/mg chl/hr) was substituted for the maximum rate value in Figure 12, and the entire scale changed accordingly. It is probably justifiable to assume that, in the absence of a "bloom," the chlorophyll at all depths above the thermocline in a lake will show the same maximum capacity, and similar behavior as a function of light intensity, since all of the water above the thermocline is ordinarily subject to frequent mixing.

Tables IX and X illustrate the method of calculation for an individual lake, Weber in this case. Light conditions were defined by choosing a clear day on August 1. Transparency data were taken from the results of measurements several years earlier (Birge and Juday, 1932). The transparency in 1939 was presumably somewhat lower, but the error involved is probably

TABLE IX

Light intensities (ergs/cm²/sec × 10⁴) in Weber Lake (August 1).

Time A.M.	P.M.	0	1	2	3	4	5	6	7	8	9	10	11	12	13
5	7	4.0	1.1	.79	.56	.40	.29	.20	.146	.104	.074	.053	.038	.027	.020
6	6	15.0	3.7	2.5	1.76	1.22	.84	.58	.40	.28	.193	.134	.092	.064	.044
7	5	33	8.2	5.7	3.9	2.7	1.89	1.31	.91	.63	.44	.30	.21	.147	.102
8	4	52	13.7	9.7	6.8	4.8	3.4	2.4	1.70	1.20	.85	.60	.42	.30	.21
9	3	70	19.9	14.3	10.3	7.4	5.4	3.9	2.8	2.0	1.44	1.04	.75	.54	.39
10	2	84	25	18.6	13.6	10.0	7.3	5.3	3.9	2.9	2.1	1.53	1.12	.82	.60
11	1	93	29	22	16.0	11.8	8.4	6.4	4.7	3.5	2.6	1.91	1.41	1.04	.77
12 M		97	31	23	17.0	12.6	9.4	7.0	5.2	3.8	2.8	2.1	1.57	1.17	.82

Depth (meters)

TABLE X

Photosynthesis (mg O_2/mg chl/hr) in Weber Lake (August 1).

Depth (meters) / Time	0	1	2	3	4	5	6	7	8	9	10	11	12	13
5 A.M.	4.4	3.1	2.4	1.8	1.3	1.0	0.7	0.5	0.3	0.2	0.2	0.1	0.1	0.1
6	6.9	5.7	4.9	4.1	3.3	2.6	1.5	1.3	0.9	0.6	0.5	0.3	0.2	0.1
7	6.4	6.9	6.5	5.7	5.1	4.3	3.5	2.7	2.0	1.4	1.0	0.7	0.5	0.3
8	4.9	6.8	7.0	6.8	6.2	5.5	4.8	4.0	3.3	2.6	1.9	1.4	1.0	0.7
9	3.5	5.9	6.7	7.0	6.9	6.4	5.8	5.1	4.4	3.7	3.0	2.3	1.8	1.3
10	2.6	5.0	6.1	6.8	7.0	6.8	6.4	5.8	5.2	4.5	3.8	3.1	2.5	1.9
11	2.0	4.4	5.5	6.5	6.9	7.0	6.7	6.2	5.6	5.0	4.3	3.6	3.0	2.4
12 M.	1.8	4.1	5.4	6.3	6.9	7.0	6.8	6.3	5.8	5.1	4.5	3.9	3.2	2.5
1-7 P.M.	30.7	37.8	39.1	38.7	36.7	33.6	29.8	25.6	21.7	18.0	14.7	11.5	9.1	6.8
Totals	63.2	79.7	83.6	83.7	80.3	74.2	66.4	57.5	49.2	41.1	33.9	26.9	21.4	16.1

Total oxygen production in day by a column one square meter in cross-section and 13.5 meters in depth: 2323 (0-7.5 meters) + 1032/3 (7.5-13.5 meters)

= 2667 milligrams
= 25 kilograms of glucose per hectare cross-section.

not very great. Transparency data from the same source, or from unpublished results, were used in calculations for the other lakes. As shown in Table IX, the day was divided into one-hour periods, and the lake into one-meter strata. Half-meter strata were used in similar calculations for the less transparent lakes, Helmet and Scaffold. The intensity for each hour in each stratum is entered in the table. The change in path-length for solar radiation, due to changes in the solor elevation, was taken into account. Photosynthesis per milligram of chlorophyll for each hour at each depth was obtained by using Figure 12 in conjunction with Table IX. The results were entered as shown in Table X. In the thermocline and below (from seven meters down in Weber) the values become uncertain, and probably much too high, for two reasons. One is the rapid decrease in temperature. This is partially compensated by the decrease in light intensity, since the rate of photosynthesis becomes independent of temperature at sufficiently low intensities. The second reason is the much lower photosynthetic capacity, per unit of chlorophyll, observed for deep water samples (see above). In most lakes, the uncertainty is not serious, since the light intensity in and below the thermocline is too low for much photosynthesis. Of the lakes studied in this work, the uncertainty is greatest for Weber and Crystal, the two clearest lakes.

Since the present calculations are principally for illustrative purposes, the average chlorophyll concentration for the various

lakes, rather than individual concentrations, were used as a basis of calculation. Thus, for Weber Lake, the total daily photosynthesis by one milligram of chlorophyll in each stratum was multiplied by the average concentration in that stratum (obtained from Fig. 1 by interpolation). The products for the different strata were added to give the total daily photosynthesis in a column of one square meter extending from top to bottom of the lake in its deepest part. Below seven meters, the total figures were more or less arbitrarily divided by three in order to compensate roughly for the lesser efficiency of the deep-water chlorophyll. The final calculation is outlined at the bottom of Table X.

The result, together with the results for other lakes, is given in Table XI. In this table, the productivity is calculated as glucose production in kilograms per hectare per day, both for the maximum depth of the lake and, as an average, for the entire lake surface. In the case of Trout Lake, similar calculations were made for July 14 and August 15. Assuming the same chlorophyll distribution, the August 15 figure was just ten per cent lower than the July 15 figure.

It will be noted from Table XI that the productivity is far from being proportional to the average chlorophyll concentra-

TABLE XI

Productivities (in terms of glucose) on a clear day (August 1).

Lake	Ave. chl. conc. in epilimnion	Char. trans.* below one meter	Glucose production (kgs /hectare /day)	
			Max. depth	Average
Helmet	22.5	.13 (1 m-2 m) .28 (2 m-3 m)	14	13.5
Trout	3.3	.67	16	14
Crystal	2.2	.82	17	11
Muskellunge	3.8	.67	17	10
Weber	4.2	.76	25	17
Nebish	5.2	.74 (1 m-5 m) .60 (5 m-10 m)	26	15
Scaffold	41.1	.48 (1 m-3 m) .12 below 3 m)	44	
Chlorella culture (theoret.)			430	
Corn field (Transeau)			216	

* The characteristic transmissions, given for a path length of one meter, are from Birge and Juday (1932) and unpublished data.

tion, even assuming, as has been done, a constant capacity for chlorophyll at a given intensity. This is because of the varying competition for light by the lake water itself. Thus, Crystal Lake is more productive than Helmet Lake, although the latter has ten times the chlorophyll concentration. In Helmet Lake, the brown stain in the water absorbs light so rapidly that the chlorophyll has much less chance to function than in the very clear waters of Crystal Lake.

The glucose production by a culture of the green alga, *Chlorella,* shown in Table XI, was calculated on the assumption that all the light is absorbed by *Chlorella* cells, with a photosynthetic efficiency of 0.10 molecules of oxygen evolved per quantum absorbed at low intensities (Emerson and Lewis, Stauffer, Moore and others, unpublished data), and a behavior at higher intensities like that shown in Figure 12. Thus, even the most productive of the lakes studied (Scaffold) falls far short of the theoretical maximum. The figure given in Table XI for a corn field is based on calculations by Transeau (1926) and represents an average over a 100-day growing period.

Concluding remarks.—The methods used in calculating the results in Table XI are perhaps more refined than the accuracy of the assumptions justify. However, a table such as Table X, aside from its use in the productivity calculation, gives a valuable picture of the influence of time of day and light intensity on photosynthesis at each depth. Aside from the absolute productivity calculations, which can be only approximately correct, the results given in Table XI are useful in showing, somewhat quantitatively, the importance of lake transparency in determining productivity.

Without doubt, further experimental data would make possible an improvement in the accuracy of the assumptions used in these calculations,, with a corresponding improvement in the accuracy of the calculated results.

SUMMARY

Repeated observations, during July and August, have been made on the concentration and distribution of chlorophyll in several lakes in northeastern Wisconsin. In some of the lakes,

e.g., Trout and Nebish, the chlorophyll distribution remained fairly constant during the period of observation. In others, e.g., Weber, marked changes were observed in the type of depth distribution.

It was found that, with certain limitations, chlorophyll may be used as an index of the photosynthetic capacity of epilimnion waters. At optimal light intensity, the average capacity was found to be seven milligrams of oxygen produced per milligram of chlorophyll per hour. This corresponds to a reduction of one molecule of carbon dioxide by one molecule of chlorophyll every eighteen seconds.

The chlorophyll and photosynthesis data have been used to calculate approximate productivities (in terms of glucose production) for seven lakes. Using a clear day on August 1 as a basis of calculation, the highest productivity calculated was 44 kilograms of glucose per hectare per day, for Scaffold Lake, while the lowest value was 14 kilograms per hectare per day, for Helmet Lake.

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THE SURFACE TENSION OF WISCONSIN LAKE WATERS*

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Introduction

In 1937 Adam described a simple field method for determining the surface tension of natural waters, dependent upon the spreading properties of various solutions of a surface active compound in a pure mineral oil. Working on the English coast, he found that in general the surface tension of coastal waters was that of clean sea water (1-2 dynes per centimeter above that of fresh water). Near sewage outlets or other obvious sources of contamination the tension was shown to vary, and in creeks and small harbors it was often considerably lowered. While muddy, fast streams might have a normal tension, stagnant or slow-flowing waters which appeared to be clean could be seen by this method to be covered by surface tension depressant films.

STANDARDIZATION OF SOLUTIONS

In accordance with the directions given by Adam (1937), a series of solutions was prepared of different concentrations of n-dodecyl alcohol ($C_{11}H_{22}CH_2OH$) in a clear, white mineral oil. The author is grateful to Dr. Homer Adkins for supplying these reagents, and to Mr. H. G. Tennent for his valuable assistance in standardization of the solutions. The spreading power of each solution was standardized against a monofilm of stearic acid on distilled water, under known surface pressure, using a Cenco hydrophile balance. Standardization was carried out at three temperatures, corresponding to those met in the field; a drop

was considered to have spread when its diameter reached approximately 2.5 centimeters. The solution concentrations and the surface pressure against which a drop of each would just spread are given in Table 1. The surface tension in each case may be calculated by subtracting the determined pressure from the original surface tension of pure water at that temperature. For the data in Tables 2 to 4, readings were made to the nearest 0.5 dyne for surface pressure and calculated to the nearest degree Centigrade, as given in the International Critical Tables (1928).

TABLE 1. *Spreading power of oil solutions used.*

Dodecyl alcohol, per cent	Surface pressure, dynes/cm
13-16° C.	
0.2	0.0
0.3	4.0
0.4	6.0
22.5-24°	
0.3	1.0
0.4	3.0
0.5	5.0
0.7	7.5
0.8	8.5
1.0	11.5
1.5	19.5
26.2-27°	
0.4	2.0

By plotting the concentration of the oil solution against the degrees of torsion shown on the hydrophile balance, and comparing this with the curve obtained by plotting the degrees of torsion against dynes per centimeter, the standardization was found to be reproducible within 2 degrees of torsion, or 0.4 dynes/cm. The field accuracy of the method is somewhat less than this, due in part to the necessity for estimating the concentration of alcohol which would just spread where the concentrations actually used were too far apart in the higher dilutions. While this difficulty could be obviated by using solutions at closer intervals of concentration, it is doubtful if results so obtained would be significant in the study of natural waters. In the present paper a general accuracy of about one dyne per centimeter is assumed.

TABLE II. *Surface tension of pure water against air.*

Temperature, C.	Surface tension, dynes/cm
10	74.4
15	73.5
20	72.7
21	72.6
22	72.4
23	72.3
24	72.1
25	72.0
30	71.2

RESULTS

During the summer of 1939 more than one hundred determinations were made on about 40 lakes in northern and southern Wisconsin. Other data on most of these lakes have been accumulated over many years by the Wisconsin Geological and Natural History Survey and will be used here without specific reference. Temperatures were taken with all readings. Of the total number of determinations, 59 per cent gave the same surface tension as pure water, namely 72 dynes/cm at 25° C; 25 lakes showed a normal tension in at least one reading, but only 9 of them were that high in all determinations made.

The surface tension data obtained could best be correlated with the lake classification according to productivity. Table 3 shows general ranges covering the whole series of results obtained.

TABLE 3. *Range of surface tension depressions in various situations.*

Situation	Surface tension depression, dynes/cm
Oligotrophic lakes	0-2
Eutrophic lakes	0-20
Bog lakes	0-20
Lakes with foam	2-9
Near *Lemna* and lillies	5-20
During plankton bloom	0-20

The oligotrophic lakes tested, of which Crystal Lake and Trout Lake are typical, showed very little variation. This type of water compares closely in organic content with sea water,

which was tested by Adam. Two series of measurements on
Trout Lake were made, one on the same day at different stations
and the other at a single station over a period of a week. No
difference in tension was found in open water, in shore stations,
in shallows over a sand bar and in water surrounding an emer-
gent stand of *Carex* rooted in sand. A slight diurnal variation
in tension, correlated with change in temperature, was noted.
The surface tension of Weber Lake, an oligotrophic lake which
has been made more productive by artificial fertilization over a
period of several years, was depressed by about 2 dynes/cm.

<div align="center">CHEMICAL FACTORS</div>

In both the highly productive eutrophic lakes and in the
deeply stained dystrophic lakes, the surface tensions appeared
to vary with several factors. Since the surface tension of a
mixture of two substances will depend upon that of the original
compounds, it might be expected that lakes varying widely in
chemical composition would have different surface tensions.
Further, since inorganic solutes are known to raise the tension
of water somewhat when in concentrated solution, while small
amounts of polar organic compounds may lower it greatly, the
biological and organic conditions might be expected to exert a
stronger influence than other chemical factors. This was found
to be the case. No difference was observed between the northern
soft-water and southern hard-water lakes, nor did variations in
pH from 4.5 to 8.5 appear to affect the surface tension, unless,
as in some of the bog waters, organic acids presumably were
present. Readings taken over a mud flat near the shore of Alle-
quash Lake, where the water contained continually rising bub-
bles of gas (hydrogen sulfide, carbon dioxide and probably
methane), showed no decrease nor increase in tension. It may
be mentioned here that salts or small amounts of acid and alkali
were reported by Adam to make no appreciable difference in the
standardization of his solutions. It would be of interest to test
the surface tension of waters containing a very large concentra-
tion of inorganic solutes, such as Great Salt Lake or the alkali
lakes of arid regions.

The colored bog lakes have, on the whole, lowered surface
tensions. Surface tensions in this group ranged from 72 dynes

to about 50 dynes/cm, having depressions of from 0 to more than 20 dynes/cm. The average of over 30 readings taken on these lakes was 6 or 7 dynes below normal. Open water in Helmet Lake on a calm day was depressed by 6 dynes/cm, while water pumped from a subsurface outlet in the Forestry Bog and tested in a cleaned pan was 4 dynes/cm lower than normal. A channel of calm, deep water between Lake Mary and Lake Adelaide was depressed by 20 dynes/cm. However, no direct correlation between color intensity and surface tension can as yet be made. The above data are of especial interest in view of the fact that the chemical nature of the brown suspensoid material in these lakes is not known. It has been suggested that such plant derivatives as tannins, glucosides and saponins may be involved, and the surface active nature of such compounds would be attested by the results here given. The presence of organic acids in those bogs having a low pH would likewise tend to lower the surface tension. Here also might be noted the fact that water from below the thermocline in Scaffold Lake, a curious lake containing a large amount of organic matter, is depressed by about 4 dynes/cm below the normal tension at that temperature (10.7° C). There is less organic matter at the surface in this lake than at the deeper stations, and the surface water was depressed by only 2 dynes/cm.

BIOLOGICAL FACTORS

The most important factors in lowering the surface tension of a lake appear to be those directly connected with biological activity. The tension may be strongly affected by a high plankton count or bloom in a eutrophic lake. Lake Monona, during a heavy surface bloom of blue-green algae, showed a surface tension of less than 52 dynes/cm (representing a depression of over 20 dynes). Wildcat Lake, its water turbid with plankton, was depressed by 3 dynes/cm, and Muskellunge Lake under similar conditions had a surface tension of 64 dynes/cm in the open lake and only 60 dynes/cm in Crystal Bay, where the water is shallower, the temperature higher and more plankton was present. Lake Mendota during a bloom of *Anabaena* and attached Vorticellids was down to 67 dynes/cm at a shore station. The open water of this lake ordinarily exhibits the tension of pure water.

Higher aquatic plants, particularly those with floating leaves, lower the tension of the water in their immediate vicinity, in both eutrophic and dystrophic lakes. The tension of Helmet Lake water in a stand of emergent *Potamogeton* and lilies was less than 52 dynes/cm. In Three Grass Lake the main lake body at a shore station showed 72 dynes, but a small arm full of lily pads and *Utricularia* had only 56 dynes/cm. In but one case did the water surrounding lily pads have the tension of pure water, and that was when a reading on Fishtrap Lake was taken during a steady rain. Some interesting observations on Boulder Lake were made. The open water of this lake has a normal tension. At one side is a small, weed-choked bay, containing *Castalia*, wild rice and many kinds of submerged plants. As the lilies in the bay are approached the tension begins to be altered, and in among the plants is depressed by 15 to 20 dynes. When the behaviour of a single oil drop floating toward a lily pad was followed, it could be seen to contract as it came close to the plant and then spread again as it was carried farther away. This would be repeated near the next leaf; the influence became apparent within 5 to 10 centimeters of the lily. This behaviour may be exactly duplicated on a hydrophile balance by alternately raising and decreasing the pressure exerted upon the surface film.

Lemna and some species of emergent *Potamogeton* show similar effects. A small, stagnating stream leading into Lake Mendota, covered with *Lemna,* had a surface tension of only 58 dynes/cm. Submerged vegetation, on the other hand, has little if any influence; a shallow station taken on Lake Mendota, above a submerged weed bed, was depressed by only 1 or 2 dynes. Thus some dependence of these phenomena upon the waxy character of floating leaves seems evident; but precisely what compounds may be given off into the water by such leaves is unknown. One possibility may be suggested by the analyses of Schuette on aquatic plants from Wisconsin Lakes (quoted from Welch, p. 281) ; his figures show the ether-extractable materials to form a higher percentage of the total sand-free dry weight in those plants having floating leaves than in those which grow completely submerged. Emergent reeds and grasses seem to have no influence upon the surface tension; this was found to be true in Trout Lake, Rudolph Lake and others.

PHYSICAL FACTORS

The fact that stagnant water is likely to have a decreased surface tension, noted by Adam and observed repeatedly in the Wisconsin series, is probably due to two major factors: the increased opportunity for bacterial and other biological activity and the production of surface active compounds, and the lack of any physical mechanism for dispersing such compounds once they have entered the surface layer. Physical factors of various kinds are of great importance in determining the tension of lake waters. Temperature is of course important for all lake types, but the variation caused is usually slight. The most extreme example of temperature effect was found in a very shallow, mud-bottomed flat caused by a widening of the bed of Token Creek, fed by subterranean springs. Here, on a warm day, the shallow water over the flats had reached a temperature of 28° and had a surface tension of 71.5 dynes, while the water immediately above the springs was at 10°, with a tension of about 74 dynes/cm. Both tension readings were normal for the respective temperatures.

Wave action often initiates a regular spreading and contracting of the organic surface depressant film. This has been noticed on many lakes, and causes an analogous but inverse phenomenon in the testing drop. Any mechanical breaking of the water surface may be effective in temporarily lowering the tension. The clearest exhibition of this kind was about a dam, with a fairly high waterfall, at the outlet of Rest Lake. Directly above the fall, and in a calm basin having direct connection with the channel below, the surface tension was normal. In the channel just below the fall, however, where the water was continually being churned and broken, the tension was depressed by 4 to 5 dynes; the testing drops here, instead of spreading evenly, would form long streamers. A steady wind tends to blow any organic film before it. If the rate of this wind action is greater than the rate of diffusion of new substances into the surface, then the tension of a given lake may be found to be higher on a windy day than when it is calm. Thus while on a calm day the tension of Helmet Lake was depressed by 6 dynes/cm, on a windy day the open water showed no depression; but a leeward dip of the shore contained water depressed by 7 dynes/cm. During a strong

onshore wind the surface of the open water of Lake Adelaide was normal, but the tension at the lee shore was depressed by 8 dynes/cm. The same effect of wind action has been observed on Mendota and other lakes, and has also been remarked by Adam (1937).

It has been suggested that a decreased surface tension may be partially responsible for the phenomenon of frothing or foaming of lakes. This occurs usually after a steady onshore breeze; the contributory conditions are not entirely clear. The few cases of frothing observed in this series were accompanied by decreases in surface tension ranging from 2 to 9 dynes/cm. Not enough measurements could be made to indicate any definite conclusion. While it seems likely that the piling up of the organic film by an onshore wind might tend to cause a lasting emulsion, analogous conditions were often seen without any foam at all. It might be noted here that the bottom water of Scaffold Lake (see above), higher in organic content and having a lower tension than the surface water, would also hold an emulsion much longer when shaken in a test tube. Thus there does seem to be some degree of correlation between frothing and a decreased tension, but no evidence of a strictly causal relationship has as yet been presented.

Table 4 summarizes data on three lakes studied intensively, showing many of the factors above ennumerated.

DISCUSSION

No quantitative treatment of data has been attempted. Although a large number of determinations were made, it has been considered important first to cover as wide a variety of conditions as possible in the allotted time, rather than to accumulate precise knowledge of smaller variations. Sufficient evidence has been acquired to justify listing the factors above discussed. For exact quantitative correlations to be of value a much larger series of tests would be necessary, made over longer periods and accompanied by simultaneous measurements of the other factors to be cited.

Little work has been done which might serve to show the possible ecological significance of the surface tension factor in aquatic environments. It is well known that many animals live

TABLE 4. *Surface tension data on three typical lakes.*

Lake	Type	Stations and conditions	Surface tension depression, dynes /cm
Trout	Oligotrophic	Open water	0
		Shallows over sand bar	0
		Around emergent *Carex*	0
		Laboratory pier, calm day	0
		Laboratory pier, windy day	0
		Laboratory pier, foam on surface	2
Mendota	Eutrophic	Open water, calm day	0
		Near shore above sand bottom	0
		Bay above submerged vegetation	1-2
		Stream covered with *Lemna*	15
		Shore, bloom of Vorticellids and *Anabaena*	5
Helmet	Dystrophic	Open water, calm day	6
		Shore, bed of floating vegetation	20+
		Open water, windy day	0
		Lee shore, windy day	7

associated, either permanently or temporarily, with the surface film. This association has been mentioned briefly by Welch (1935) ; and the paper by Scourfield (1908) gives a survey of the adaptations of aquatic animals to such existence. The only experimental data of which the author knows dealing with the effect of *variation* of surface tension upon aquatic animals are in some unpublished preliminary notes of Mr. G. Evelyn Hutchinson. Using surface skating insects, he was able to show that *Hydrometra* and a Gerrid behaved differently toward changes in tension caused by the addition of ethyl alcohol. While at a given percentage of alcohol the Gerrid would fall through the surface, its legs held rigid in the normal position, *Hydrometra* would first collapse, lying flat on the water. It is of interest to note that the *Hydrometra* collapsed in this experiment at a surface tension of approximately 50 dynes/cm, within the range which has been observed among Wisconsin lakes. Further investigation along this line should be carried out.

CONCLUSIONS

The presence of such surface films as are detected by this method depends most often upon biological activity, and some-

times upon the dissolved organic content of the lake.   Their distribution is determined largely by winds and currents.

The possible ecological significance of these films has been mentioned.

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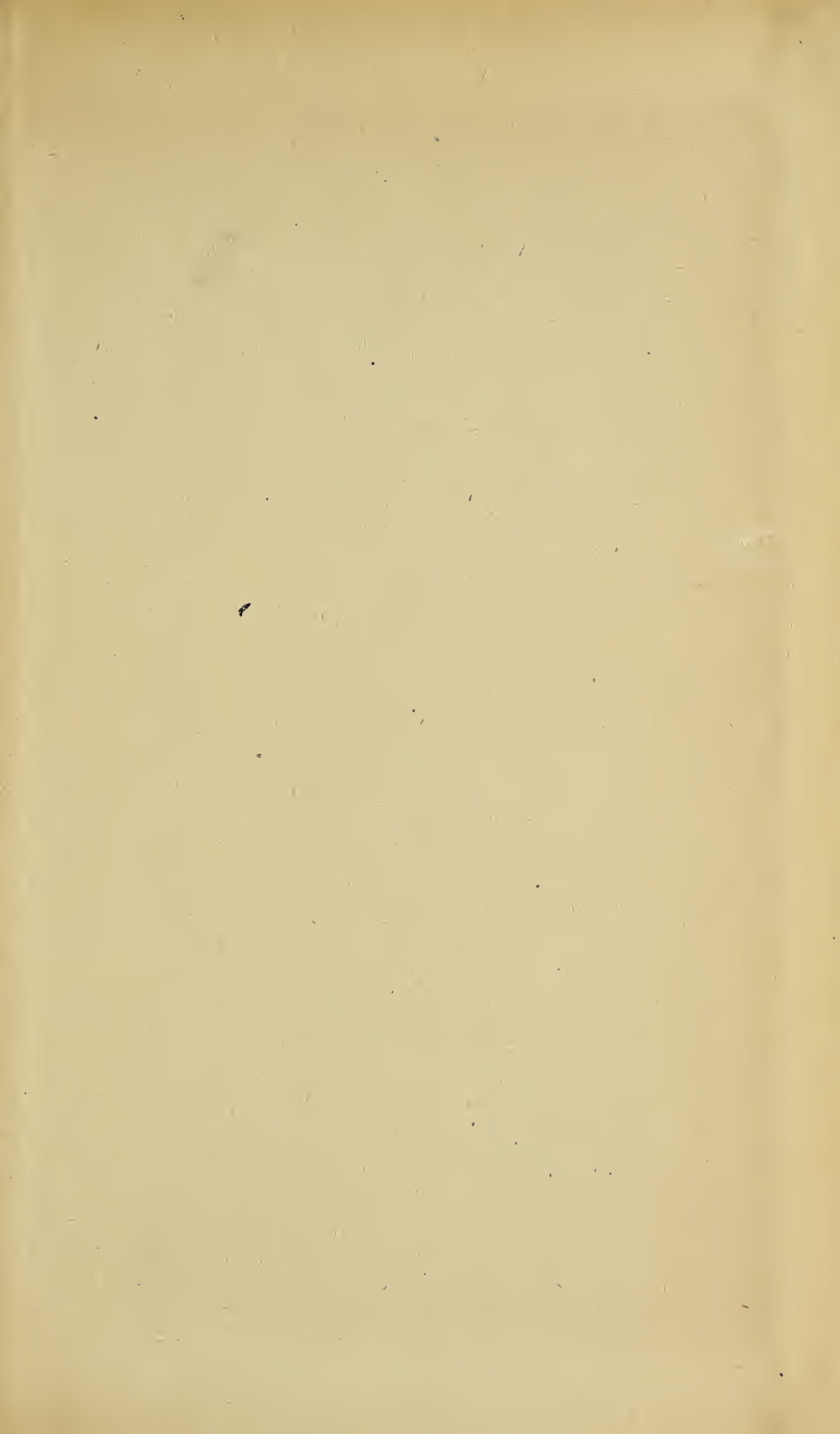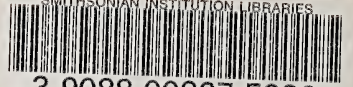Welch, Paul S. 1935. Limnology. 471 pp. McGraw-Hill, New York.