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VALIDITY OF AGE DETERMINATION FROM
SCALES, AND GROWTH OF MARKED
LAKE MICHIGAN LAKE TROUT

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VALIDITY OF AGE DETERMINATION FROM SCALES, AND GROWTH OF MARKED LAKE MICHIGAN LAKE TROUT

BY LOUELLA E. CABLE, *Fishery Research Biologist*

The lake trout, *Salvelinus n. namaycush* (Walbaum), was once the leading fish in the Great Lakes from the standpoint of monetary returns to the fishermen. The normal catch in the years before the invasion of the sea lamprey was 15,375,000 pounds, valued at \$7,688,000 by present day market prices.¹

Depredations of the sea lamprey² had so reduced the stock of lake trout by 1953 that only 4,128,000 pounds were taken. Lakes Erie and Ontario never supported large fisheries for lake trout, and, as the 1953 catch in Lake Superior was near normal, most of the 11,247,000-pound loss in total production was sustained in Lakes Huron and Michigan. Between 1932 and 1953 the catch in Canadian waters of Lake Huron was reduced gradually from an annual average of 3,596,000 pounds to 344,000 pounds, and in United States waters the catch dwindled from 1,400,000 pounds in 1936 to practically none in 1953 (Hile 1949, Hile and Buettner 1954).

The collapse of the lake trout fishery in Lake Michigan, though later than that in Lake Huron, has been equally dramatic. Annual production from 1885 to 1945 held between 5 and 9 million pounds. The decline was first apparent about 1946, but by 1953 the catch amounted to only 402 pounds. For a record of the annual production of this fishery from 1885 to 1949, see Hile, Eschmeyer, and Lunger (1951).

It now seems probable that the sea lamprey can be brought under control by the use of electrical barriers (Applegate, Smith, and Nielsen 1952; Applegate and Moffett 1955) placed near the mouths of streams into which adult lampreys run to spawn. When this has been accomplished, rehabilitation of lake trout stocks will be possible.

Meanwhile, information about the growth and habits of these fish must be gathered as a basis for an intelligent program for restoration and management of the fishery.

In the study of the lake trout, it is imperative first to assess the reliability of ages determined from scales of the fish to validate them for the many uses to which age statistics and calculated lengths, based on measurements of scales, are put in population studies.

Although determination of the age of lake trout from scales was considered difficult by Royce,³ Cooper, and Fuller (1945), and by Miller and Kennedy (1948), several investigators, including Greeley (1934 and 1936), Fry and Kennedy (1937), Fry (1949, 1953), and Van Oosten (1950), have read them with apparent assurance, but without establishing the validity of their readings.

The purpose of the present examination of the scales from lake trout of known age is not to offer an estimate of any person's skill in reading ages of the fish, but rather to ascertain whether recognizable markings of any kind, formed one each year, may be judged to be annuli. As scales of lake trout of known age have not been studied critically before, criteria for distinguishing annuli as they occur in this species are set forth in the paper. Time of annulus formation, development of marginal growth, calculated lengths, and growth of the marked lake trout also are discussed.

The cooperative work of the Conservation Departments of Michigan and Wisconsin and the Branch of Game-fish and Hatcheries of the United States Fish and Wildlife Service provided material for the present investigation. The author is indebted to Dr. Ralph Hile and Dr. James W. Moffett for reading the manuscript and for valuable suggestions, to Dr. Paul Eschmeyer for per-

¹ Further research and control of sea lampreys of the Great Lakes area. Hearings of the Subcommittee Merchant Marine and Fisheries, 82d Cong., U. S. House of Representatives, 1952, page 28.

² See Applegate (1951), and Van Oosten (1949 a, b) for accounts of the invasion and spread of the sea lamprey in the upper Great Lakes.

³ The reproduction and studies on the life history of the lake trout *Cristivomer n. namaycush* (Walbaum). By William F. Royce. Doctoral thesis submitted to Cornell University in 1943. Manuscript.

TABLE 1.—*Marked lake trout released in Lake Michigan*

Mark (fin removed)	Date of release	Number released	Average total length (inches)	Average weight (ounces)	Place of release
Dorsal and adipose.....	Sept. 6-16, 1944.....	100,280	2.9	0.11	NW shore South Fox Island. SE shore North Fox Island.
Right pectoral.....	Sept. 4-11, 1945.....	159,712	3.2	.16	8 mile course from Charlevoix toward Fox Island. Between North and South Fox Islands.
Left pectoral.....	Sept. 16-18, 1946.....	151,402	3.2	.14	

mission to publish information on young lake trout from his collections, also to George Lunger for recommendations regarding statistical treatment of data. Photographs of the scales were made by William L. Cristanelli. Scale samples were taken and measurements of the fish were made by Kiyoshi G. Fukano.

MATERIALS AND METHODS

Scales from lake trout of known age were obtained from fish recovered during a marking experiment inaugurated in 1944 as part of a program for the study of lake trout in Lake Michigan by the Great Lakes Lake Trout Committee.⁴

Early attempts to mark various species of fish in the Great Lakes (Milner 1874; Cole 1905; and others) met with small success. Most of the fish were "never heard from again" after release. Smith and Van Oosten (1940) reported the recovery of 218 or 15.4 percent of 1,416 lake trout caught commercially, tagged, and released between June 20, 1929, and August 4, 1931, in Lake Michigan at Port Washington, Wis. Although Smith and Van Oosten estimated the growth of the tagged fish, they made no study of the scales of the recovered fish to establish the validity of the ages of the fish as determined by examination of their scales.

Two later plantings of tagged lake trout in Lake Michigan resulted in sparse returns. The Wisconsin Conservation Department (Schneberger 1936) tagged and liberated 650 lake trout in Green Bay during the fall of 1935. Only 13 of these fish were recaptured subsequently. Three years later in November 1938, Shetter⁵ tagged 28 lake trout which were released about three-fourths of a mile

⁴ The committee, composed of representatives of the Great Lakes States, the Province of Ontario, and the Fish and Wildlife Service, was organized in 1943. It was combined with the Great Lakes Sea Lamprey Committee in 1952 to form the Great Lakes Lake Trout and Sea Lamprey Committee. In 1953, the functions of the committee were broadened, representation from the Canadian Federal Department of Fisheries added, and the name changed to Great Lakes Fishery Committee.

⁵ Tagging of Lake trout in Lake Michigan, November 7, 1938. By David S. Shetter. Michigan Institute for Fisheries Research, Ann Arbor, Mich. Report No. 502 (unpublished).

WNW by W of Seven Mile Point in northeastern Lake Michigan. The following November two fish from this planting were recovered within 5 miles of the point of release.

RELEASE OF MARKED LAKE TROUT

Considerable success in the capture of marked lake trout was attained from plantings made according to plans of the Great Lakes Lake Trout Committee. Although the original purpose of these plantings was to obtain definite information on the survival of hatchery-reared fingerlings, later destruction of a large part of the lake trout population by the sea lamprey disrupted the experiment. Some of the marked fish were recovered, however, and they form the basis for this study.

Over a period of 3 years, the conservation departments of Michigan and Wisconsin, participating with the United States Fish and Wildlife Service, distributed lake trout reared through their first summer in the United States Fish Hatchery at Charlevoix, Mich. The plantings were made each year during the first 3 weeks in September. About 10 percent of the fingerlings were marked by the removal of fins. Pertinent data on the marking and release of the young lake trout are shown in table 1. Control groups of marked and unmarked fingerlings were transferred each year to ponds at the Michigan State Hatchery near Marquette, Mich. The effect of removal of the fins from these lake trout was reported by Shetter (1951).

RECOVERIES

Recoveries of marked lake trout in Michigan and Wisconsin waters of Lake Michigan were made by commercial fishermen, who were paid \$2 for each fish sent in.⁶ Slightly more than half of the recovered lake trout were taken in chub gill nets 2½ to 2¾ inches, stretched mesh; the remainder were from large-mesh gill nets (4½ inches and greater).

⁶ In 1952, when numbers of the marked fish were approaching or had reached legal size (1½ pounds minimum weight or larger), a \$4 reward was established for marked lake trout. Relatively few of these larger rewards were claimed.

TABLE 2.—Recoveries of "marked" lake trout from Lake Michigan, by year of capture

Year marked	Year of capture													
	Areas 1-6 ¹							Area 8						
	1947	1948	1949	1950	1951	Total number	Percentage returns ²	1947	1948	1949	1950	1951	1952	Total number
1944.....	23	10	24	57	0.06	1	1
1945.....	37	199	570	257	14	1,077	.67	13	5	11	10	3	42
1946.....	2	12	60	173	24	271	.18	4	13	14	17	8	3	59
Total.....	62	221	654	430	38	1,405	4	27	19	28	18	6	102

¹ Includes 2 fish from extreme northern part of area 7. See figure 3 for boundaries of the statistical areas.

² See table 1 for number of marked lake trout released.

Marked lake trout captured by fishermen in Michigan waters of Lake Michigan were delivered to local conservation officers who recorded data given by the fishermen. Initially, the officers removed the fin scar from each fish (in some cases, also a scale sample) and sent them to the Institute for Fisheries Research of the Michigan Department of Conservation in Ann Arbor for payment of the reward. Later, however, most of the fish were shipped iced, either in the round or dressed,⁷ to the Institute where the scale samples were taken, measurements recorded, and the deformed or missing fin described in some detail. Sex was not recorded.

Up to July 22, 1952, 1,603 fish had been sent to the Institute for Fisheries Research. Of this number, 96 could not be identified with any one of the three plantings or lacked essential records: *i. e.*, record of the missing fin was lacking, the fin or combination of fins reported missing or abnormal had not been used in the experiment, or fins were reported by the State observer as normal in every respect, length measurement was not recorded, or scale sample was not taken.

For the 1,507 fish that, on the basis of fin records alone, could have been marked lake trout, the annual recoveries were as given in table 2. Although this group includes individuals with "naturally deformed" fins (malformations not resulting from earlier clipping), the data of table 2 give a rough estimate of the percentage return from the several plantings. Because it is doubtful that the recoveries from area 8 were fish with bona fide markings, the percentage of returns are shown for areas 1-6 only. Recoveries from the 1945 planting exceeded those from the 1946 planting almost 4:1, and exceeded recoveries from the 1944

planting 11:1, but the recoveries of marked lake trout from all plantings were in exceedingly small percentages of the numbers of fish released. About 0.67 percent of the marked lake trout released in 1945 but only 0.06 percent of the 1944 planting and 0.18 percent of those planted in 1946 were recovered. The low percentages of return and abrupt termination of captures probably were due to the rapid reduction of the population by the sea lamprey. No explanation can be offered for the higher percentage of return from the 1945 than from the 1944 and 1946 plantings.

A large majority of the recoveries of marked lake trout in northern Lake Michigan (areas 1-6) were made in the fourth year after planting. The fish had evidently reached a sufficiently large size at that age to be most easily caught in the nets employed in the fishery at the time.

The localities and relative numbers of recoveries are shown in sectional maps of Lake Michigan (figs. 1 and 2). Boundaries of these sections are superimposed on a map of the entire lake (fig. 3) to indicate their position with reference to the boundaries of the statistical areas or districts 1-8 regularly employed in analyses of commercial fishery statistics for the State of Michigan waters of Lake Michigan (Van Oosten, Hile, and Jobses 1946; Hile, Eschmeyer, and Lunger 1951).

The largest catches of marked lake trout were made out of Manistique, Mich., in area 2, and in the vicinity of the islands of area 3, with the greatest concentration about Beaver Island and the shoals to the east of this island. A few specimens were caught in each of areas 1, 5, and 6; 2 trout, taken just across the line in the northern part of area 7 by fishermen from Pentwater, are included with those caught in area 6. No recoveries were made between Little Sable Point in the northern

⁷ Gills and viscera removed.

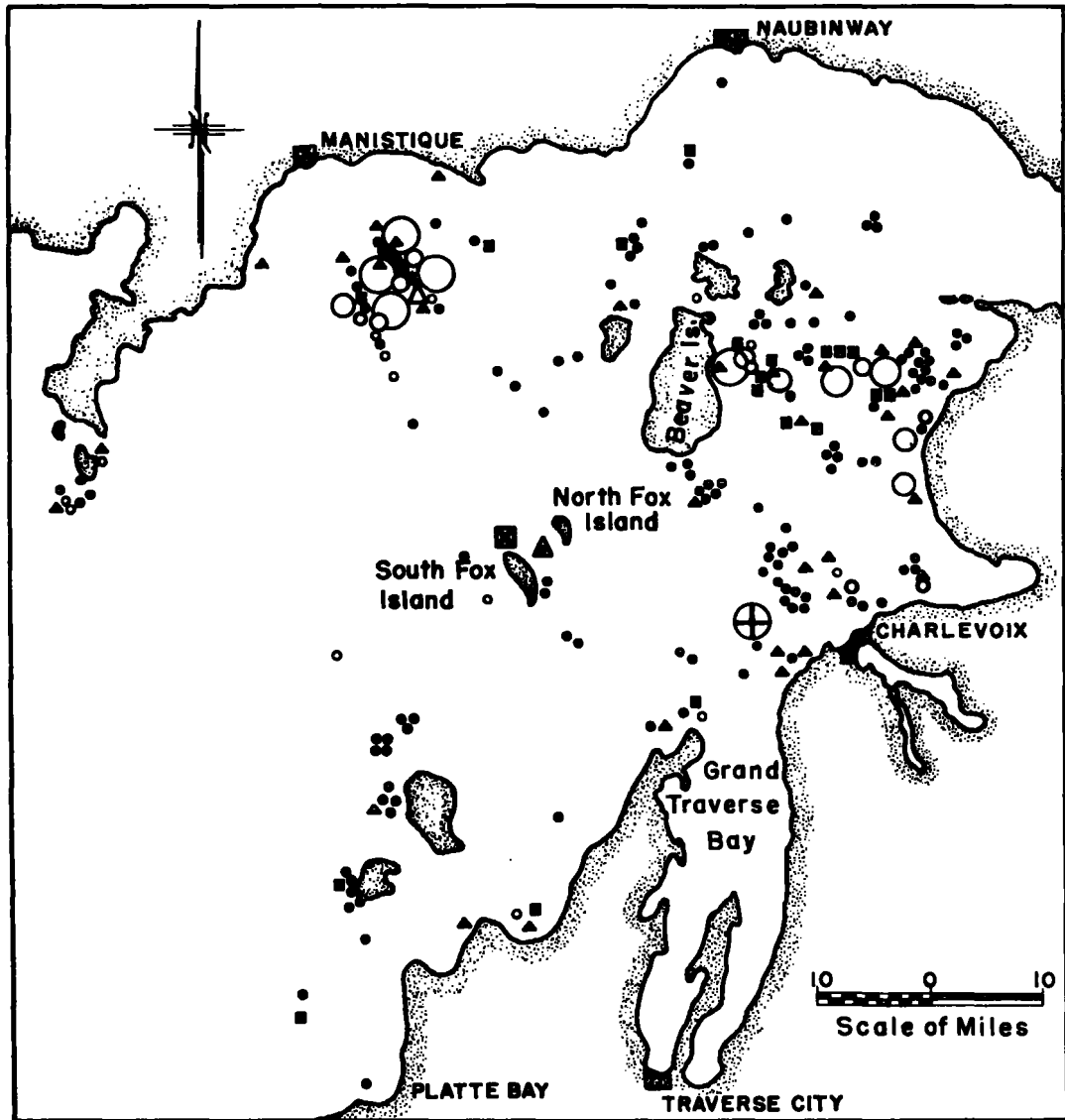


FIGURE 1.—Northern Lake Michigan showing points of release and capture of marked lake trout. Planting locations designated as follows: 1944, square enclosing an X; 1945, circle enclosing a +; 1946, triangle enclosing dot. Recoveries from the three plantings are indicated as follows: 1944, squares; 1945, circles; 1946, triangles. The sizes of the symbols indicate numbers of fish recaptured at the various points, the smallest symbol of each year class is for 1-4 fish through the largest for more than 49 fish.

part of area 7 and the vicinity of South Haven (area 8), more than 60 miles distant, where 102 lake trout with deformed or missing fins were taken.

Lake trout with abnormal fins, captured on the Wisconsin side of the lake, are not shown on the map. Most of the 142 fish taken were caught north of Algoma; a few, 1 or 2 off each port, were taken off Two Rivers, Cedar Grove, Milwaukee,

and Racine. The records on these fish are not sufficiently detailed for profitable study.

Rather than reject individual fish arbitrarily all samples, properly documented and having "possible" fin markings, were accepted for study. The large size of certain lake trout whose missing fins indicated ages of 1 or 2 years made it certain they were not from the plantings, but size alone cannot be used as a general criterion for the sepa-

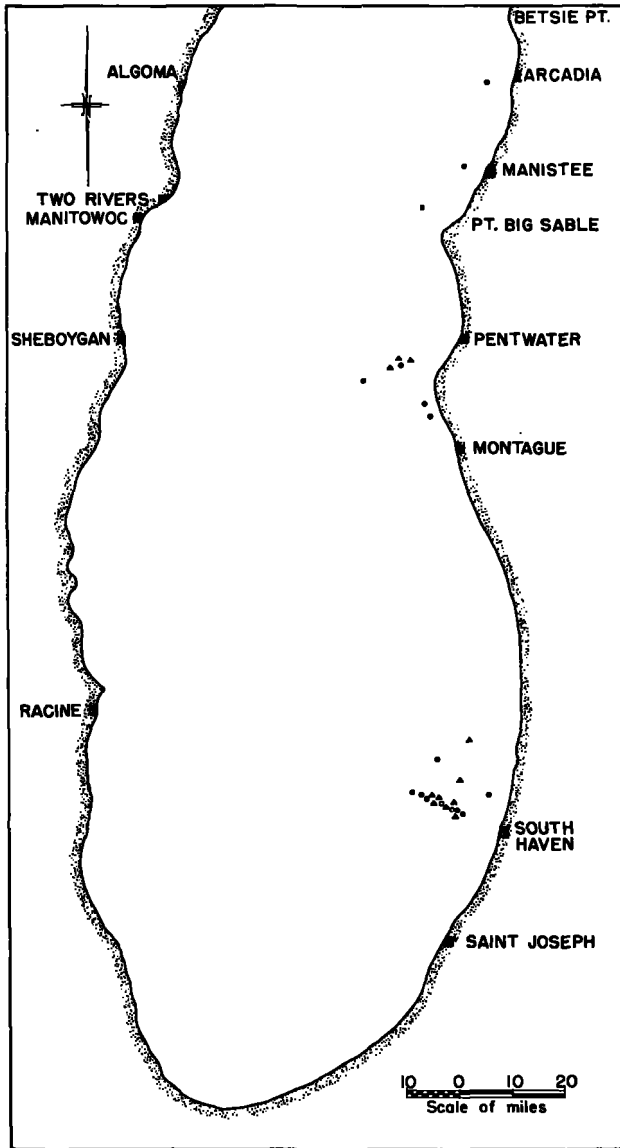


FIGURE 2.—Southern Lake Michigan showing points of capture of lake trout having deformed or missing fins. Year class indicated by fin mark is as follows: 1944, squares; 1945, circles; 1946, triangles. The sizes of the symbols indicate numbers of fish captured at the various points, the smaller size of each symbol represents 1-4 fish, the larger one represents 5-9 fish.

ration of fin-clipped fish from those with deformed fins. Small lake trout with abnormalities resulting from causes other than clipping undoubtedly were included.

PREPARATION AND EXAMINATION OF SCALES

The scales were made ready for examination by preparing impressions in plastic. Washed

scales were mounted, still damp, on 3- by 5-inch cards of gummed Kraft paper. Scale samples from 9 to 30 fish were mounted on each card in 2 or 3 rows depending on the size of the scales and the number per sample to be mounted. Three to 6 symmetrical scales from each fish were mounted; usually at least one scale was mounted with the smooth or inner surface up, as the annuli often were prominent on that side

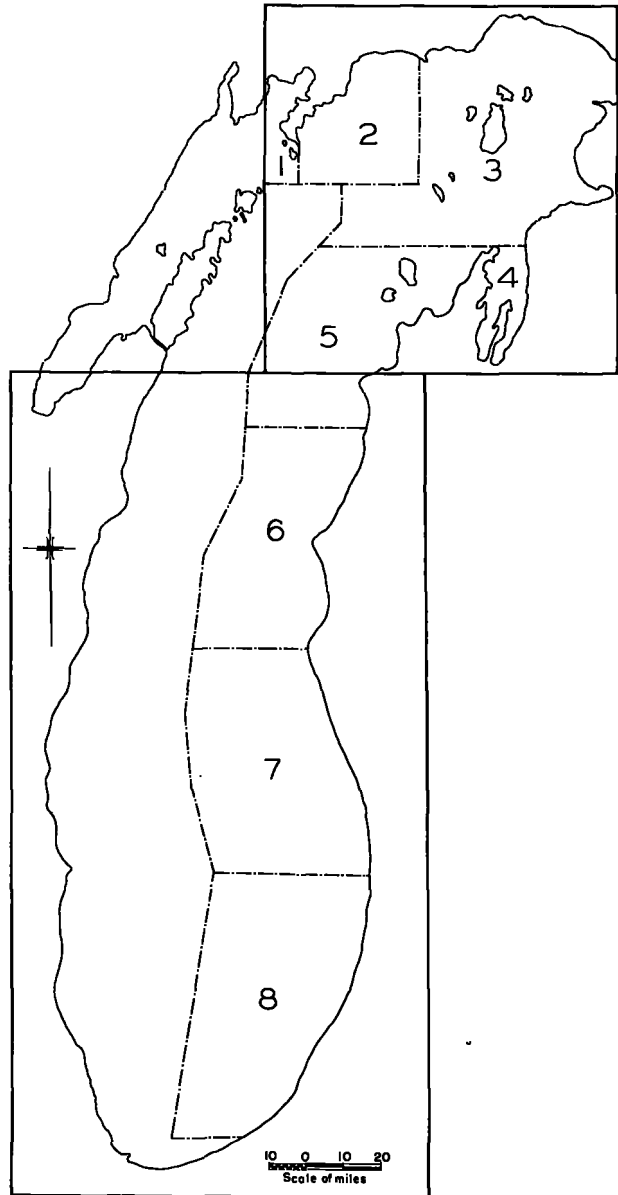


FIGURE 3.—Map of Lake Michigan showing boundaries of the statistical areas or districts 1-8, and of sectional maps in figures 1 and 2.

(fig. 4). Annuli seen first on the inner surface could then be located more readily in the sculptured pattern of the outer surface. Labels bearing specimen numbers were typed on rag paper with hectograph ribbon, laid face down on the gummed paper, and secured at the ends by bits of Scotch tape; then 3- by 5-inch sheets of cellulose acetate 0.020-inch thick were inserted between the label and the gummed Kraft paper card on which the scales had been affixed.

The labeled, mounted scales were impressed by the exertion of about 12 tons of pressure on 8- by 8-inch platens, preheated to 230° F.⁸

The impressions were studied at a magnification of 83.5X on the microprojection machine described and illustrated by Moffett (1952). The annuli found on each scale were traced on the viewing screen with a glass-marking pencil. The diameters of the entire scale and of fields within the several annuli were measured along the antero-posterior axis through the center of the focus. Measurements of the diameters of the annuli were more suitable than measurements of either anterior or posterior radii for the estimation of past growth.

BASIS FOR REJECTION OF SAMPLES FROM SOUTHERN LAKE MICHIGAN

It was realized early that by no means all lake trout represented in the 1,507 scale samples were authentic recoveries of fin-clipped fish. That occasional naturally propagated lake trout may lack fins or have abnormally formed fins has been established.⁹ Hatchery-reared lake trout rarely develop deformed fins of the types that would be mistaken for clipped fins (see footnote 20).

Even though the percentage of naturally occurring malformations may be small, it was anticipated that most of the fish bearing them would be reported by the fishermen. The marking experiment was widely publicized and the operators were urged strongly both by the officers of their own trade association and conservation officials to cooperate by reporting all recoveries.

Various aspects of the data were studied in detail

⁸ Details of this procedure, basic features of which were developed by R. A. Nesbit, unpublished.

⁹ John Van Oosten reported in 1949, at the spring meeting of the Great Lakes Lake Trout Committee, that Frank W. Jobs and Howard J. Buettner examined 1,850 lake trout from Lake Michigan and found 4 (0.22 percent) with deformed fins. Three fish (0.20 percent) also with deformed fins were found among 1,462 lake trout from Lake Superior. It was believed only one of these fins could have been mistaken for a regenerated fin which had previously been removed by clipping.

In order to judge the reliability of measurements made of impressions of lake-trout scales, measurements of scales mounted in gelatin were compared with those of impressions of the same scales. Gelatin mounts are wet scales whereas plastic impressions are made from dry scales, yet the difference in scale size was not significant and was no greater than occurs regularly between independent measurement of the same scale. It appears from this comparison that dehydration causes no appreciable decrease in size of lake trout scales. Butler and Smith (1953), who compared dry mounts, gelatin mounts, and Plastacele impressions of the thicker scales of the walleye, *Stizostedion vitreum*, found significant differences among them but the differences were "reflected proportionally at each annulus."

In this paper, age groups are designated by Roman numerals corresponding to the number of annuli (fish in their first year are members of age-group 0). A "virtual" annulus is credited at the edge of the scale from January 1 to the time of annulus formation. Year classes are identified by the calendar year of hatching (which takes place in the spring; spawning occurs the preceding fall).

to obtain reasonably objective standards for distinguishing between marked and unmarked lake trout. Among the points considered were: geographical distribution of recoveries from the 3 years' plantings; condition of abnormal fins in terms of numbers of regenerated rays and length of fin; growth shown by the fish at ages indicated by the deformed fins; discrepancies between ages indicated by abnormal fins and those shown by the scales. Data on the last of the aforementioned points may be used, of course, only as indicative of general relationships and trends, since a mere disagreement between these ages does not in itself constitute acceptable evidence that individual fish had not been marked by fin clipping.

The analyses led to the rejection of the entire sample from southern Lake Michigan (area 8) as containing few or no marked lake trout. For the samples from the northern part of the lake (areas 1-6), objective standards were not furnished for the separation of the marked from the unmarked or wild fish. By other methods, it was possible to point out most of the unmarked fish there with

a high degree of confidence. The findings on these fish are detailed more appropriately in later sections but a summary of the basis for the rejection of the samples from area 8 is given at this point.

GEOGRAPHICAL DISTRIBUTION OF RECOVERIES

In areas 1-6, the earliest recoveries were made near the locality of planting. As the fish grew older and larger the captures were more widely distributed. They scattered to some extent in all directions, but the principal movement was in a northwesterly direction toward Manistique and thence westerly and southwesterly until some fish were recaptured along the Wisconsin shore. Captures of lake trout with deformed fins were fewer and the distribution was discontinuous southward from the localities in which the plantings were made. No recoveries at all were made between the extreme northern part of area 7 and the neighborhood of South Haven.¹⁰ If it is assumed that lake trout reported off South Haven were actually marked fish, it is difficult to understand why none were caught in the heavily fished 60-mile-long area en route to the more southerly waters. On the other hand, if the lake trout reported from area 8 are considered to be wild-stock lake trout with abnormal fins, the troublesome question arises as to why no trout of the same category were reported from that 60-mile stretch.¹¹ The discontinuity of distribution of the recoveries does not provide convincing evidence, but does, nevertheless, give cause to regard with suspicion the genuineness of the mark (deformed fin) on the fish caught at South Haven.

FINS ON RECOVERED LAKE TROUT

Records of degree of regeneration of the pectoral fins¹² in terms of regenerated rays (table 3) and lengths of the abnormal fins (table 4) on recovered lake trout were similar in that they suggested no basis for the separation of marked

¹⁰ Van Oosten (1950) described the distribution of recoveries of these same fish through 1949. Subsequent captures did not change the general situation greatly, except that the progressive scattering of the growing fish continued.

¹¹ The answer possibly may lie in the enterprise of a single fisherman. Of the 102 recaptures from southern Lake Michigan, 94 were turned in by the same operator. Conceivably fishermen in the waters to the north observed similar abnormalities but did not believe them to be the result of fin-clipping.

¹² The collection of fish with dorsal and adipose fins clipped is too small to give reliable results, but 43 (75.4 percent) of a total of 57 specimens were judged to have true marks. Just one lake trout with this mark was caught in area 8. The mark (dorsal and adipose fins removed) proved somewhat confusing because of the presence of fish with one fin deformed and the other normal.

lake trout of areas 1-6 from naturally propagated individuals of this region, but did indicate rather conclusively that the samples from areas 1-6 and area 8 could not have been drawn from the same population. Despite certain disagreements as to detail between data on the right and left pectoral fins of trout from areas 1-6 (discrepancies which could have been the result of the small number of fish recaptured with a deformed left pectoral fin), the general situation can be described satisfactorily from the combined records of the two fins. The extent of regeneration of fins on lake trout from areas 1-6 was relatively small. In a total of 1,348 individuals, 57.5 percent had no regeneration of the fin rays, and 77.5 percent had fewer than 5 rays regenerated. With respect to length of regeneration, 58.2 percent of the fins were without regeneration, and 75.2 percent were not more than $\frac{1}{2}$ normal length. In area 8, to the contrary, regeneration of most fins was advanced. Of 74 fish, for which there were records of the number of rays in the deformed fin, but 1.4 percent had no rays regenerated, and only 4.1 percent had fewer than 5 rays regenerated as compared with 77.5 percent in areas 1-6. Of 89 fish, for which the length of the fins was recorded, just 1.1 percent of the fins were without regeneration, and only 13.5 percent were not more than $\frac{1}{2}$ normal length as compared with 75.2 percent in areas 1-6. The very small percentage (1.1) of fins showing no regeneration in area 8 is strikingly different from that (58.2) of fins on fish from areas 1-6.

The data of tables 3 and 4 have a usefulness in addition to that of demonstrating that samples from areas 1-6 and area 8 were drawn from stocks that were dissimilar with respect to the characteristics of abnormal fins. If the thesis is accepted that most or all of the lake trout from area 8 were unmarked, it can be anticipated that most of the unmarked lake trout in the samples from areas 1-6 also will be among the fish whose fins exhibit more advanced regeneration.

DISCREPANCIES BETWEEN AGES READ FROM SCALES AND INDICATED BY ABNORMAL FINS

Agreement between ages indicated by fins and read from scales was high (substantially above 90 percent) in fish from areas 1-6, but in area 8 only 39.2 percent of the scale readings agreed with the ages indicated by abnormal fins. Even

TABLE 3.—Extent of regeneration of the pectoral fins, expressed as number of rays, on lake trout marked in 1945 and 1946

Locality of recovery and mark; year of planting	Number of fish	Number of rays regenerated										
		0	1	2	3	4	5	6	7	8	>8	Unknown
Areas 1-6:												
Right pectoral (1945).....	1,077	679	91	46	31	36	48	30	25	17	41	33
Percentage ¹		65.0	8.7	4.5	3.0	3.4	4.6	2.9	2.4	1.6	3.9	3.1
Left pectoral (1946).....	271	95	20	9	10	10	13	17	14	28	33	13
Percentage.....		36.8	11.2	3.5	3.9	3.9	5.0	6.6	5.4	10.9	12.8	4.8
Right and left pectorals.....	1,348	774	120	55	41	46	61	47	39	45	74	46
Percentage.....		57.5	9.2	4.2	3.1	3.5	4.7	3.6	3.0	3.5	5.7	3.4
Area 8:												
Right pectoral (1945).....	43				1		3	1	1	2	25	10
Percentage.....					3.0		9.1	3.0	3.0	6.1	75.8	23.3
Left pectoral (1946).....	59	1			1			2		2	35	18
Percentage.....		2.4			2.4			4.9		4.9	85.4	27.1
Right and left pectorals.....	102	1			2		3	3	1	4	60	28
Percentage.....		1.4			2.7		4.1	4.1	1.4	5.4	81.1	27.5

¹ Fish with unknown number of fin rays not included in percentages.

TABLE 4.—Extent of regeneration of the pectoral fins, expressed (for most fish) as a fraction of the normal length of the fin, on lake trout marked in 1945 and 1946

Locality of recovery and mark; year of planting	Number of fish	Extent of regeneration								Full normal length	No record of length
		No regeneration	Less than 1/2-inch long	1/4 normal length	1/3 normal length	1/2 normal length	2/3 normal length	3/4 normal length	4/5 normal length		
Areas 1-6:											
Right pectoral (1945).....	1,077	679	124	18	21	128	45	42	8	8	12
Percentage.....		63.8	11.6	1.7	2.0	12.0	4.2	3.9	0.8	0.8	1.1
Left pectoral (1946).....	271	95	48	7	8	60	27	17	2	2	7
Percentage.....		36.0	18.2	2.7	3.0	22.7	10.2	6.4	0.8	0.8	2.6
Right and left pectorals.....	1,348	774	172	25	29	188	72	59	10	10	19
Percentage.....		58.2	12.9	1.9	2.2	14.1	5.4	4.4	0.8	0.8	1.4
Area 8:											
Right pectoral (1945).....	43		1	1	2	15	13	6			5
Percentage.....			2.6	2.6	5.3	39.5	34.2	15.8			11.6
Left pectoral (1946).....	59	1	2	4	1	18	10	14	1	1	8
Percentage.....		2.0	3.9	7.8	2.0	35.3	19.6	27.5	2.0	2.0	13.8
Right and left pectorals.....	102	1	3	5	3	33	23	20	1	1	13
Percentage.....		1.1	3.4	5.6	3.4	37.1	25.9	22.5	1.0	1.0	12.7

¹ Fish with fins of unknown length not included in percentages.

though this percentage was somewhat higher than would be expected from an assumption of complete independence of age shown by abnormal fins and by scale markings, it does indicate that if the sample from area 8 contained any authentic marked lake trout, their number was extremely small.

GROWTH AS INDICATED BY ABNORMAL FINS

Presentation here of details on length frequencies and average sizes of various age groups of the different year classes as established by abnormalities of the fins and by the examination of the scales would be little to the point as the situation is described adequately by the data of table 5 which shows the mean lengths and ranges of length for the several age groups (year classes combined) as indicated by fins. If these lake trout are taken as bona fide fin-clipped fish, we must accept also the conclusion that the trout were largest in the first and second years of life (average lengths of age-groups I and II, 23.8 and

17.1 inches, respectively), were smaller, and, for the most part, without growth in later years (range of 12.5 to 12.7 inches for average lengths of age-groups III-VI, and only 13.7 inches for age-group VII).¹³ Despite the considerable range of length for each age group of lake trout of known

TABLE 5.—Average lengths and ranges in length of age groups as indicated by the occurrence of abnormal fins (assumed to be true marks) of lake trout from southern Lake Michigan

[See text discussion of the probability that few or none of these fish could have come from the various fin-clipping experiments]

Age group	Number of fish	Total length (inches)	
		Average	Range
I.....	4	23.8	22.5-24.0
II.....	13	17.1	10.4-24.0
III.....	28	12.7	7.4-21.0
IV.....	22	12.7	10.4-23.0
V.....	19	12.5	10.4-15.2
VI.....	13	12.6	10.0-16.6
VII.....	3	13.7	13.2-14.5

¹³ According to Smith and Van Oosten (1940) lake trout tagged at Port Washington, Wis., that averaged 12.8 inches long at tagging were 19.8 inches long about 2 years later.

age that will be demonstrated later, some of the ranges in table 5 cannot be considered reasonable.

These lines of evidence, even though they do not exclude the possibility of the presence of a few marked lake trout in the samples from area 8, demonstrate conclusively that the great majority were unmarked wild stock, and that the occurrence of abnormal fins among these fish was not related

to the age of the fish. The sample is, therefore, considered unsuitable for use in the present study. Samples from areas 1-6 undoubtedly also include some unmarked fish with abnormal fins; and convincing evidence of their presence will be offered. There is no reason to believe they were sufficiently numerous there to harm seriously the materials for the purposes of this investigation.

VALIDITY OF AGE DETERMINATIONS FROM SCALES

The study of the scales of lake trout, presumably of known age, offered the rather perplexing problem of using the same materials for two purposes which, in a sense, are mutually exclusive. It was, of course, imperative to examine carefully the scale characteristics of a large series of fish of known age to establish, as exactly as possible, criteria for the determination of age. It was equally necessary to use the same fish as the basis for an objective estimate of the degree of accuracy to be expected in the reading of the scales of lake trout for which the ages are not known.

With a small series of fish, accomplishment of both purposes would be impossible, for the investigator would become so well acquainted with the scales of individual specimens as to remember their characteristics, especially their unusual features, and hence would be unable to make objective age determinations. In the present large series of 1,405 fish from northern Lake Michigan (areas 1-6), however, memory of scales of individual fish probably had no biasing effect on the accuracy of successive readings. Even so, precautions were taken to keep the tests objective. A brief statement of the general procedure follows.

In a preliminary examination, designed to establish whether or not the scales of lake trout bear markings that can be interpreted as annuli corresponding in number to the supposed age of the fish (as indicated by a deformed or missing fin), the scales of several hundred lake trout were read objectively. They were studied for the occurrence of repetitive irregularities in the sculptured pattern without reference to any information about the fish except the date of its capture. When such markings were found, readings and measurements made from them were compared with the full data on the individual fish. Another important aspect of the first series of examinations

was the establishment of the time of annulus formation and the progress of the season's growth, without knowledge of which it is difficult to make accurate readings from scales of fish caught over much of the growing season.

After the characteristics of the annulus and the time of annulus formation were well established, the entire series of scales was read twice. During both readings the only information available was date of capture, and each second reading was made without knowledge of the age assigned at the first. After completion of the two readings, a careful study was made of the scales of all lake trout for which the ages assigned were not the same at the first and second examination and a best estimate of the correct age was made.

EARLY GROWTH OF SCALES

The scales of lake trout are cycloid, oval to egg-shaped. Concentric ridges or circuli, arranged about a focus, roughen the outer surface of the scale. The focus may be central or slightly anterior or posterior to the center of the scale (see figs. 8 and 11). Neither radii nor transverse grooves are present. The inner surface of the scale lacks circuli but is not utterly smooth and characterless. Annuli sometimes are clearly visible on this side. The scales are so small, thin, and deeply embedded in the skin as to be relatively inconspicuous. They are dislodged with such difficulty that few are regenerated. Variation in the number of scales, in series along the lateral line, is large, from 180 to more than 200. Squamation of the body is complete. Only the head, which is well supplied with mucus pores, and fins, are unscaled.

The size of the scale varies greatly from one location on the fish to another. In general, the larger scales are on the posterolateral surfaces of the body and the smaller scales about the fin bases

and on the anteroventral and anterodorsal surfaces. Samples for study were taken from a mid-point on the body, below the anterior part of the dorsal fin, immediately above the lateral line, and thus did not include either the smallest or the largest scales of the individual fish. However, scales from rather limited areas show considerable variation in size and shape. Scales chosen from the sample for study were those which seemed most representative of the larger symmetrical scales.

The scales of lake trout appear during the summer of the first year of development. However, neither the age nor the length of the fish at the time of scale formation has been determined definitely for the lake trout in Lake Michigan. Both salt-water and fresh-water fishes that have been studied develop platelets, the beginnings of scales, when the young fish are from about 18 to 50 millimeters in total length (Fish 1932; Hildebrand and Cable, 1930, 1934, and 1938; Cooper 1951; Brown and Bailey, 1952; and others). Fish (1932) described a lake trout larva 21.5 millimeters long from Cape Vincent Hatchery, but did not mention the development of scales. A yolk sac was still present at this size and the appearance of scales would scarcely be expected before absorption of the yolk.

In 1953, young lake trout 26 to 56 millimeters long, were taken in Lake Superior in the middle of June and the middle of August by the Fish and Wildlife Service research vessel *Cisco*. The largest of those caught in August was 56 millimeters or $2\frac{3}{16}$ inches long. It had a band of scale pockets containing platelets along the entire length of the lateral line. This band consisted of several rows of platelets on either side of the lateral line. The sizes of the platelets were graduated; the larger ones were adjacent to the lateral line; the others became smaller and farther apart with each successive row. Only in the lateral line did the scale structures take alizarin stain readily. These structures were concave ovoids, two in each pocket, one dorsal to and the other ventral to the lateral-line organ, forming partial sidewalls to it. The platelets, situated in dermal pockets, were protected from immediate contact with the alizarin. Consequently, the scale pockets stood out as clear areas after staining. The largest scale platelets, when teased out of the pockets, measured about 0.2 millimeter long. Some were clear and smooth; the first circulus was formed on

others. Although some fish such as brook trout form scales first along the posterior part of the lateral line (Cooper 1951), a young lake trout 53 millimeters long had platelets scattered in one or two interrupted rows and in small groups here and there along the anterior end only of the lateral line. The lateral line itself was not in evidence posteriorly. The largest platelets on this lake trout were about 0.1 millimeter long and lacked circuli. Probably scales begin to form on lake trout in Lake Superior when the fish are about 50 millimeters long but no histological sections were made to determine this point.

It is not known whether young lake trout growing in Lake Michigan develop scales at the same size as those in Lake Superior. One hundred fingerlings, all of the same age but ranging in length from 35 to 85 millimeters, which were reared in the fish hatchery at Charlevoix, Mich., in 1948 and preserved on September 17, were examined. The smallest of these lake trout having scales was 47.5 mm. long. This fish had scales with as many as 4 circuli the full length of the lateral line. Other specimens 35 to 43 mm. long were without scales and no evidence of a lateral line was seen. Although these young lake trout grew under artificial conditions, development of the scales began at about the same body length as on young fish that had grown under natural conditions in Lake Superior. The lake trout from the hatchery were caught about a month later than those from Lake Superior, which may account for the presence of scales on somewhat smaller fish. Season of the year and age as well as body size may be factors in determining the time for the formation of scales.

The average total length of the lake trout marked by removal of fins and planted in Lake Michigan in early September 1944, 1945, and 1946 was 81 mm. or 3.2 inches (range 2.1–4.3 inches¹⁴). It probably is safe to assume, therefore, that nearly all were fully scaled when planted and would not pass through the first year without the formation of an annulus. As soon as the scales appear on the fish, squamation proceeds rapidly to comple-

¹⁴ Measurements were of random samples of the general stock of lake trout reared in the fish hatchery at Charlevoix, Mich., for the 1945 experiments. The range for 1,000 unmarked lake trout used as controls was 55–105 mm.; that for 1,000 marked lake trout also used as controls was 54–100 mm.; and the range for 490 lake trout held for studies on regeneration of fins was 53–105 mm. I thank David S. Shetter, Michigan Institute for Fisheries Research, for permission to publish this information.

tion. Further growth of the scales is approximately proportional to the growth in length of the fish.

The spacing of circuli on the scales of lake trout appears to indicate periods of fast and slow growth. The wider spacing is found typically at the beginning of each new band of growth. The closely spaced circuli are laid down on the scale at the end of the growing season. Widely spaced circuli have been found in narrow annual growth zones (fig. 10, first year), and conversely, closely spaced circuli sometimes occur in wide annular growth zones. Both types probably are true records of growth. Fish may grow a small amount but grow rapidly during a short period of the year and not at all or very little the rest of the year, or they may grow at a slow rather uniform rate during a much longer period of the year.

CHARACTERISTICS OF THE ANNULUS

Because annular markings on lake trout scales are rather difficult to locate, a detailed description of the annuli and a statement of criteria for their recognition are apropos. The annulus is more distinct on the scales of some lake trout than others; it is also more easily seen on some parts of a scale than elsewhere. Its location is revealed by one or more of the following characteristic arrangements of the circuli.

The most common and most easily recognized arrangement of the circuli in the normal growth pattern consists of a gradual narrowing of the spacing outward from the focus to the annulus, then an abrupt change to wider spacing. This feature is well illustrated by the scales in figures 5 and 6 and to a varying degree by all other scales reproduced here.¹⁵ The closely spaced circuli give the appearance of incomplete bands on the scale which are usually, but not always, most conspicuous in the posterolateral fields. Figure 12 shows a scale on which all the circuli are widely spaced and the annular narrowing, though barely perceptible, offers a definite and reliable criterion. However, the annuli cannot be traced completely around the scales by this characteristic alone. Other criteria must be used in combination with it.

Traces of annuli also may be observed in the posterior field (shown at the bottom of all figures

of scales). Here, the annulus often is seen distinctly as a ridge on the scale or as a groove on the impression. The groove is well illustrated by the second and third annuli in figure 10, and the third and fourth annuli in figure 9. Another characteristic pattern in the posterior field results at points where circuli of the preceding growing season end and the first circulus of a new season crosses their paths at angles that bring the pattern to a crude V in which the angle of the V points toward the annulus. These V's are in evidence somewhere on nearly every scale, but on the scale shown in figure 7, it is doubtful whether the fourth annulus would have been located but for the V on the lefthand side, as the annulus is indistinct elsewhere around the scale. The V's are also clearly represented in figure 5 by the second and third annuli, and in figure 8 by the first, second, and third annuli.

Frequently, part of the posterior area of the scale is almost devoid of sculpturing. Only ragged bits of crooked, discontinuous circuli are scattered about, but even then, circuli extend farther out into this part of the scale at the annulus than between annuli, pointing it out like a crooked finger.

In the anterior and lateral fields, three characteristics of the pattern of circuli, usually occurring in combination, indicate the location of the annulus. First is the narrowing of the spacing between circuli at the end of a growing season, mentioned earlier and seen in most figures. Usually, in addition, there is a broken circulus here or there along the annulus with another circulus crossing the ends in a "cutting-over" pattern (as in the V formations of the posterior field). The longer circulus which does the cutting-over is the first circulus of the new growth. It is often continuous through the anterior field from the posterior field on one side to the posterior field on the other side of the scale, and may cross or extend partly across the posterior field itself, as shown by the first annulus in figure 12, and by all annuli in figure 11. The third characteristic pattern results from the appearance of one or two very fine, broken lines¹⁶ at the annulus. This feature is illustrated by the scale shown in figure 10. Note especially the second and third annuli.

The scales shown in figures 5 to 12, also 15A and 16A, are from fish representative of lake trout

¹⁵ All scales were studied at the same magnification (X83.5). Illustrations of the scales have been reduced X66.8. See p. 59 for significance of the check labeled "O."

¹⁶ These do not appear to be true circuli.



FIGURE 4.—A scale from a 4-year-old lake trout 15.3 inches long, marked in September 1945 and recovered May 7 or 9, 1949, showing the degree to which annuli mark the inner surface of the scales. The outer surface of another scale from the same fish is seen in figure 8. The photograph is a negative of an impression in plastic.

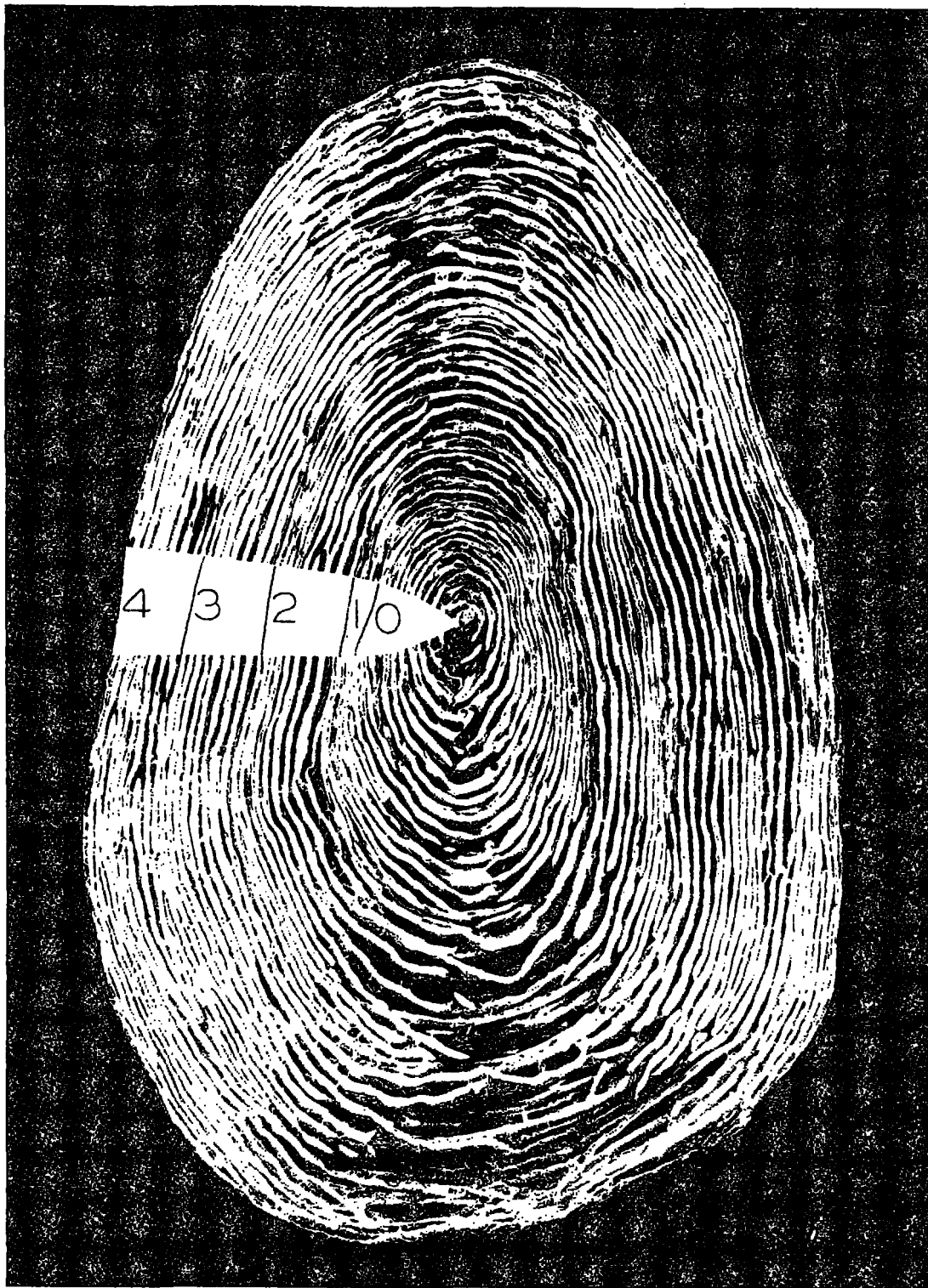


FIGURE 5.—Scale of a lake trout marked in September 1945 and recovered June 11, 1949. A negative photograph of an impression in plastic.



FIGURE 6.—Scale of a lake trout 14.8 inches long, marked in September 1945 and recovered July 8, 1949. The O-mark and first annulus appear to occur together. A narrow band of new growth is present.

presumably of known age. Scales of lake trout whose age, as read from the scales, did not agree with the supposed age of the fish are shown in figures 13 and 14, also 15B and 16B. All were read in accordance with the criteria described.

An annulus is usually located by a combination of the criteria, rather than by any one of them

alone. False annuli were the exception and did not extend completely around the scales. Interpretation of the structures near the center of the scale is the most difficult. A true estimate of first-year growth, even the age of a lake trout may depend on correct interpretation of the pattern there.



FIGURE 7.—Scale of a lake trout 17.7 inches long, marked in September 1946 and recovered August 28, 1950. A narrow band of new growth is present.



FIGURE 8.—Scale of a lake trout marked in September 1945 and recovered May 7 or 9, 1949. Note that focus of the scale is located posterior to the center. No new growth.



FIGURE 9.—Scale of a lake trout 13.5 inches long, marked in September 1945 and recovered August 13 or 16, 1949. Note that the band of new growth is wider than in figure 7 even though this fish was caught 2 weeks earlier.

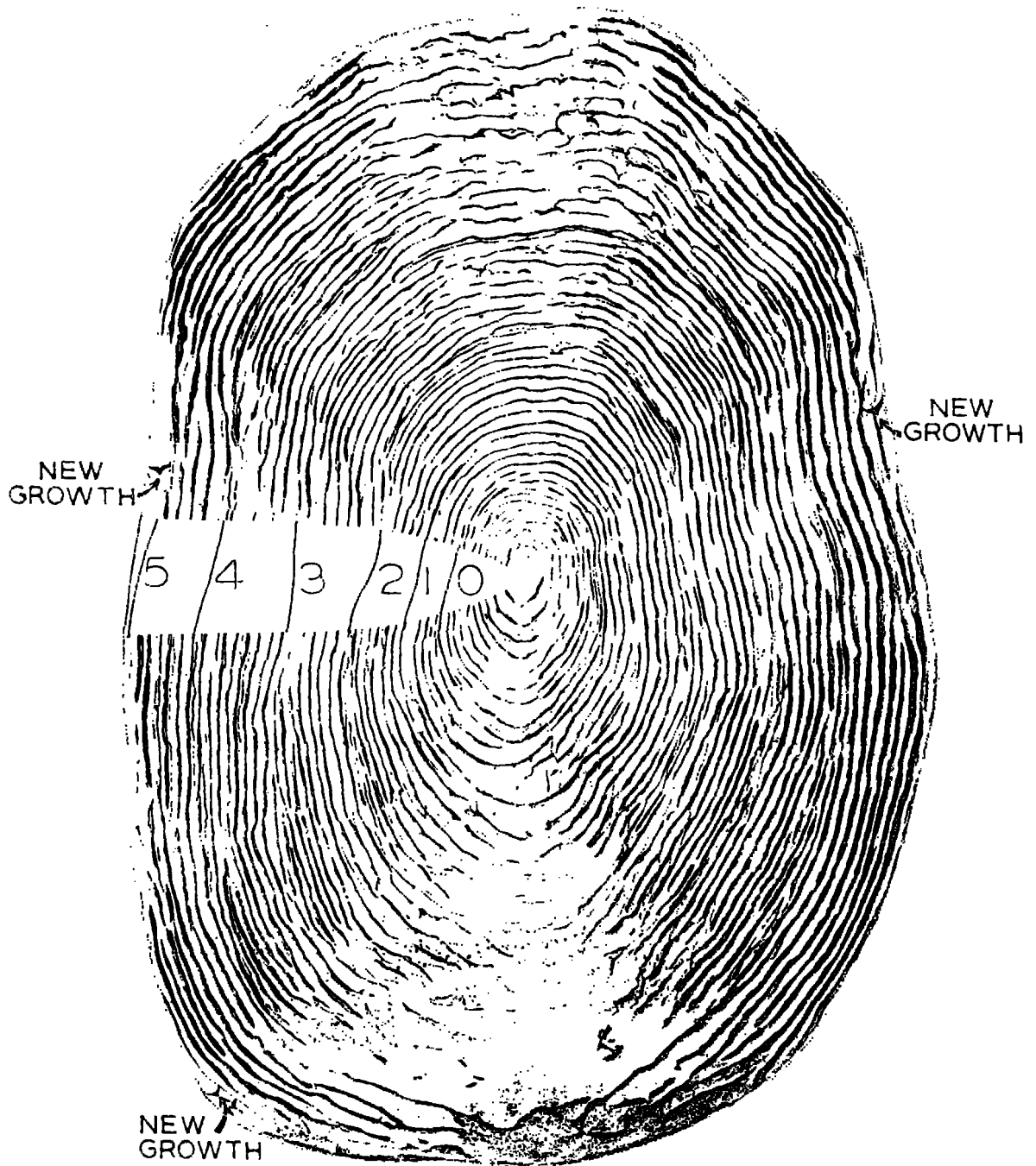


FIGURE 10.—Scale of a lake trout 15.9 inches long, marked in September 1945 and recovered April 17, 1950. The O-mark is more conspicuous than the first annulus on this scale. The band of new growth is narrow, but wider laterally than terminally.



FIGURE 11.—Scale of a lake trout 15.1 inches long, marked in September 1945 and recovered April 25, 1950. The focus of this scale is located anteriorly. The annuli are indistinct. Such a scale is difficult to read. The band of new growth is narrow.

TIME OF ANNULUS FORMATION

New growth on lake trout scales is first seen as a narrow, clear band outside a darker band of the closely spaced circuli of "winter growth." In the early part of the season, new growth is too narrow to be distinguished from spacing between winter circuli. For this reason, new growth was identified and measured only when it had attained a width greater than that of the spacing between preceding circuli and an outer circulus had formed

at least part way around the scale. Hence, in this study, the scales had grown an undetermined, though short, time before growth was recorded. One lake trout had some new growth on its scales January 19, but no others appeared with new growth until the latter part of March. Similarly, a single specimen without new growth was caught September 23, more than a month after new growth was started on the scales of all other fish in the sample. The two aberrant specimens are



FIGURE 12.—Scale of a lake trout 16.8 inches long, marked in September 1945 and recovered April 25, 1950. The O-mark is more conspicuous than the first annulus. The band of new growth is wider than is usually found on scales of the fish caught in April.

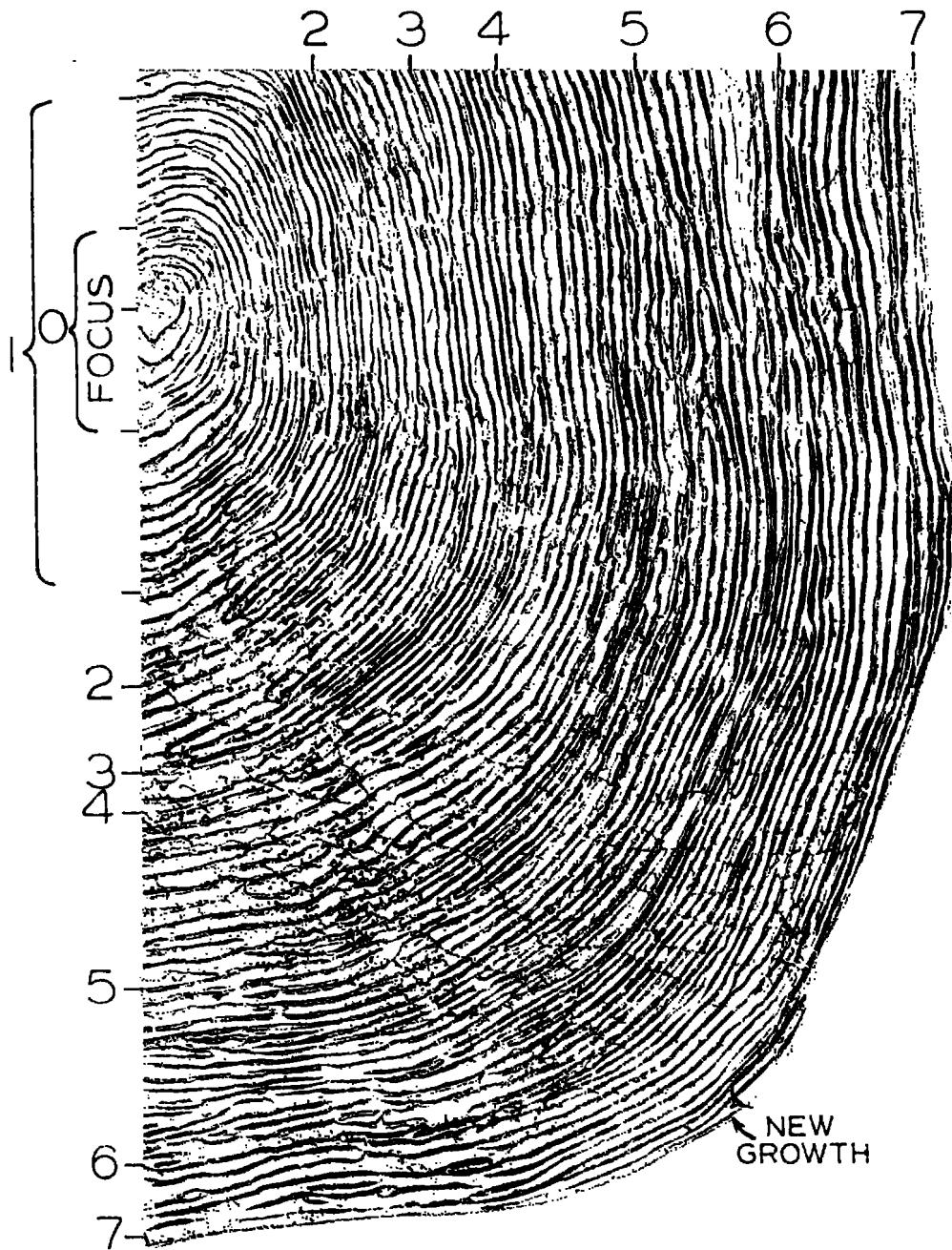


FIGURE 13.—Scale of a lake trout 26.2 inches long with left pectoral fin abnormal although the type of abnormality was not described. Caught June 13, 1947. If this lake trout had been marked by the removal of the left pectoral fin, it would have been 1 year old, but it is too large for that age, and 8 checks were on the scales. (See text for discussion of the central check). New growth was not uniform in width. On this section, new growth appears only in the lower right area. The deformed fin was an abnormality.



FIGURE 14.—Scale of a lake trout 31.8 inches long with left pectoral fin missing; no regeneration. Caught September 10, 1947. Lake trout with left pectoral fin removed were released in September 1946. If marked, this fish should have been 1 year old. Because of its large size, it probably was of more advanced age. Ten checks were read on the scale. (See p. 59 for a discussion of the central check). The band of new growth is wide. The missing fin was an abnormality.

listed in table 6 because a fin of each appeared to have been clipped and the annuli on the scales seemed well defined. However, the dates on which new growth on the scales was begun are sufficiently unusual to throw some doubt on the authenticity of the fin-clip and the accuracy of the age determination from the scales.

The percentage of lake trout with new growth on their scales increased slowly through April and May, but rose rapidly through June and July, passed the 50-percent level during the last week of June, and reached the 100-percent level the last half of August (table 6; fig. 17). Although the season's growth was detectable on the

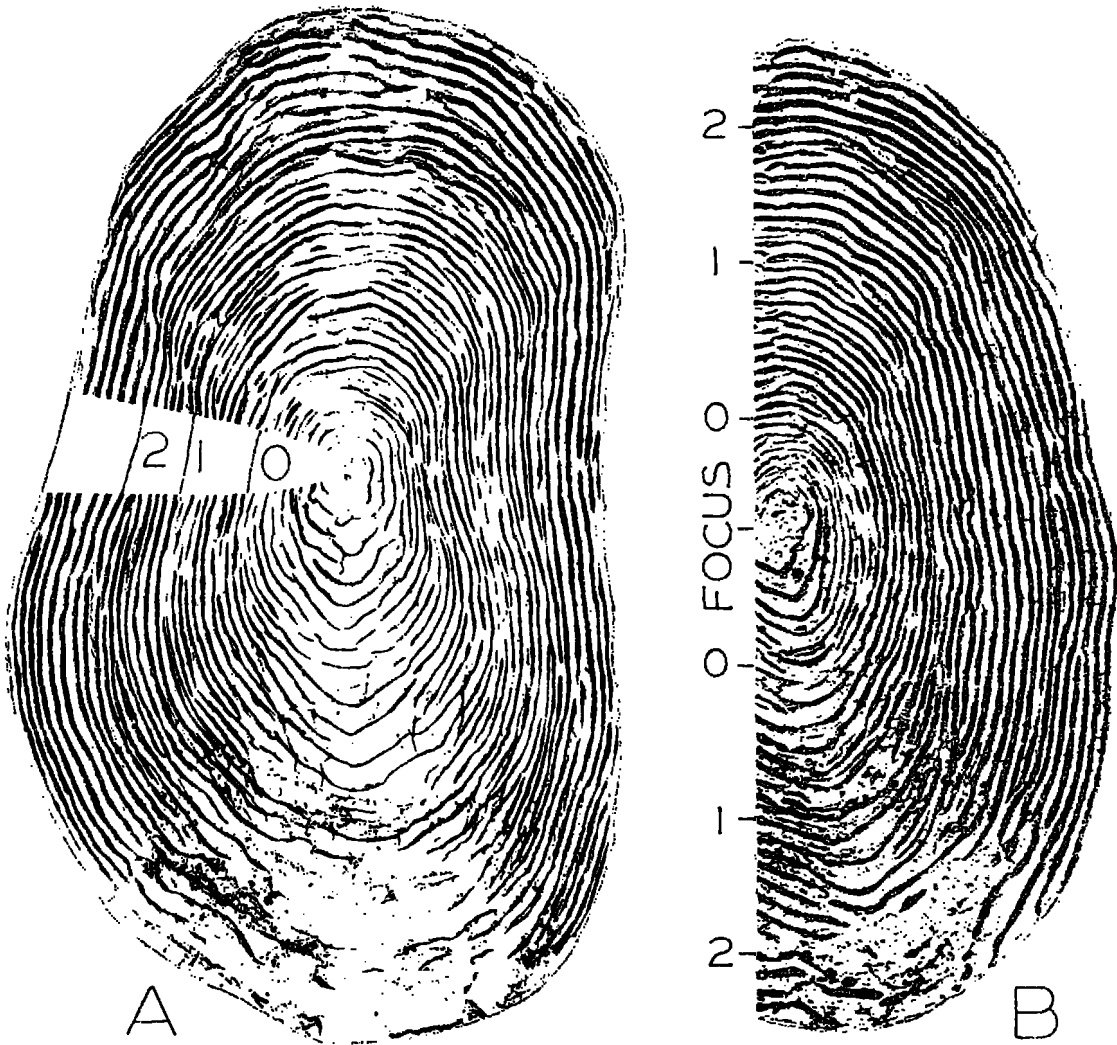


FIGURE 15.—(A) Scale of a lake trout 8.6 inches long, marked in September 1945 and recovered October 8, 1947. The band of new growth is wider than the entire growth zone of the previous year. (B) Scale of a lake trout 10.8 inches long with a right pectoral fin missing; no regeneration. Caught November 4, 1948. Only 3 checks were found on the scales. As lake trout with the right pectoral fin removed were released in September 1945, the scales should have had 4 checks, 3 annuli, and O-mark, if the fish were one of those marked. The missing fin was, therefore, abnormal.

scales of some lake trout by the latter part of March, it could not be seen on others until August. The period for the start of new growth, therefore, extends through 5 months. Possibly, the period would be shorter for groups of fish, all caught from a small, localized area. The present collection of marked lake trout came from contiguous but relatively extensive areas in the northeastern part of Lake Michigan. A diversity of environmental conditions in various localities, about which there is at present very little information, may cause growth on the scales of local groups of

lake trout to begin at different times so that when the groups are combined, as in the present study, the semblance of a long period for the beginning of growth would result.

Assuming normal distribution, the combined data fit, within the confidence limits at the 5-percent level of probability, a normal cumulative curve with the $\sigma=20$ days and the 50-percent level on June 18. The test used for goodness of fit was the Kolmogorov-Smirnov test described by Massey (1951). Whereas the 50-percent level of the theoretical normal population falls on

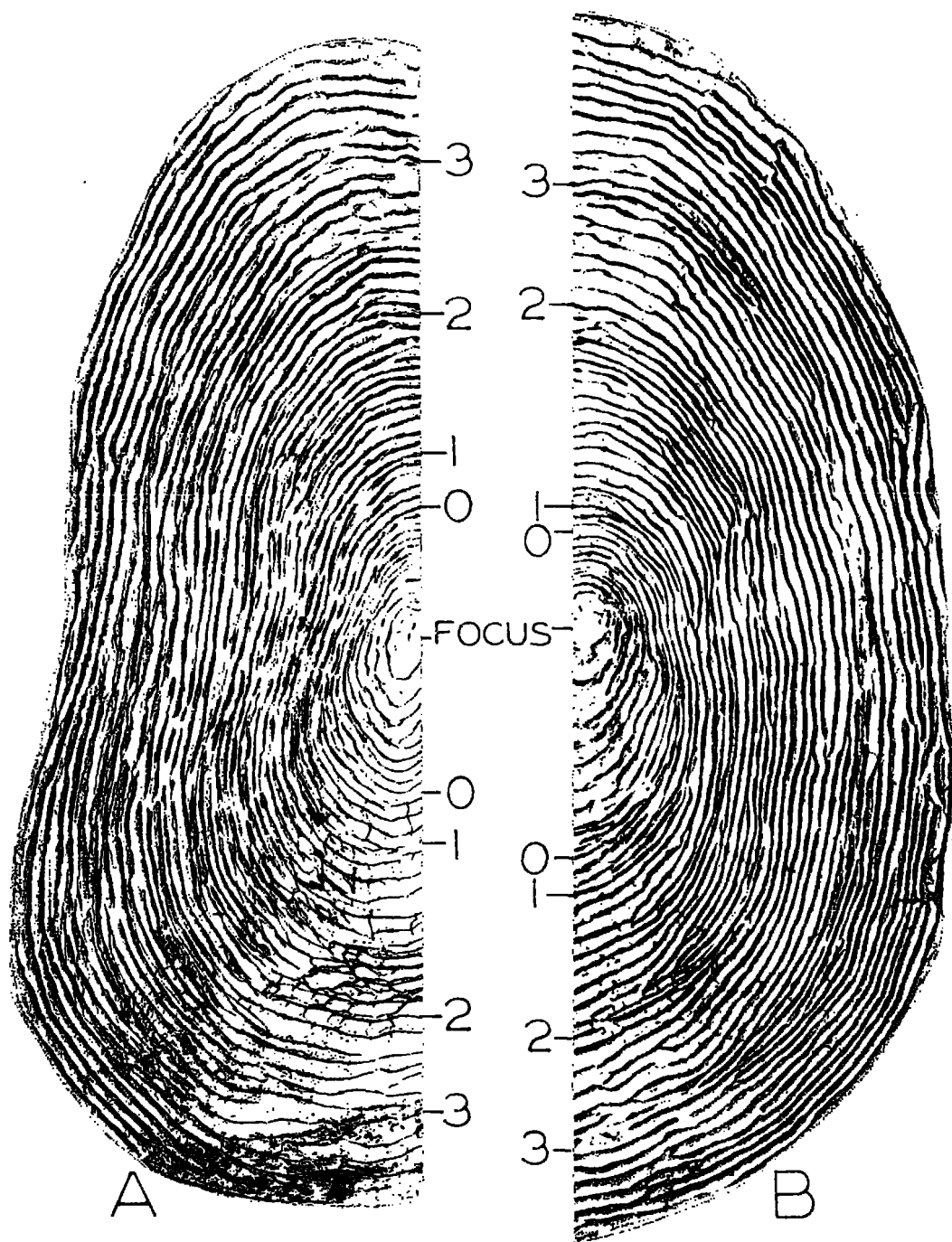


FIGURE 16.—(A) Scale of a lake trout 16.5 inches long, marked in September 1945 and recovered October 5, 1948. Note partial check between the second and third annuli. There was no evidence of a check on the righthand side of the scale. (B) Scale of a lake trout 13.5 inches long with left pectoral fin consisting of 9 twisted rays one-half normal length. Caught December 18, 1948. Four checks appear on the scales. As lake trout with left pectoral fin removed were released in September 1946, the scales should have had 3 checks, 2 annuli, and O-mark, if the fish were one of those marked. The fin was, therefore, deformed.

TABLE 6.—Progress of annulus formation on the marked lake trout

[Based on recoveries for the calendar years 1947-51 and age groups II-VI. No consistent differences could be detected among age groups in collections from different years]

Date	Number without new growth	Number with new growth	Percentage with new growth	Date	Number without new growth	Number with new growth	Percentage with new growth
Jan. 1-15.....	29	0	0.0	July 1-15.....	48	104	68.4
16-31.....	23	1	4.2	16-31.....	7	96	93.2
Feb. 1-15.....	8	0	0.0	Aug. 1-15.....	2	151	98.7
16-28.....	13	0	0.0	16-31.....	0	60	100.0
Mar. 1-15.....	1	0	0.0	Sept. 1-15.....	0	62	100.0
16-31.....	20	4	16.7	16-30.....	1	47	97.9
Apr. 1-15.....	25	3	10.7	Oct. 1-15.....	0	17	100.0
16-30.....	67	17	20.2	16-31.....	0	3	100.0
May 1-15.....	140	30	21.8	Nov. 1-15.....	0	3	100.0
16-31.....	55	24	30.4	16-30.....	0	9	100.0
June 1-15.....	71	31	30.4	Dec. 1-15.....	0	16	100.0
16-30.....	66	56	45.9	16-31.....	0	16	100.0

† See page 19 for comments on these specimens.

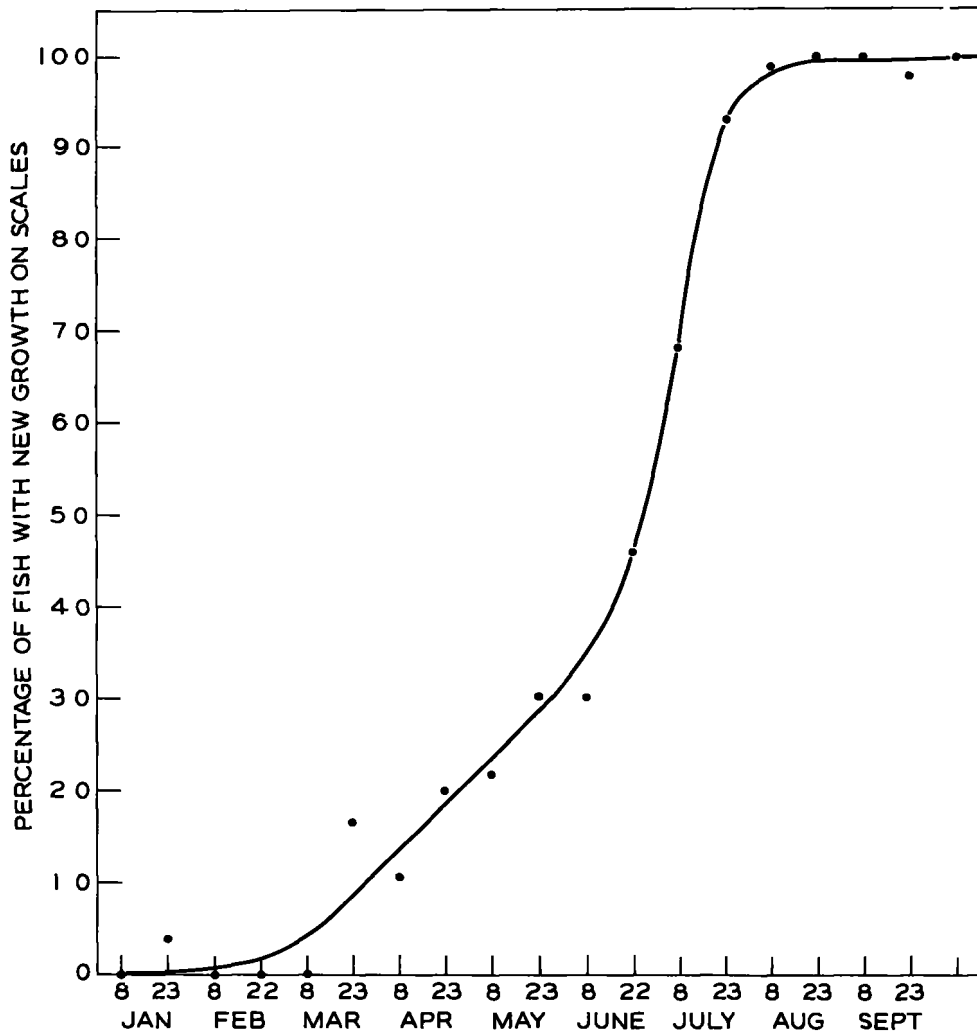


Figure 17.—Percentage of marked lake trout showing new growth on their scales. Empirical data indicated by dots; curve drawn by inspection.

June 18, the date on which 50 percent of the marked fish had started new growth on the scales was June 26. Within the 5-percent confidence limits for samples of the same size, new growth on the scales of lake trout in other years would be expected to reach the 50-percent level during the last 3 weeks of June. New growth may be identified, then, on the scales of individual lake trout in northern Lake Michigan any time between the middle of March and the middle of August, and about 50-percent of the lake trout will show new growth on their scales by the latter part of June.

Because of the long time interval in which new growth may begin, the numbers of lake trout with narrow spacing between the circuli at the margin of their scales diminish gradually from January through August and the numbers with wide spacing between these circuli increase correspondingly. In July and August some scales, that began growth early in the season, already had a wide band of new growth with narrowing spacing between the circuli near the edge of the scales. The age of unmarked fish would be difficult to interpret from such scales. Whether the band of growth had been formed during the current or the previous season would be a matter of the reader's judgment. On most scales from fish caught at this season, the growth of the current season was narrower than the growth of the previous year, but there were exceptions which gave difficulty.

The end of the growing season for the scales of lake trout could not be determined definitely from the scales themselves. As new growth on the scales of individual fish in the sample began at different times during the spring and summer, they may also have completed growth at different times. In summer and early fall, scales having wide bands of marginal growth with narrowing spacing between the outer circuli had the appearance of completed growth, but it is not known that additional circuli do not form later in the season. It remains uncertain, therefore, whether the scales of lake trout attain the full growth of a season shortly after the beginning of growth or continue to increase in size, however slowly, until time for the next annulus to form.

SUPERNUMERARY OR O-MARK

During the first examination of the scales, it was a surprise to discover that the number of annulus-

like markings observed was almost invariably greater, by one, than the number of years of age indicated by the clipped fin. Upon further investigation, the reason for the discrepancy was found in the interpretation of the mark nearest the focus. Comparisons of lengths at capture of lake trout of a known age group (age-groups II to V) with calculated lengths for the same year of life showed the outermost markings to be annuli. Although no lake trout of age-group I were captured, it is logically to be expected that on their scales, also, the outermost mark would be an annulus, hence that the central check is supernumerary. This check or mark appears to have been formed during the fall of the fish's first year when they were only slightly larger than at the time of planting.

The innermost marking on the scales, referred to hereafter as the O-mark, is interpreted to be a line of demarcation between an initial slow rate of growth and a later sudden increase in the rate as indicated by a change in spacing of the circuli at this point. The circuli within the central mark are more broken and more closely spaced than circuli laid down later (figs. 5 and 12). The mark is usually fainter than the annular rings on the scales and is not present on the scales of all specimens.¹⁷ Rarely, scales show the central marking so closely approximated to the first annulus (figs. 7 and 11) as to suggest that on other scales it might coincide with the annulus and thus be lacking altogether as on the scale in figure 6; a few have it very close to the focus, but for most specimens the inner mark is a little over halfway from the focus to the first annulus. Although this mark is typically indistinct (figs. 5 and 9), it sometimes is the most conspicuous mark on the scales (figs. 10 and 12). Such outstanding marks might easily be taken to be first annuli on fish of unknown age unless the reader were expecting to find, and looking for, a mark within the true first annulus.

The O-mark can only be surmised, at this time, to record some drastic change in the young fish's environment or habits of life. A possible explanation is that the check results from handling (anaesthetization, removal of fin, transportation) at the time of planting and the change from hatchery to lake environment. In support of this view is

¹⁷ A separate inner marking was not found on the scales of 4 (0.3 percent) of the marked specimens and it is believed the inner mark on these scales coincided with the first annulus.

the fairly close agreement between the average calculated length of 3.7 inches (range 1.5–5.9) at time of formation of the O-mark (computed from scale measurements of recovered marked fish) and the average measured length (3.2 inches; range 2.1–4.3) of samples of fingerlings at time of release into the lake.

On the other hand, the examination of scales of lake trout that almost surely were not marked fish (lake trout from northern Lake Michigan that were unreasonably large for the ages indicated by their deformed fins and fish from area 8 that included few, if any, marked fish) suggested strongly that naturally hatched lake trout in Lake Michigan also form a O-mark. Such a mark could arise, for example, from a change in environmental conditions, a change of diet, or a shift by the fish to different grounds upon attainment of a particular length (about 3.7 inches in the northern part of the lake).

The scales of lake trout for which there was disagreement between the age, as indicated by scales and fin, consistently exhibited a first check that resembled in every way the O-mark on the scales of marked specimens. The scales in figures 13 and 14 were from fish turned in as recoveries of marked lake trout but they were unquestionably from fishes of natural origin. Fish marked in 1946, averaging 3.2 inches long, could not have attained lengths of 26.2 and 31.8 inches before they were caught in 1947. Actually, the scales showed 8 and 10 checks, respectively. The central checks resemble closely the O-marks of the scales from bona fide recoveries. This is brought out forcefully by figures 15 and 16 in which the lefthand scales are presumably from bona fide recoveries (age read from the scales and age indicated by the deformed fin in agreement); and the righthand scales are probably from natur-

ally propagated fish (ages from scales in disagreement with age indicated by fin). It is readily apparent that the structure and size of the central areas of these scales are similar.

That the central check on the scales of wild-stock lake trout was in fact a O-mark and not the first annulus was strongly supported by the good agreement between the average calculated lengths of the naturally propagated fish and the marked, hatchery-reared fish at each of the first three checks on the scales. A few lake trout captured by large-mesh nets in northern Lake Michigan during 1947 could be identified, without question, as wild stock because they were too large to have belonged to any group of marked fish. The calculated lengths of these fish at all three first checks were greater than for the marked lake trout caught in all nets over a period of years, 1947–51 (columns 2 and 4, table 7). The differences were no larger, however, than would be expected from the small number of fish in the sample and from the powerful selective influences that bore on the older age groups of the more recent year classes in the collections. The calculated lengths of the wild stock caught in nets of all mesh sizes¹⁸ differed little from the marked fish caught in similar nets (columns 2 and 6, table 7). Calculated lengths of wild-stock lake trout caught by all nets in the southern part of the lake were 0.8–1.0 inch shorter at each of the first 3 checks than those of wild stock caught in more northern waters (columns 6, 8, table 7). This large difference between calculated lengths of lake trout from the 2 sections of the lake is indicative of the racial separation of the 2 populations.

¹⁸ This group of lake trout includes, in addition to those positively identified as wild stock, other lake trout for which the age read from the scales differed from that indicated by the deformed fin. Evidence is presented later to show that most, if not all, of these fish were also wild stock.

TABLE 7.—Calculated total lengths (inches) and increments of growth in length of marked lake trout recaptured in northern Lake Michigan and of naturally propagated fish from northern and southern Lake Michigan year classes combined

Check or annulus	Marked lake trout, ¹ Northern areas 1-6, from all nets		Unmarked lake trout					
			Northern-areas 1-6				Southern-area 8	
	Length	Increment	From large-mesh nets		From all nets		From all nets	
			Length	Increment	Length	Increment	Length	Increment
0.....	3.7	4.0	3.5	2.7
1.....	5.9	2.2	6.9	2.9	5.6	2.1	4.8	2.1
2.....	8.7	2.8	10.0	3.1	8.3	2.7	7.3	2.5
Number of fish.....	1,319		216		99		102	
Age groups in sample.....	II-VI		III-IX		II-IX		II-VIII	

¹ The marked lake trout averaged 3.2 inches long at time of planting.

² This total includes 9 fish obviously too large for their supposed age (see p. 30) and also 7 that could not be assigned to a particular planting (more than one fin deformed or the deformed fin not one used as a mark), but which were too large to have been from any of the three plantings. All fish were caught in 1947.

Discrepancies between increments of growth were also small. At the second check the difference was 0.1 inch between marked and unmarked fish from all nets in areas 1-6, but was nil between unmarked or wild stocks from the northern and southern parts of the lake. At the third check the increment of growth of the unmarked fish in areas 1-6 was 0.1 inch smaller than that of the marked fish from the same areas and 0.2 inch larger than that of the unmarked fish in area 8.

With regard to the central check on the scales of the naturally reared lake trout, two assumptions are possible. First, that these fish did in fact form a O-mark during their first growing season; under this assumption these data exhibit no particular conflict with those for planted lake trout. Second, it may be assumed that naturally reared lake trout do not complete a O-mark, and hence that the calculated lengths for the first three checks on the scales describe the fish at completion of their first, second, and third growing seasons.

A corollary to this thesis, namely, that the average length of the unmarked, wild fish from all nets in areas 1-6, at the end of their first year (3.5 inches), was about the same as that of the marked, hatchery fish at formation of the O-mark (3.7 inches), might be accepted without misgivings as the hatchery and naturally propagated lake trout spent much of their first year in different environments. If this corollary is accepted, however, it follows that the increment of growth in length of the wild stock in northern Lake Michigan during their second growing season would be only 2.1 inches which is considerably less than the growth indicated for this group during either the first or third (2.7 inches) years. A growth of 2.1 inches the second year would be 0.7 inch less than the growth made in the same environment by the hatchery fish in their second year and 0.6 inch less than the growth made by the marked hatchery fish between their introduction into the lake in September at a length of 3.2 inches and formation of the first annulus when they were 5.9 inches long.

The growth made by the wild stock between formation of the first two checks on their scales, nevertheless, was very nearly the same as that made by the marked fish between formation of the O-mark and the first annulus. It would be expected that the wild stock would grow at about the same rate as the introduced fish after Sep-

tember, but if they did, and the first check on the scales were the first annulus, they could not have grown any the fore part of the season. The length of the wild stock at the end of the second year would be 5.6 inches or 0.3 inch shorter than the marked stock at the end of their first year and 3.1 inches shorter than the marked fish at the end of their second year. To justify this relationship, it is necessary to assume that the wild stock grew erratically during their first or second year. The rates of growth in later years were about the same for the marked and unmarked lake trout. Although it cannot be stated categorically that the central check on the scales of the unmarked fish was not the first annulus, neither does it seem reasonable to assume that it is. The evidence strongly favors the belief that the first check on the scales of the naturally propagated lake trout is a O-mark formed during the first growing season. This view is supported further by the appearance of the check itself (pattern, and location on the scales). See figures 15 and 16.

The contribution of data on lake trout from southern Lake Michigan to the problem of the O-mark is greatly limited by the lack of recoveries of planted fish from this area for comparison with the wild stock. Nevertheless, the much smaller increment of growth before formation of the first check on the scales of lake trout in southern than in northern waters makes it difficult to assume that the O-mark of these naturally propagated fish is a first annulus. If this assumption is made, it is necessary to believe that these fish were only 4.8 inches long at the end of two full growing seasons or 1.1 inches shorter than the marked fish from northern Lake Michigan at the end of one year (5.9 inches). Alternatively, if it is assumed that the first check is a O-mark, the calculated length at that point is somewhat smaller than that for the northern fish at formation of this check. Subsequent growth is only slightly less for the southern than the northern fish. This growth pattern follows closely that of the marked fish.

If the hypothesis, that most or all naturally reared lake trout do form a O-mark on their scales during their first growing season, is accepted, the question then arises as to the extent of error that this structure might introduce into the work of a competent and careful scale reader who is not aware of its existence. The only objective information on this point comes from

records of calculated lengths for 97 lake trout captured in large-mesh gill nets off Montague, Mich., October 1, 1947 (Van Oosten 1950). The scales of these fish were read by Dr. Frank W. Jobes who did not record having observed the O-mark. The calculated lengths from 82 of the fish in the year classes 1939-43 yielded an average length of 5.1 inches at the end of the first year of life. This average is between (1.5 inches higher and 1.0 inch lower than) the averages 3.6 and 6.1 inches obtained in the present study for the lengths at formation of the O-mark and the first annulus, respectively, from 17 lake trout of the same year classes from southern Lake Michigan (off South Haven in area 8) caught in the same year and in nets of the same mesh size (table 23). These differences suggest that on some scales Dr. Jobes may have measured the first annulus to the O-mark rather than to the first annulus. However, the calculated lengths¹⁹ for the later years of life of the lake trout from Montague and South Haven were close enough to indicate good agreement on the assessment of age.

From these data, it appears that without a knowledge of the O-mark, errors in measuring to the first annulus of lake trout scales, due to misinterpretation of the central check, might be numerous enough to bias seriously an estimate of the first-year growth of Lake Michigan lake trout, but errors of age determination would be few.

AGREEMENT BETWEEN FIRST AND SECOND READINGS

The two readings of lake trout scales, mentioned previously, were made on the scales of all fish in the collection. No samples were discarded, however difficult to read. The second series of readings was begun several months after the first was completed and, for each fish, a second scale was read and measured, after comparison with the other mounted scales in the sample. The two readings agreed on age for 96.8 percent of the fish. Errors of interpretation, not involving change in age, reduced agreement to 91.4 percent of the specimens. Because of experience gained during the first reading, and standardization of procedures, the second reading disclosed errors in the earlier work as shown in table 8. Many of the disagreements resulted from the omission of a

measurement of the central or O-mark, and the mistaken location of annuli. However, there were also disagreements on the number of annuli. The number of annuli located during the second reading varied from that recorded during the first reading for 45 (3.2 percent) of the fish as follows: 1 annulus more for 18 fish, 1 annulus less for 24 fish, 2 less for 2 fish, and 3 less for 1 fish. The differences in percentage of such disagreements among the data for the three plantings were not large. Disagreements in measurement, not resulting in change of age, occurred for scales of 76 (5.4 percent) of the fish.

TABLE 8.—Comparison of first and second readings by the same person, of scales from the "marked" lake trout

Item	Year of planting			Totals
	1944	1945	1946	
Number of fish.....	57	1,077	271	1,405
Differences from first to second reading				
Resulting in change of age:				
One annulus added.....		14	4	18
One annulus subtracted.....	2	13	9	24
Two annuli subtracted.....		2		2
Three annuli subtracted.....	1			1
Total.....	3	29	13	45
Percentage.....	5.3	2.7	4.8	3.2
Not resulting in change of age:				
Assumption of marginal growth in error.....		4	4	8
Current season's marginal growth not seen.....	1	10	1	12
Age same but one or more annuli mismeasured.....	2	45	9	56
Total.....	3	59	14	76
Percentage.....	5.3	5.5	5.2	5.4
Total changes.....	6	88	27	121
Percentage.....	10.5	8.2	10.0	8.6

Disagreements in readings due to omission of the central check at the first reading were recorded, but were not considered to be errors in reading because the importance of measuring the O-mark was not fully understood at the beginning of the first reading. Measurements of the central mark had been taken commonly, however, when location of the first annulus was made easier by definitely locating the central check.

The scales of some lake trout present such problems of interpretation that readings made at different times are likely to disagree. Much of this uncertainty is dispelled by long familiarity with scales from fish of known age. Most readers discard the more difficult scales (usually about 5 percent of the total) as unreadable. If this practice had been followed in the present study, some of

¹⁹ Sums of the increments of growth. Those for the lake trout from Montague, Mich., were obtained from the published data.

the disagreements between readings might have been eliminated.

AGREEMENT BETWEEN AGES READ FROM SCALES AND AGES FIXED BY DEFORMED FINS

The final readings of the lake trout scales agreed with the supposed ages of the fish for 1,319 of the 1,405 or 93.9 percent of the specimens from northern Lake Michigan. The presumed age is determined as the time between the date of capture and the year the fish would have been hatched if the damaged fin were a true mark of identification.

Detailed information is given in table 9 for the 86 lake trout for which the supposed ages and the ages as read from the scales were in disagreement. Of this number, 9 fish (indicated by asterisks in the table) were so large in relation to their supposed age that it may be assumed with confidence that they were unmarked fish with malformed fins. No dependable objective standard was found from which to judge whether or not the remaining 77 lake trout were bona fide recoveries of marked lake trout. They must accordingly be classed collectively as of "uncertain status." Data presented in a later section, however, give evidence that a large percentage of these fish had not been marked.

A summary of the discrepancies in age with respect to the degree of divergence (including the 9 fish designated in table 9 as too large for their supposed age) is given in table 10. Disagreements on age were mostly of 1 year (68.6 percent); but were of 2 years for 18.6 percent and more than 2 years for 12.8 percent.

TABLE 9.—Information on 86 lake trout from northern Lake Michigan for which age indicated by the mark did not agree with age read from the scales

[Asterisks designate fish that obviously were too large in relation to their supposed ages to have been bona fide recoveries of marked fish]

Total length (inches)	Supposed age	Age read from scales	Year marked	Condition of fin
31.8*	1	9	1946	No regeneration, or fin missing.
12.3*	1	3	1946	3/3 normal length.
21.2*	2	4	1945	No information.
20.0*	2	5	1945	Do.
14.8*	2	3	1945	1/2 normal length, rays twisted.
13.3*	2	3	1945	Short stub, 2 twisted rays.
12.7.	2	5	1945	1/2 normal length.
20.0*	2	6	1946	No information.
19.0*	2	7	1946	Small stub.
16.5*	2	6	1946	No information.
12.0.	2	3	1946	Do.
22.0.	3	5	1944	Do.
21.5.	3	4	1944	Do.
20.0.	3	7	1944	Adipose missing, dorsal normal.
20.0.	3	6	1944	Do.
17.5.	3	5	1944	Do.
14.1.	3	5	1944	Do.

TABLE 9.—Information on 86 lake trout from northern Lake Michigan for which age indicated by the mark did not agree with age read from the scales—Continued

Total length (inches)	Supposed age	Age read from scales	Year marked	Condition of fin
17.5.	3	4	1945	No regeneration, or fin missing.
15.4.	3	5	1945	Do.
14.8.	3	4	1945	Do.
13.3.	3	4	1945	Do.
11.7.	3	4	1945	Do.
11.5.	3	4	1945	Do.
11.2.	3	4	1945	Do.
10.8.	3	2	1945	Do.
10.0.	3	4	1945	Little regeneration.
9.5.	3	2	1945	No information. Fin scar not seen in Ann Arbor.
22.0.	3	5	1946	No regeneration, or fin missing.
16.8.	3	4	1946	Do.
15.9.	3	5	1946	1/2 normal length, 8 rays.
12.7.	3	4	1946	1/4 normal length, 1 curved ray.
12.7.	3	4	1946	1/2 normal length, 10 twisted rays.
12.1.	3	4	1946	1/2 normal length, rays twisted.
12.1.	3	4	1946	1/2 normal length, 4 twisted rays.
11.9.	3	4	1946	1/2 normal length, 4 twisted rays.
11.6.	3	5	1946	1/2 normal length, 12 twisted rays.
11.3.	3	2	1946	No regeneration, or fin missing.
11.0.	3	4	1946	3/8 inch long, 1 twisted ray.
14.1.	4	3	1944	Adipose missing, 4 rays in dorsal.
21.8.	4	5	1945	3/4 normal length, some rays fused and curved.
20.5.	4	7	1945	3/4 normal length, 6 twisted rays.
20.0.	4	5	1945	8 rays.
19.3.	4	6	1945	No regeneration, or fin missing.
18.2.	4	6	1945	1/2 normal length, 4 rays.
18.0.	4	7	1945	3/4 normal length, 8 rays.
16.1.	4	3	1945	No regeneration, or fin missing.
16.0.	4	5	1945	Do.
15.6.	4	5	1945	Do.
14.7.	4	5	1945	Almost normal length, 7 rays.
13.9.	4	5	1945	2/3 normal length, 9 twisted rays.
12.5.	4	5	1945	1/2 normal length, rays twisted.
12.1.	4	3	1945	No regeneration, or fin missing.
11.7.	4	3	1945	1/2 inch long, 7 rays.
9.7.	4	2	1945	1/2 inch long, 1 curved ray.
18.0.	4	5	1946	No regeneration, or fin missing.
14.9.	4	5	1946	2/3 normal length, 8 rays.
14.3.	4	5	1946	1/2 normal length, 6 rays.
13.4.	4	5	1946	No regeneration, or fin missing.
13.1.	4	5	1946	Do.
12.0.	4	5	1946	3/8 inch long, 2 twisted rays.
17.3.	5	6	1944	Adipose missing, dorsal normal length but with all rays crooked 3/8 distance from back.
14.4.	5	4	1944	Adipose torn, dorsal normal.
13.7.	5	4	1944	Do.
13.0.	5	4	1944	Do.
12.8.	5	3	1944	Adipose missing, dorsal normal.
11.8.	5	4	1944	Adipose: small, dorsal normal.
11.8.	5	4	1944	Adipose missing, dorsal normal.
20.0.	5	6	1945	1/2 inch long, 2 twisted rays.
19.4.	5	6	1945	1/2 normal length, 5 rays.
19.0.	5	6	1945	No regeneration, or fin missing.
18.8.	5	6	1945	Do.
18.7.	5	6	1945	Do.
18.6.	5	6	1945	Do.
18.0.	5	6	1945	1/2 inch long, 2 twisted rays.
17.0.	5	6	1945	1/2 normal length, 5 rays.
17.0.	5	4	1945	No regeneration, or fin missing
15.3.	5	6	1945	3/4 normal length, 2 rays.
14.0.	5	4	1945	3/4 normal length, rays broken.
13.8.	5	3	1945	Normal length.
12.4.	5	2	1945	2/8 normal length, 4 curved rays.
12.2.	5	4	1945	3/4 normal length, 8 normal rays, 6 twisted rays.
11.3.	5	4	1945	3/4 normal length, 14 twisted rays.
11.2.	5	4	1945	3/4 normal length, 9 rays.
10.8.	5	3	1945	1/2 normal length, 3 twisted rays.
13.4.	6	6	1946	2/3 normal length, 10 rays.
13.0.	6	4	1945	3/4 normal length, 9 twisted rays.

TABLE 10.—Summary of the extent of disagreements on lake trout showing discrepancies between supposed ages and those read from the scales

Age discrepancy	Areas 1-6	
	Number of fish	Percentage
1 year	59	68.6
2 years	16	18.6
>2 years	11	12.8

FACTORS OF DISAGREEMENT

Disagreements between ages as read from scales and supposed ages can arise from misinterpretation of the scales from bona fide recoveries, and also from the inclusion in the sample of lake trout that had not been marked. Both types of errors may be represented in the disagreements discussed in the preceding section. Although the relative importance of these factors cannot be estimated closely, the data do provide some instructive information in the matter.

Errors of Reading

Errors of reading may originate in the interpretation of scale patterns which, properly diagnosed, could lead to a correct determination of the age of the fish. Errors may arise also from defective scales, that is, scales that failed to form certain annuli, developed accessory checks indistinguishable from annuli, or had a pattern so diffuse that any reading is questionable. As was pointed out earlier, the present collection certainly contained some lake trout that were not recoveries from plantings of fin-clipped fish. It is impossible, therefore, to attribute any individual disagreement strictly to error on the part of the scale reader.

It is possible, however, to gain a general idea of the clarity and dependability of scale patterns from the examination of a large series of scales, a high percentage of which must be from bona fide recoveries of planted fish, even though the status of an individual specimen must be recognized as uncertain. Careful study of the hundreds of scales from which readings agreed with supposed age led to the conclusion that over the age-span represented, the markings were almost always clear, and that failure to form an annulus must be rare. Some annuli were extremely faint, especially in the posterior field but faint year-marks usually could be detected in the lateral fields. The presence of an occasional indistinct annulus does, nevertheless, indicate the possibility of others so weak as to be overlooked.

Accessory checks between annuli, other than the O-mark discussed in the preceding section, were not common and when present caused little trouble because they rarely, if ever, extended completely around the scale.

Another factor which may have been a source of some error is the interpretation of marginal growth. During the period of annulus formation

it is occasionally difficult to decide whether the marginal band represents completed growth of the previous year or rapid growth of the current season.

Inclusion of Unmarked Fish With Abnormal Fins

Overwhelming evidence was presented earlier that the "recoveries" from southern Lake Michigan (area 8) included few, if any, marked lake trout. Since there is no reason to believe that the development of abnormal fins among naturally propagated fish is exclusively a property of the stock of lake trout in southern Lake Michigan, it was to be anticipated that the recoveries from northern Lake Michigan, though principally marked fish of hatchery origin, would also include some naturally hatched lake trout (and possibly some unmarked hatchery-reared lake trout that developed abnormal fins).²⁰

Relation of disagreements to appearance of the fin

If data on the "extent of regeneration" of the fins of lake trout from area 8 (tables 3 and 4) are typical for abnormal fins on wild fish, then, in samples from northern Lake Michigan (areas 1-6), the great majority of fish with fewer than 5 rays regenerated or with fins less than $\frac{1}{2}$ normal length would be bona fide recoveries of marked specimens, whereas most unmarked fish with abnormal fins would appear in the group showing greater regeneration. If these conclusions are valid and if the collection of lake trout from northern Lake Michigan contains appreciable numbers of wild fish, a correlation should be found between the extent of regeneration and the percentage of disagreement between supposed ages and ages read from scales.

This expectation is met by the data of table 11, for the lowest percentage disagreement (3.8 percent) occurred among fish with fewer than 5 fin rays regenerated less than half normal length. For the other three groups in the main body of the table the percentages ranged from 6.3 (trout with fewer than 5 fin rays regenerated but half normal length or longer) to 10.7 (fish with fins less than half normal length but having 5 or more fin rays regenerated). The value of 6.9 percent

²⁰ Although the percentage of wild-stock lake trout with abnormal fins is small, the total number reported by fishermen can be considerable when all catches are being scrutinized for deformed fins. The percentage of hatchery fish with abnormal fins is also low. Dr. Paul Eshumeyer, who has been in charge of fin-clipping operations at the United States Fish and Wildlife Service Fish Hatchery near Charlevoix, Mich., several seasons, states that an occasional fingerling lake trout reared in the hatchery has an accessory fin but very few fingerlings have deformed fins.

for trout with more than 5 fin rays at least half normal length offers a slight inconsistency, since, on the basis of the assumptions made, this percentage should have been the largest.

TABLE 11.—*Relation of extent of the regeneration of pectoral fins, expressed in terms of number of regenerated rays and length (fraction of normal) to percentage disagreement between ages as determined from scales and as indicated by deformed fins*

Length of fin	Item	Numbers of regenerated rays		Totals ¹
		Fewer than 5	5 or more	
Less than half normal.	Number of fish.....	953	28	981
	Number of disagreements.....	36	3	39
	Percentage disagreement.....	3.8	10.7	4.0
Half normal or longer.	Number of fish.....	79	233	312
	Number of disagreements.....	5	16	21
	Percentage disagreement.....	6.3	6.9	6.7
All lengths.....	Number of fish.....	1,032	261	1,293
	Number of disagreements.....	41	19	60
	Percentage disagreement.....	4.0	7.3	4.6

¹ Information not available on both the number of rays regenerated and the length of regeneration for 55 specimens.

Despite the one inconsistency, the data of table 11 provide evidence that the collections from northern Lake Michigan did contain enough unmarked fish to affect appreciably the percentage of disagreements between supposed ages and ages as read.

Relation of disagreements to year and locality of capture

Evidence from the capture of marked fish has been presented by Smith and Van Oosten (1940), and Eschmeyer and others (1953), that lake trout tend to remain local in habit but that their movements lead to a gradual scattering from a point of release. If this concept of the behavior of the young fish is accepted as established, and if it is assumed that marked lake trout entered the fishery gradually over a period of years and then disappeared from the fishery gradually, and assumed further that fishermen of northern Lake Michigan in their search for marked fish, found and turned in most or all of the wild-stock lake trout with natural abnormalities of the fins involved in the marking experiments, it is possible to set up, a priori, an expected relation for disagreements between supposed ages and ages read from the scales. It should be expected first that the percentage disagreement would be high when the marked fish of a particular planting were just entering the fishery, for they would be taken only in small numbers and thus would make up a small

percentage of the combined total of marked and unmarked fish with abnormal fins. The percentage disagreement should decrease as marked fish become more abundant and hence dominate strongly this same combined total, but should increase again as the marked fish disappear from the grounds. It should be anticipated further that within a single year the percentage disagreement would be least among lake trout taken in areas in which marked fish are plentiful and greatest where marked fish are scarce. These expectations are fulfilled rather well by the records of the 1945 year class, the planting from which the greatest number of "marked" fish was recovered (table 12).

TABLE 12.—*Annual distribution of the "marked" lake trout of the 1945 year class, and the relation of the locality of capture to the percentage disagreements between supposed age and the age read from the scales*

Year of capture and distance from point of release (miles)	Number of recaptures ¹	Percentage of total recaptures	Number of disagreements ²	Percentage disagreements
1947:				
<20.....	19	52.8	0	0.0
20-40.....	5	13.9	0	0.0
40-60.....	9	25.0	2	22.2
>60.....	3	8.3	3	100.0
Total or average.....	36		5	13.9
1948:				
<20.....	123	61.8	3	2.4
20-40.....	61	30.7	6	9.8
40-60.....	15	7.5	1	6.7
>60.....	0			
Total or average.....	199		10	5.0
1949:				
<20.....	91	17.2	3	3.3
20-40.....	251	47.5	2	0.8
40-60.....	156	29.6	3	1.9
>60.....	30	5.7	4	13.3
Total or average.....	528		12	2.3
1950:				
<20.....	59	23.4	2	3.4
20-40.....	48	19.0	4	8.3
40-60.....	138	54.8	8	5.8
>60.....	7	2.8	3	42.8
Total or average.....	252		17	6.7
1951:				
<20.....	0	0.0	0	0.0
20-40.....	5	18.5	0	0.0
40-60.....	9	33.3	1	11.1
>60.....	13	48.2	8	61.5
Total or average.....	27		9	33.3

¹ Some lake trout were omitted from this table because the description of the locality of capture was indefinite.

² All disagreements were on lake trout captured along the north and east shores of Lake Michigan, areas 2, 3, 5, and 6. There were no disagreements on those captured in areas 1 and 4.

The sequence of changes through the years followed the expected pattern. The percentage disagreement (between supposed age and age read from scales) was relatively high (13.9 percent) in 1947 when only 36 recoveries were made. As the number of recoveries rose to a maximum of 528 in 1949, the percentage disagreement declined to

a minimum of 2.3. Decreases in the number of recoveries to 252 fish in 1950 and a mere 27 in 1951 were accompanied by increases in percentage disagreement to 6.7 and 33.3 percent, respectively. The order with respect to the size of the annual total number of lake trout recaptured was practically the reverse of the order of the percentage disagreements. The one exception was between ranks 2 and 3 where the differences in percentage disagreement were small but sufficient to reverse the order of the ranking as shown:

Year	Number of fish	Rank	Percentage disagreements	Rank
1949.....	528	1	2.3	5
1950.....	252	2	6.7	3
1948.....	199	3	5.0	4
1947.....	36	4	13.9	2
1951.....	27	5	33.3	1

Still another significant feature of the annual totals is the limited range in the number of disagreements (from 5 in 1947 to 17 in 1950). The indicated variability is much below that of total recaptures for corresponding years. For example, from 1947 to 1949 the catch of fish with deformed fins increased 14.7 times but the number of disagreements increased only 2.4 times. Thus it appears that the number of disagreements tended to fluctuate about a fairly stable level and to be relatively independent of the number of recaptures of marked fish. This relation is precisely the one which should obtain if a high percentage of the disagreements were caused by the presence of unmarked fish.

The data on the relation between locality of capture and percentage agreement within and between calendar years exhibit certain inconsistencies most of which can be attributed to the small numbers of fish in some entries. Definite trends can be detected, nevertheless. It is seen, for example, that the percentage disagreement between supposed ages and ages read from scales was invariably nil or small (0.0 to 3.4 percent) for lake trout recaptured within 20 miles of the point of release. The percentages were large, on the other hand, for trout recaptured more than 60 miles from the locality of planting. Only in 1949, when 13.3 percent of the fish were in disagreement on age, was there evidence of considerable numbers of bona fide marked fish in this area. In the remaining 3 years in which recaptures were reported

from distances greater than 60 miles, the percentages ran from 42.8 to 100.0 (numbers of fish were small but the figures probably are significant because of consistently high values).

For lake trout captured at the two intermediate distances, the percentage disagreement was nil at 20 to 40 miles in 1947 and 1951, but only 5 fish were reported each year. The remaining records for fish captured at 20 to 40 or 40 to 60 miles indicate a general inverse relationship between percentage disagreement and number of lake trout reported. In the largest sample, 251 fish at 20 to 40 miles in 1949, the percentage disagreement was only 0.8; the two samples in the range of 100 to 200 fish had percentages of 1.9 and 5.8; and the four samples containing fewer than 100 fish had percentages ranging from 6.7 to 22.2.

The data of table 12, taken as a whole, lend strong additional support to the belief that a considerable part of the disagreements between supposed ages and ages read from the scales can be attributed to the presence in the sample of unmarked lake trout with abnormal fins.

Relation of disagreements to size of fish

It was stated in an earlier section that 9 of the 86 lake trout, for which the supposed ages and ages read from scales did not agree, were too large for their supposed age and hence almost certainly were not recoveries of marked fish, but merely had abnormal fins (these fish are designated by asterisks in table 9). The basis for this conclusion is to be found in the length-frequency distributions of table 13. The 9 fish include 2 members of age-group I (marked lake trout of this age seemingly were still too small to be captured in commercial nets) and the 7 lake trout of age-group II that lay well outside the range of length for lake trout of the same age for which scale reading and supposed age agreed.

For the remaining fish, length does not appear to offer a safe criterion for judgment as to whether any particular individual in a "no" column was or was not a marked fish. The frequencies and mean lengths for the paired groupings are so different, however, as to leave no doubt that the lake trout, for which supposed age and age as read did not agree, included considerable numbers of unmarked fish. Despite the wide ranges in length of individual age groups and the extensive overlap between successive age groups, the distribution of

TABLE 13.—Length-frequency distribution of "marked" lake trout at capture, in age groups indicated by deformed or missing fin (all year classes combined)

[Fish in "yes" column of each age group are those for which age read from scales agreed with age indicated by abnormal fin, and fish in the "no" column are those for which ages disagreed. Total lengths in inches]

Total length	Age group								
	I		II		III		IV		V
	No ²	Yes	No	Yes	No	Yes	No	Yes	No
7.0-7.4		1							
7.5-7.9									
8.0-8.4		4							
8.5-8.9		7							
9.0-9.4		4							
9.5-9.9		2		4	1		1		
10.0-10.4		7		2	1	1		2	
10.5-10.9		5		12	1	2			1
11.0-11.4		3		28	3	7		3	2
11.5-11.9		4		33	4	19	1	2	2
12.0-12.4	1	1	1	31	2	44	2	6	2
12.5-12.9		1	1	39	2	84	1	4	1
13.0-13.4			1	31	1	74	2	10	2
13.5-13.9				27		84	1	5	2
14.0-14.4				20	1	111	2	18	2
14.5-14.9			1	8	1	90	2	15	
15.0-15.4				9	1	68		24	1
15.5-15.9				5	1	56	1	41	
16.0-16.4				3		26	2	23	
16.5-16.9			1	1	1	27		31	
17.0-17.4						18		26	3
17.5-17.9					2	8		17	
18.0-18.4						3	3	14	1
18.5-18.9						3		14	3
19.0-19.4			1			3	1	10	2
19.5-19.9						1		5	
20.0-20.4			3	1	2	1	1	6	1
20.5-20.9							1		
21.0-21.4			1			2		1	
21.5-21.9					1		1	2	
22.0-22.4				1	2			1	
31.5-31.0	1								
Number.....	2	39	10	255	27	732	22	280	25
Mean length...	22.0	10.0	17.0	12.8	14.5	14.3	15.5	15.9	15.0

¹ Later age groups not included because the number of fish in each was too small to yield useful information.
² No fish were captured for which the age read from the scales agreed with this supposed age.

the lengths and the progressive shift of modes and means of fish in the "Yes" columns are much as would be expected. The frequencies in the "no" columns do not exhibit a similarly consistent relationship. They show a random scatter greater than that which can be ascribed to the small numbers of fish. Modes are lacking, and the means give no indication of the progressive increase in size that should accompany increase in age. The differences between the two groups with respect to indicated growth is demonstrated by the summary in table 14. Here, as was true for fish from southern Lake Michigan, the lake trout for which there was disagreement on age present the ridiculous spectacle of diminishing length with increase in age. A high percentage of them obviously could not have been from plantings of marked fingerlings.

Another approach to the question of the presence of unmarked lake trout in the samples lies in the

comparison of the growth of lake trout for which there was agreement on age with the growth of those for which there was not agreement on age. In this comparison it was assumed that none of the lake trout for which there was disagreement were marked fish and that the scales rather than fin abnormalities offer the correct estimate of age. Table 15, which gives the result of this comparison, is so arranged that the vertical columns give the average lengths at ages indicated by abnormal fins and diagonal rows (from upper left to lower right) contain a series of estimates of the length of lake trout of the same age, as read from the scales. As would be anticipated, if the readings are correct, the lake trout with agreement on age were shorter than those whose ages, read from the scales, were one or more years older than the ages indicated by the deformed fins. Conversely, the lake trout with agreement on age were larger than others whose ages were read one or more years younger than the ages indicated by the fins. In general, the magnitude of this difference in lengths was progressively greater with each increase in the number of years of disagreement between the supposed age of the fish and the age read from the scales. Despite the considerable variability expected because of the small numbers of fish in some samples and the known large range of lengths within age groups, the means in each diagonal, in the main, fluctuate normally about the average length determined for lake trout for which ages from scales and fin marks agreed.

Data in summary table 16 support the contention that lengths of age groups determined by

TABLE 14.—Comparison of average lengths of lake trout, for which the ages as indicated by scales and fins were the same, with average lengths as indicated by abnormal fins of lake trout for which ages indicated by fins and scales were different

[Data from table 13. Number of fish in parentheses]

Age group	Total length (inches)	
	Scales and fins in agreement	Scales and fins not in agreement
I.....	22.0 (2)	22.0 (2)
II.....	10.0 (39)	17.0 (10)
III.....	12.8 (255)	14.5 (27)
IV.....	14.3 (732)	15.5 (22)
V.....	15.9 (280)	15.0 (25)

TABLE 15.—Comparison of the average lengths of lake trout whose scale readings disagreed with their supposed age with the average lengths of lake trout for which the reading agreed with the supposed age¹

[In all readings, it was assumed that the central check was a 0-mark]

Departure of age read from expected age	Age indicated by fin mark reported					
	I	II	III	IV	V	VI
5 years more:						
Age from scales.....		VII				
Average length.....		19.0				
Number of fish.....		1				
4 years more:						
Age from scales.....		VI	VII			
Average length.....		18.2	20.0			
Number of fish.....		2	1			
3 years more:						
Age from scales.....		V	VI	VII		
Average length.....		16.4	20.0	19.2		
Number of fish.....		2	1	2		
2 years more:						
Age from scales.....		III	IV	V	VI	VII
Average length.....		12.3	21.2	16.1	18.8	22.0
Number of fish.....		1	1	6	2	1
1 year more:						
Age from scales.....		III	IV	V	VI	
Average length.....		13.4	13.4	15.4	17.8	
Number of fish.....		3	15	13	11	
As expected:						
Age from scales.....		I	II	III	IV	V
Average length.....		5.6	10.0	12.8	14.3	15.8
Number of fish.....		1,319	39	255	732	280
1 year less:						
Age from scales.....			II	III	IV	
Average length.....			10.5	13.5	13.0	
Number of fish.....			3	4	10	
2 years less:						
Age from scales.....				II	III	IV
Average length.....				9.3	12.5	13.0
Number of fish.....				1	3	1
3 years less:						
Age from scales.....					II	
Average length.....					12.4	
Number of fish.....					1	

¹ In addition to the fish listed in the table, the collection contained 1 lake trout, 31.8 inches long, which, according to the fin, should have belonged to age-group I but the scales indicated it to be a member of age-group IX.

² A mean calculated length based on all lake trout for which ages from scales and fin marks agreed. The samples contained no fish whose scales indicated that they belonged to age-group I.

scale readings give a reasonable estimate on growth of the lake trout for which ages from scales and fins disagreed. In this table age groups, as established from the scales, have been combined regardless of discrepancies between supposed age and age as read. For age groups II to V, the differences in average lengths between the lake trout with and without agreement on age fell within the range of 0.1 inch (age-group V) to 0.8 inch (age-group IV). The difference was fairly large (2.5 inches) for age-group VI, but here the average length for trout with agreement (15.6 inches) must be viewed with skepticism as it was 0.2 inch below the mean length for age-group V (15.8 inches). Despite this discrepancy, the data, as a whole, show that the scale readings gave reasonable estimates of the growth of the 86 fish with disagreement on age, and hence provide still further evidence of a high percentage of unmarked lake trout among them.

TABLE 16.—Comparison of average lengths of lake trout for which the ages as indicated by scales and fins were the same, with average lengths as indicated by scale readings for the 86 lake trout for which ages indicated by fins and scales were different

[Data from table 15. Number of fish in parentheses.]

Age group	Total length (inches)	
	Scales and fins in agreement	Scales and fins not in agreement
II.....	10.0 (39)	10.6 (5)
III.....	12.8 (255)	13.1 (11)
IV.....	14.3 (732)	13.5 (27)
V.....	15.8 (280)	15.7 (21)
VI.....	15.6 (13)	18.1 (16)

¹ This low figure is probably due to selective destruction of the lake trout population in Lake Michigan.

CONCLUSIONS AS TO THE DEPENDABILITY OF SCALE READINGS

The study of the scales of lake trout presumably of known age has proved scale readings to be highly dependable over the age span represented in the sample. In the original collection of 1,405 recaptured lake trout from northern Lake Michigan, ages as read from scales agreed with ages as indicated by fin marks for 1,319 or 93.9 percent of the individuals. The actual degree of dependability is much greater, however, than this percentage suggests. The evidence is strong that the 86 fish, for which ages were in disagreement, actually included many unmarked individuals on which fin development had been abnormal. Nine lake trout could be designated with confidence as "unmarked" because of their unreasonably large size in relation to their supposed age. Criteria were lacking for an objective decision as to whether any one individual among the remaining 77 fish could have been a bona fide recovery, but a series of analyses on the relation of the disagreements to appearance of the deformed fins, year and locality of recapture, size and growth of fish yielded convincing evidence of the presence of considerable numbers of unmarked lake trout. Although an exact figure can not be given, it can be stated with confidence that, had the original sample been composed entirely of recaptures from the three plantings of marked fish, the agreement between supposed ages and ages read from the scales would have been well above 95 percent.

The O-mark, a check in the field of first-year growth, was present on the scales of nearly all

marked lake trout recaptured and, according to the best available evidence, was also a characteristic of the scales of most wild fish.

It should be emphasized that, dependable as lake trout scales may be as indicators of age, they are not read easily. Considerable experience is

required before a reader's interpretation of the scale pattern becomes highly reliable. Even the experienced reader can do accurate work only if the scale preparations are clear and they are studied carefully with the aid of the best optical equipment.

GROWTH OF MARKED LAKE TROUT

The study of the growth of marked lake trout is based principally on the 1,319 specimens for which the age as read from the scales agreed with the supposed age. This restriction excludes any bona fide recaptures for which errors were made in scale readings. The 1,319 fish may include a few unmarked fish with abnormal fins that happened to be of the correct age at capture. There is no reason to believe, however, that the number in either of the groups is large; the restricted sample, therefore, may safely be presumed to consist almost entirely of marked fish and also to include nearly all of the true recoveries.

Measurements of the marked lake trout were made in Ann Arbor before the fish were preserved but after they had been shipped in ice from the port where they were landed. Although most of the fish were in good condition upon arrival, a few were in advanced stages of decomposition so that length and weight measurements could not be determined accurately. Such fish have been excluded from tables and calculations for which those measurements are requisite. In some tables the total number of fish was further reduced by dropping from consideration the older age groups which were poorly represented. More lengths than weights were obtained because some of the lake trout were dressed (gills and viscera removed) upon arrival in Ann Arbor.

LENGTH-WEIGHT RELATION

The commonly accepted formula expressing the length-weight relation in fishes is:

$$W = cL^n$$

or $\log W = \log c + n \log L$

where $W = \text{weight}$

$L = \text{total length}$

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

As the measurements of length and weight alike are subject to error, a method developed by Bartlett (1949) was used in fitting a line to the logarithms of individual lengths and weights of

1,197 lake trout²¹ from northern Lake Michigan. The resulting estimate of the relation between weight in ounces and total length in inches was:

$$\log W = -2.4698 + 3.1125 \log L$$

The value of 3.1125 for n (which measures the relative rates of increase of weight and length) shows that in these lake trout the weight increased somewhat faster than the cube of the length. In other words, the body form became more robust as the fish grew longer.

The departure of the length-weight relationship of the lake trout of northern Lake Michigan from the "cube law" probably was significant. The 5-percent confidence interval of the true slope β with $t = 1.962$ for 1,195 degrees of freedom, when calculated by Bartlett's method was 3.13718 ± 0.90129 . At the same level of significance, the least squares method gave $b_{xy} = 3.08414 \pm 0.04332$.

Comparisons between empirical weights and theoretical weights (as computed from the length-weight equation) are to be found in table 17 and figure 18; the straight line of figure 18 is a graph of the equation. Because table 17 contains actual and computed values of both length and weight, an explanation of the arrangement may be helpful. The first row of figures in the left section, for example, states first that the single lake trout 7.2 inches long had a weight of 1.2 ounces at capture (fourth column). In the same row, it is shown further that the expected weight for a 7.2-inch fish was computed to be 1.6 ounces (fifth column) and that the expected length for a 1.2-ounce lake trout would be 6.6 inches (third column).

Agreement between most empirical and calculated weights and lengths can be termed good. Discrepancies usually are small (full agreement at 14 lengths). The larger disagreements occur at

²¹ This number included all the lake trout weighed in the round, 1,118 presumably marked and 79 for which the ages from scale readings and deformed fins did not agree.

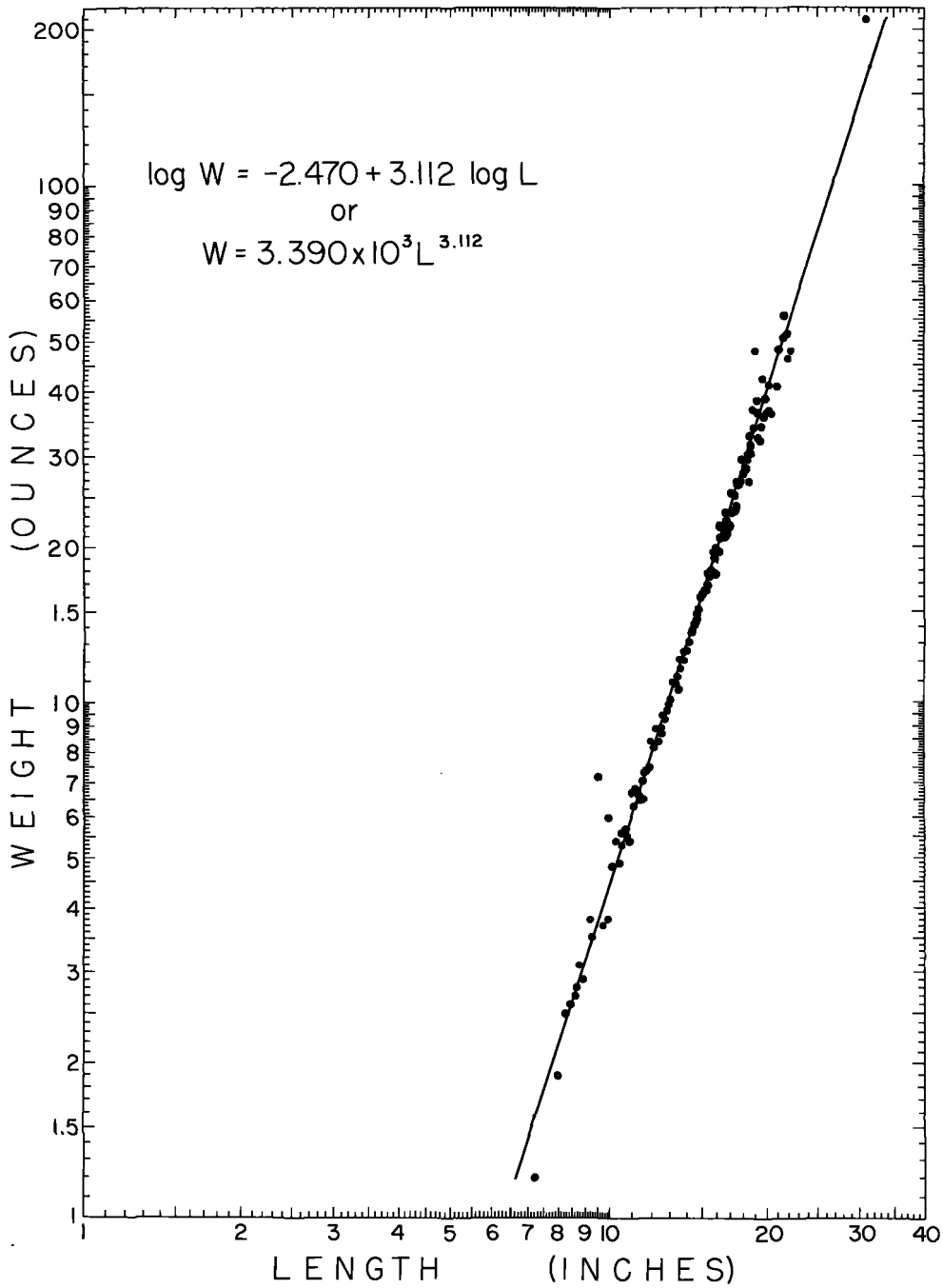


FIGURE 18.—Length-weight relation of 1,197 lake trout from northern Lake Michigan. [Dots give empirical values; line represents values obtained from solution of the length-weight equation].

TABLE 17.—Relation between total length (inches) and weight (ounces) of lake trout from northern Lake Michigan, also lengths and weights calculated with the length-weight equation

[Based principally on lake trout recaptured from the 1944-46 plantings of marked fish. See text for details]

Number of fish	Total length		Weight		Number of fish	Total length		Weight		Number of fish	Total length		Weight	
	Actual	Calculated	Actual	Calculated		Actual	Calculated	Actual	Calculated		Actual	Calculated	Actual	Calculated
1.....	7.2	6.6	1.2	1.6	24.....	13.0	13.0	9.9	9.9	10.....	17.2	17.5	25.2	23.8
1.....	8.0	7.6	1.9	2.2	15.....	13.1	13.1	10.1	10.2	8.....	17.3	17.5	25.1	24.2
1.....	8.3	8.3	2.5	2.5	19.....	13.2	13.1	10.1	10.4	3.....	17.4	17.1	23.4	24.6
2.....	8.4	8.4	2.6	2.6	20.....	13.3	13.4	10.9	10.7	6.....	17.5	17.8	26.6	25.1
2.....	8.6	8.6	2.7	2.8	32.....	13.4	13.4	10.8	10.9	6.....	17.6	17.3	24.0	25.5
2.....	8.7	8.6	2.8	2.8	25.....	13.5	13.5	11.2	11.2	10.....	17.7	17.8	26.3	26.0
1.....	8.8	8.9	3.1	3.0	19.....	13.6	13.2	10.5	11.4	3.....	17.8	17.9	26.8	26.4
1.....	8.9	8.8	2.9	3.1	23.....	13.7	13.7	11.6	11.7	3.....	17.9	18.4	29.4	26.9
1.....	9.2	9.5	3.8	3.4	30.....	13.8	13.8	12.0	13.0	13.....	18.0	18.0	27.6	27.4
2.....	9.3	9.3	3.5	3.5	12.....	13.9	13.8	12.0	12.2	2.....	18.1	18.2	28.2	27.8
2.....	9.5	11.7	7.2	3.7	27.....	14.0	14.0	12.5	12.5	2.....	18.2	18.2	28.2	28.3
3.....	9.7	9.5	3.7	4.0	22.....	14.1	14.0	12.5	12.8	4.....	18.3	18.4	29.4	28.8
4.....	9.9	9.5	3.8	4.3	30.....	14.2	14.2	13.0	13.1	1.....	18.4	18.4	29.5	29.3
4.....	10.0	11.1	6.0	4.4	25.....	14.3	14.4	13.6	13.4	4.....	18.5	17.8	26.6	29.8
3.....	10.1	10.3	4.8	4.5	27.....	14.4	14.4	13.7	13.7	5.....	18.6	19.1	32.7	30.3
4.....	10.3	10.7	5.4	4.8	22.....	14.5	14.6	14.1	14.0	4.....	18.7	18.8	31.2	30.8
1.....	10.4	10.4	4.9	5.0	24.....	14.6	14.6	14.3	14.3	5.....	18.8	18.8	31.5	31.3
3.....	10.5	10.6	5.3	5.1	24.....	14.7	14.6	14.4	14.6	1.....	18.9	19.8	36.8	31.9
4.....	10.6	10.8	5.6	5.3	17.....	14.8	14.8	14.8	14.9	5.....	19.0	19.3	33.9	32.4
6.....	10.7	10.9	5.7	5.4	14.....	14.9	14.9	15.1	15.2	1.....	19.1	21.5	47.8	32.9
5.....	10.8	10.7	5.5	5.6	14.....	15.0	15.1	15.9	15.5	2.....	19.2	20.0	38.2	33.5
2.....	10.9	10.7	5.4	5.7	17.....	15.1	15.2	16.1	15.8	4.....	19.3	19.7	36.2	34.0
10.....	11.0	11.5	6.7	5.9	17.....	15.2	15.2	16.3	16.2	2.....	19.4	19.0	32.4	34.6
8.....	11.1	11.2	6.3	6.1	17.....	15.3	15.3	16.4	16.5	1.....	19.5	18.9	32.0	35.1
9.....	11.2	11.5	6.8	6.2	18.....	15.4	15.4	16.7	16.8	1.....	19.6	19.3	34.0	35.7
9.....	11.3	11.4	6.6	6.4	23.....	15.5	15.6	17.6	17.2	1.....	19.7	20.7	42.5	36.2
7.....	11.4	11.3	6.5	6.6	23.....	15.6	15.6	17.5	17.5	1.....	19.8	19.6	35.5	36.8
7.....	11.5	11.3	6.5	6.8	12.....	15.7	15.7	17.9	17.9	12.....	20.0	20.1	38.8	38.0
9.....	11.6	11.7	7.1	7.0	13.....	15.8	16.1	19.4	18.2	1.....	20.1	19.7	36.2	38.6
12.....	11.7	11.8	7.3	7.2	16.....	15.9	16.0	18.9	18.6	1.....	20.2	19.7	36.5	39.2
8.....	11.8	11.8	7.4	7.4	7.....	16.0	15.6	17.7	19.0	1.....	20.3	20.5	41.0	39.8
17.....	11.9	11.9	7.5	7.6	10.....	16.1	16.2	19.7	19.3	1.....	20.5	19.7	36.0	41.0
10.....	12.0	12.3	8.4	7.8	7.....	16.2	16.2	19.6	19.7	2.....	21.0	20.5	40.9	44.2
16.....	12.1	12.2	8.2	8.0	4.....	16.3	16.8	21.9	20.1	1.....	21.2	21.6	48.0	45.6
21.....	12.2	12.2	8.2	8.2	11.....	16.4	16.4	20.6	20.5	2.....	21.5	22.6	55.4	47.6
10.....	12.3	12.6	8.9	8.4	14.....	16.5	16.7	21.7	20.9	1.....	21.6	21.9	50.2	48.3
18.....	12.4	12.3	8.4	8.6	7.....	16.6	16.5	20.9	21.3	1.....	21.8	22.0	51.0	49.7
18.....	12.5	12.6	8.9	8.8	4.....	16.7	16.5	21.0	21.7	3.....	22.0	21.3	46.0	51.1
22.....	12.6	12.5	8.7	9.0	12.....	16.8	17.0	23.1	22.1	1.....	22.3	21.5	47.5	53.3
22.....	12.7	12.8	9.4	9.2	8.....	16.9	16.8	22.1	22.5	1.....	31.0	34.5	208.0	148.6
27.....	12.8	12.7	9.3	9.5	11.....	17.0	16.8	21.9	22.9					
24.....	12.9	12.9	9.6	9.7	6.....	17.1	17.1	23.2	23.3					

lengths where averages are based on one or a few fish. Other factors that possibly could have contributed to the discrepancies include: annual and seasonal fluctuations in condition; sex and state of gonads (of the larger, mature fish); and gear selection.²² It may, accordingly be held valid to use the equation to describe the general length-weight relation and thus estimate weight when length only is known or length when weight only is available.

The calculated weights (table 17) show that lake trout would be expected to attain the weight of 1 pound at 15.1-15.2 inches, 2 pounds at about 18.9 inches, and 3 pounds at 21.5-21.6 inches. The length corresponding to 1½ pounds, the minimum weight at which lake trout may be taken legally in the State of Michigan, was 17¼ inches.

To test whether the equation representing the length-weight relationship of the lake trout in the sample was also representative of younger fish,

²² See Farran (1936) and Deason and Hile (1947) for discussions of the effects of gill-net selectivity on the estimation of the length-weight relation.

calculations of weight were compared with the weights of the control groups reared in ponds at Marquette, Mich. (Shetter 1951). The lengths at which the comparisons were made are average lengths at capture of the fish in the control groups. Lengths overlapping those of the lake-reared fish up to 10.7 inches are also included in the tabulation.

Length (inches)	Number of fish (control groups)	Measured weight (ounces) of pond-reared control group	Calculated weight (ounces)
2.9.....	2,007	0.11	0.09
3.2.....	2,000	.15	.13
4.1.....	945	.26	.27
6.4.....	732	1.2	1.1
6.7.....	860	1.3	1.3
7.2.....	296	1.9	1.6
7.3.....	837	1.5	1.6
7.6.....	289	1.9	1.9
9.7.....	599	4.3	4.0
10.1.....	409	4.9	4.5
10.7.....	262	5.3	5.4

The differences between measured and calculated weights for each length given did not exceed 0.4 ounce. The average weight of the pond-reared group was only slightly heavier, 0.08 ounce, than the average calculated weight for all length-intervals represented by the group.

GROWTH IN LENGTH

The data presented on growth in length of marked lake trout include both lengths at capture and calculated lengths (based on scale measurements) at the end of the several years of life and at time of formation of the O-mark in the first field of growth. All calculations of length were made by direct proportion, that is, on the assumption that the ratio of length of fish to diameter of scale is constant at all lengths attained by the fish after completion of the O-mark. Although the materials at hand are not suitable for a discriminating test of this assumption (range in lengths is too short and lengths at the ends of the range are represented by inadequate numbers of individuals), such data as are available indicate that any systematic errors, from the use of direct proportion, must be extremely small.

Lengths at Capture

The measured lengths of the marked lake trout of each age group, at the time of capture, extended over a wide range which was somewhat greater for the older than for the younger fish (see figure 20). The range within a single age group (year classes combined) varied from 5.4 inches for age-group II to 12.6 inches for age-group III with intermediate ranges for the remaining age groups (table 18).

Despite wide ranges in lengths, the mean lengths for each year of age reached by the three year

TABLE 18.—Mean length (inches) and ranges of length, at time of capture, of the year classes of marked lake trout, by age group

Item	Age group				
	II	III	IV	V	VI
1944 year class:					
Mean length.....		13.4	15.2	15.1	
Range.....		9.9-20.0	12.8-21.0	13.4-19.7	
Number of fish.....		16	10	17	
1945 year class:					
Mean length.....	10.0	12.9	14.2	15.8	15.6
Range.....	7.2-12.6	9.7-22.3	10.5-21.0	10.0-22.0	12.2-20.2
Number of fish.....	31	190	555	240	13
1946 year class:					
Mean length.....	9.9	12.2	14.5	16.6	
Range.....	8.0-12.0	9.9-16.4	11.1-20.0	13.0-21.6	
Number of fish.....	8	49	167	23	
Combined year classes:					
Mean length.....	10.0	12.8	14.3	15.8	15.6
Range.....	7.2-12.6	9.7-22.3	10.5-21.0	10.0-22.0	12.2-20.2
Number of fish.....	39	255	732	280	

classes of marked lake trout were remarkably close together. No representatives of age-group II of the 1944 year class were taken by the fishermen, but the mean lengths of the 2-year-olds of the 1945 and 1946 year classes differed by only 0.1 inch. The mean lengths for age-groups III, IV, and V in all three year classes had maximum differences of 1.2, 1.0, and 1.5 inches, respectively.

The year classes of marked lake trout planted in Lake Michigan not only grew at similar rates but, regardless of environmental differences, they also grew at about the same rate as control groups reared in ponds at the State Fish Hatchery, Marquette, Mich. The pond-reared lake trout of the 1944 year class had grown 16.6 inches in length by October 1948 (age-group IV). None of the 1944 year class of marked, lake-reared lake trout were captured in October 1948, but the average length of trout in age-group IV caught from April through September was 15.2 inches which, as would be expected, was somewhat below the average for the fish taken only in October. The pond-reared lake trout of the 1946 year class were 10.1 inches long when they were measured in October 1948 (age-group II). Although no recoveries from the lake-reared fish of the 1946 year class were made in October 1948, the average length of 9.9 inches for fish in age-group II caught from May through September is not far below that for the pond-reared lake trout of the same year class. The best comparison of lake- and pond-reared lake trout comes from the more plentiful samples of the 1945 year class which were measured in May 1948 when they were members of age-group III. At this time the pond-reared fish were 11.7 inches long and the marked, lake-reared fish averaged 11.9 inches long (table 19).

TABLE 19.—Comparison of total lengths (inches) of lake-reared, marked lake trout with those of the pond-reared control groups

Item	Year of planting ¹		
	1944	1945	1946
Pond-reared trout:			
Average length.....	16.6 (200)	11.7 (378)	10.1 (196)
Time of measurement..	Oct. 1948	May 1948	Oct. 1948
Lake-reared trout:			
Average length ²	15.2 (10)	11.9 (20)	9.9 (8)
Time of measurement..	Apr.-Sept., 1948	May 1948	May-Sept., 1948

¹ Young of the year were planted in September of each year.

² All fish recovered from 1944 and 1946 plantings were included because few were available. None were captured as late as October.

TABLE 20.—Total length at capture and lengths calculated by direct proportion from diameters of annuli on the scales of marked lake trout

[Lengths in inches]

Age group	Year planted	Number of specimens	Length at capture	Calculated length at end of year of life						
				0	1	2	3	4	5	6
II	1945	31	10.0	13.4	5.2	8.4				
	1946	8	9.9	3.6	6.4	8.8				
	Mean		10.0	3.5	5.4	8.5				
III	1944	16	13.5	3.6	6.5	9.4	12.2			
	1945	190	12.9	3.9	5.9	9.2	11.8			
	1946	49	12.2	3.7	5.9	8.8	10.9			
	Mean		12.8	3.8	6.0	9.2	11.7			
IV	1944	10	15.2	3.6	5.9	9.0	11.9	14.4		
	1945	555	14.2	3.8	6.1	8.8	11.4	13.7		
	1946	167	14.5	3.7	5.9	8.6	11.1	14.0		
	Mean		14.3	3.7	6.0	8.7	11.3	13.8		
V	1944	17	15.2	3.5	5.7	8.0	10.4	12.7	14.8	
	1945	240	16.2	3.7	5.6	8.4	10.8	13.2	15.7	
	1946	23	16.6	3.4	5.7	8.1	10.2	13.2	16.0	
	Mean		15.8	3.7	5.6	8.3	10.7	13.1	15.6	
VI	1945	13	15.6	2.7	4.4	6.5	8.6	10.7	12.8	15.2
Number of specimens				1,319	1,319	1,319	1,280	1,025	293	13
Mean increment of growth in length				3.7	2.2	2.8	2.5	2.5	2.5	2.4
Length from summation of increments				3.7	5.9	8.7	11.2	13.7	16.2	18.6
Mean calculated length				3.7	5.9	8.7	11.2	13.6	15.5	15.2
Increments of mean length				3.7	2.2	2.8	2.5	2.4	1.9	-0.3

¹ Figures in this column are computed lengths at time of formation of the O-mark in the field of first-year growth.

Calculated Lengths

The growth history of each fish was taken as the average of the calculated lengths computed independently from the measurements of two scales selected as representative of a sample.²³ Averages of these lengths for all marked lake trout of each of the three year classes (1944-46) are shown in table 20 where they are arranged by age group. Distribution of the calculated lengths for corresponding age groups of different year classes was fairly random and agreement between them sufficiently close to warrant combination of the data from year classes. The small discrepancies that did exist among the means of different age groups are not believed to influence adversely the general mean.

The lengths for early years of life, calculated from age-groups III to VI, exhibited Lee's phenomenon of gradually decreasing values with increasing age (fig. 19). Differences in the estimates of the lengths calculated from the first three of these

²³ The larger scale in a pair from the same fish often gave a smaller calculated length for the early years of life than did the smaller scale. Although the difference between this distribution and the 50-50 relationship expected (on the theory that all scales on the fish give the same calculated lengths) was highly significant, the mean differences in calculated lengths for the sample were slight (0.05 inch at formation of the O-mark and 0.04 inch at the first annulus). The differences in the sizes of the paired scales were small, however (ranging from 0.12 to 0.96 millimeter). Because of this bias inherent to the data, and the necessity for studying the scales at high magnification (so close measurements are difficult to make), it is desirable that lengths calculated for the early years be made from measurements of two or more scales, especially when the number of fish in the sample is small. Consistent selection of either very large or very small scales could result in appreciable error.

age groups were much smaller than the differences between these and the estimates calculated from age-group VI. The 6-year-olds were not only smaller than the 5-year-olds at time of capture but, according to their calculated lengths, they started life (at planting) in the lower half of the range of length. The early disadvantage in size at formation of the O-mark was not compensated in later life.²⁴ All values for lengths at various ages, except those calculated from age-group VI, were rather closely grouped about a common mean value, hence could be combined. As age-groups II to V were represented by 1,306 lake trout and age-group VI by only 13, the averages were scarcely influenced by the latter group. Effects of selective fishing by gill nets used in the commercial fishery are discussed in the following section of this paper.

The growth history of the entire sample of marked lake trout has been described by two common methods (bottom of table 20). By the first method, and the one believed to yield the

²⁴ Reibisch (1899) in writing of the difference in size of young plaice, *Pleuronectes platessa*, caused by a long hatching period during which those that had hatched early were already large at the time others were hatching, toward the end of the season, stated that the time of hatching continues to exert its effect on the size of the individual throughout later years. More recently, Hodgson (1929) concluded from his studies that so-called compensatory growth is simply explained as the natural result of comparing the growth of fishes which are at different ages. Ford (1933) points out that with increase of age fish have less ability to increase length, but the "curve of ability to grow," which has the form of a geometric regression, may be subject to variation from fish to fish, and from population to population with different conditions of growth.

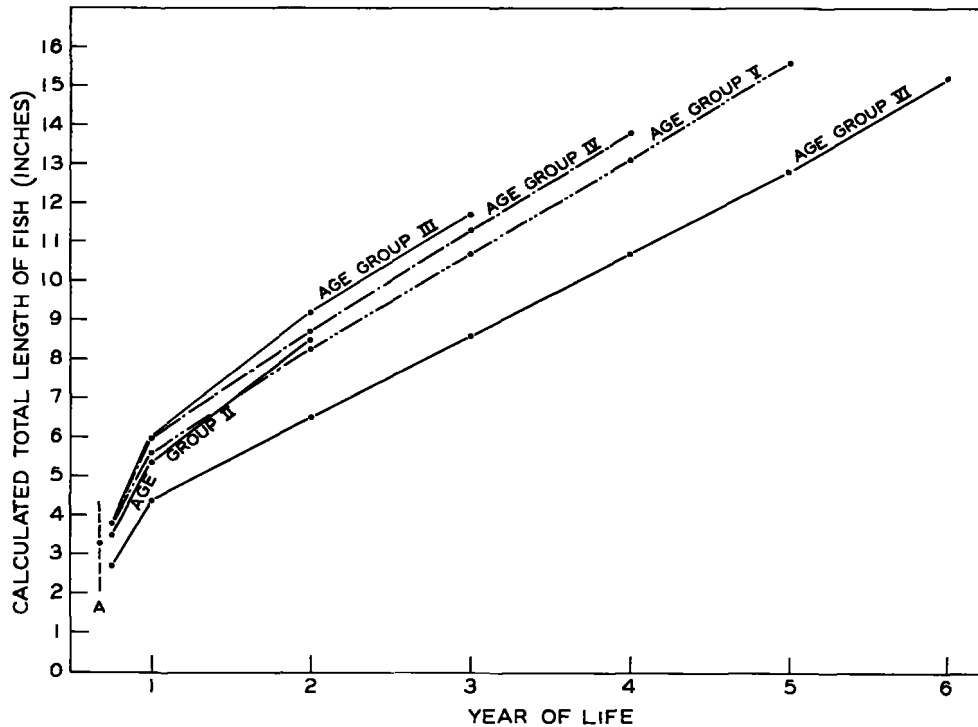


FIGURE 19.—Calculated lengths (sums of mean increments of growth in inches) of the age groups of marked lake trout.
A. Mean (dot) and range (broken line) of marked lake trout at time of planting in September.

most dependable estimate of growth rate, the mean lengths at the end of successive years of growth were obtained by the summation of mean calculated increments of length. The second general estimate of growth is composed of the weighted means of the calculated lengths. Results from the two procedures agreed for the first 3 years of life but in the later years the summation of the average increments gave decidedly higher values. The advantage of the summation of the increments is especially apparent in the data for the sixth year of life. Here the increment of mean length (-0.3 inch) obtained for the sixth year from the average lengths falsely indicates a decrease in size of the fish after the fifth year. This negative increment, or decrement, is based on lake trout caught after the year classes had been depleted of the larger fish. The sums of the increments of growth in length, on the other hand, show more reasonable figures on the rate of growth of the marked lake trout in Lake Michigan. Lengths obtained in this way were, nevertheless, somewhat smaller than the mean lengths of marked lake trout at the time of capture as the following tabulation demonstrates:

Year of life.....	2	3	4	5	6
Length (summation of calculated increments).....	8.7	11.2	13.7	16.2	18.5
Age group.....	II	III	IV	V	VI
Length at capture....	10.0	12.8	14.6	15.8	15.6

The marked fish recaptured as members of age-groups II, III, and IV measured 10.0, 12.8, and 14.6 inches long. Calculated lengths for the same years of life were 8.7, 11.2, and 13.7 inches. Whereas the calculated lengths give the size of the fish at the beginning of the growing season, the fish were caught somewhat later in the year at various times during the growing season, hence, were expected to be longer. Lengths, obtained by adding increments of growth, for fish in their fifth and sixth years of life show that in those years the lake trout actually continued to grow at rates only slightly lower than those during the earlier years of life (excepting the first year). The relation of the calculated lengths to the empirical data is shown in figure 20.

The mean annual increments of growth gradually decreased as the fish became older from 5.9 inches the first year to 2.8 inches the second

MEAN LENGTH AND RANGE IN LENGTH OF MARKED LAKE TROUT AT TIME OF CAPTURE COMPARED WITH MEAN CALCULATED LENGTHS

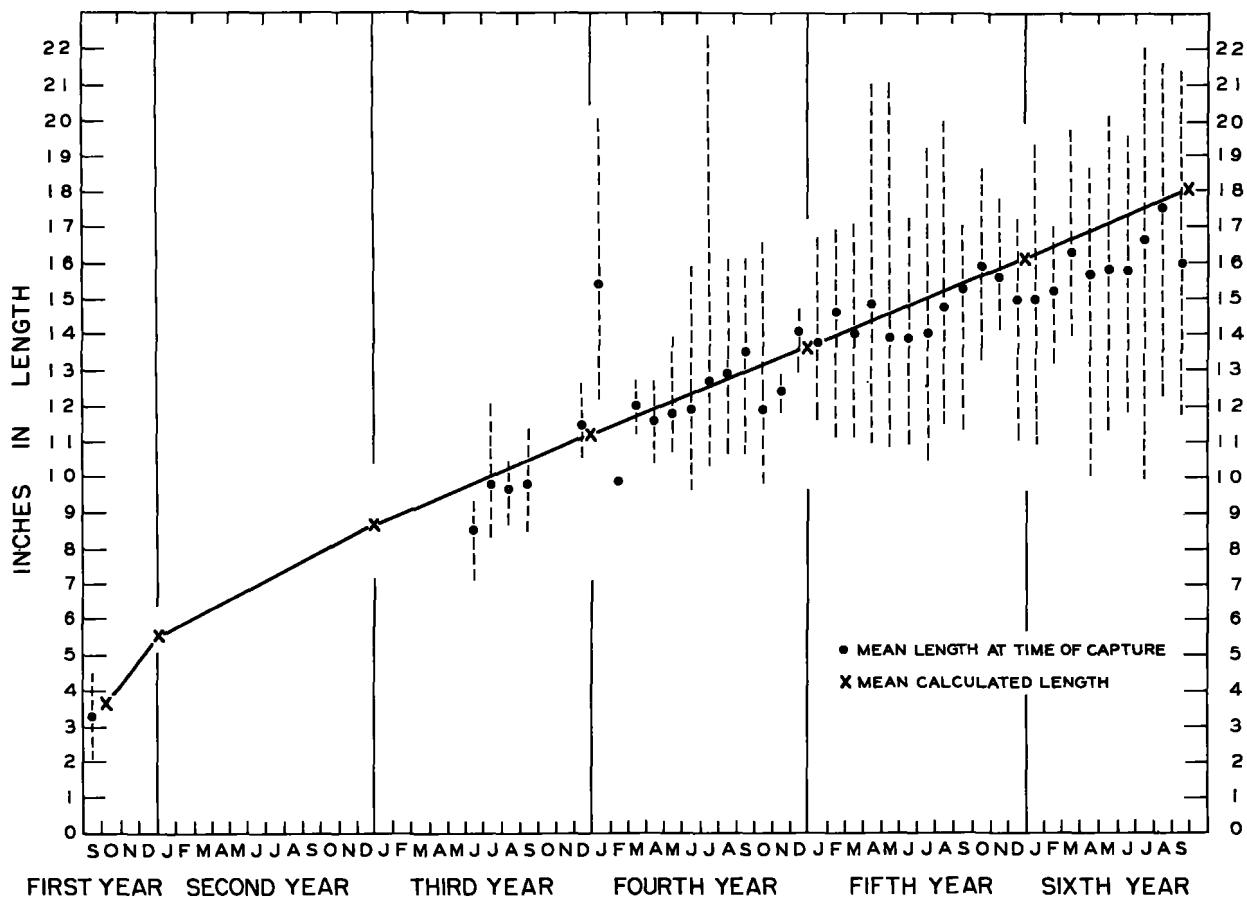


FIGURE 20.—Mean length and range in length of marked lake trout at time of capture compared with mean calculated lengths obtained by adding annual increments of growth (assuming January 1 the date growth is completed). Vertical broken lines give range of lengths, and dots the mean lengths at capture. Calculated lengths are shown along the solid, diagonal line.

year, 2.5 inches the third, fourth, and fifth years, and 2.4 inches the sixth year.

Factors of Discrepancies in Estimates of Growth

Several factors were considered as possible causes of the discrepancies in the estimates of growth made from the different age groups of marked lake trout: (1) condition of the fish; (2) sex differential in growth; (3) selectivity of nets employed by the fishery; (4) selectivity of lamprey predation. The effects of the first two were not considered important. Nearly all fish captured were taken during the summer months, thus seasonal changes in condition were not a factor. Combining data on the three year classes masked the annual differences. Sexual differences had not developed on these fish, most of which were

still immature; none caught was in gravid condition. The other two factors affecting estimates of growth are discussed later.

Selectivity of gill nets is an important factor which would have a tendency to cause discrepancies in estimates of the growth rate. Some marked lake trout (43.4 percent) were caught in the 4½-inch-mesh gill nets of the whitefish and lake trout fisheries and others (56.6 percent) were taken in the 2½-inch-mesh gill nets of the chub fishery. The percentage of the total catch of lake trout taken by the 4½-inch-mesh nets decreased from 91.3 in 1947 to 17.5 in 1950. At the same time the percentage caught in the 2½-inch-mesh nets increased from 8.7 to 82.5. During this period lake trout were becoming so scarce that fishermen were

turning more and more to chub fishing with the small-mesh nets.

A gill net made of a single size of mesh tends to catch the larger fish of the younger age groups but, as the fish grow larger in later years this relation between size of fish and size of mesh in the nets is reversed and the net then catches the smaller individuals of the older age groups. This reversal takes place when the fish are at an earlier age if small-mesh nets are used than if the fishing is done with larger-mesh nets. The marked lake trout of age-groups III and IV, caught in 2½-inch-mesh nets, were 1.3 and 0.2 inches longer than the mean calculated length for the age group, and those of age-groups V and VI were 0.4 and 4.2 inches shorter than the calculated lengths. Fish of all age groups, caught in the 4½-inch-mesh nets were longer than those caught in the 2½-inch-mesh nets and also longer than the mean calculated lengths for the age groups represented. The discrepancies for age groups II to V fluctuated between 1.7 and 1.2 inches without clear trend. For age-group VI, the difference (0.5 inch) was less than the other differences, but the reduction may not indicate

that the reversal to capture of the smaller fish of a year class was approaching for this net. Probably, larger fish were no longer available for capture.

Age group	Mean calculated length	Length at capture of fish caught in nets of:	
		2½-inch-mesh	4½-inch-mesh
II.....	8.7	-----	10.0
III.....	11.2	12.5	12.9
IV.....	13.7	13.9	14.9
V.....	16.2	15.8	17.5
VI.....	18.6	14.4	19.1

Even though the large-mesh nets consistently caught the larger fish, the average size of lake trout taken in them and in the small-mesh nets increased as the fish became larger. Nets of each mesh size were static measures of a segment of a changing range of lengths within the population as the fish of each year class became older, hence, the mode of the lengths of lake trout caught in each net shifted from the lower toward the upper limits of its segment as the average size of the fish increased (table 21).

TABLE 21.—Calculated lengths (in inches) of marked lake trout (year classes combined) caught in large- and small-mesh gill nets

[Differences are shown below the lengths of fish caught in each pair of nets]

Age group	Mesh of net (inches)	Number of fish caught	Average total length and range of length at capture ² (inches)	Calculated lengths at end of year of life						
				0	1	2	3	4	5	6
II.....	{ 4½	39	10.0 (7.2-11.9).....	3.5	5.4	8.5	-----	-----	-----	-----
	{ 2½	0	-----	-----	-----	-----	-----	-----	-----	-----
III.....	{ 4½	187	12.9 (9.7-22.3).....	3.8	5.9	9.2	11.7	-----	-----	-----
	{ 2½	64	12.5 (10.7-15.5).....	3.8	6.1	9.0	11.6	-----	-----	-----
	{ 4½	272	14.9 (10.3-21.0).....	0.0	-----	2	1	-----	-----	-----
IV.....	{ 2½	449	13.9 (10.5-19.1).....	3.9	5.9	9.1	11.8	14.3	-----	-----
	{ 4½	64	17.5 (13.0-22.0).....	3.7	5.6	8.7	11.0	13.4	-----	-----
	{ 2½	215	15.8 (10.0-20.1).....	.2	.3	.4	.8	.9	-----	-----
V.....	{ 4½	64	17.5 (13.0-22.0).....	3.8	6.0	8.8	11.4	14.0	16.7	-----
	{ 2½	215	15.8 (10.0-20.1).....	3.7	5.5	8.2	10.6	12.9	15.4	-----
	{ 4½	3	19.1 (17.7-20.3).....	.1	.5	.6	.8	1.1	1.3	-----
VI.....	{ 2½	10	14.4 (12.2-18.0).....	3.2	5.1	8.1	10.8	13.6	16.0	18.9
	{ 4½	10	14.4 (12.2-18.0).....	2.6	4.2	6.0	8.0	9.9	11.8	13.9
	{ 2½	10	-----	.6	.9	2.1	2.8	3.7	4.2	5.0
Increments of length.....	4½	-----	-----	3.8	2.1	3.2	2.6	2.5	2.7	2.9
Length from summation of increments.....	-----	-----	-----	3.8	5.9	9.1	11.7	14.2	16.9	19.8
Increments of length.....	2½	-----	-----	3.7	1.9	3.0	2.3	2.4	2.5	2.0
Length from summation of increments.....	-----	-----	-----	3.7	5.6	8.6	10.9	13.3	15.8	17.8

¹ Size of mesh in net not recorded for 16 fish.

² Fish caught at different times during the growing season. Their total lengths are not comparable with the calculated lengths.

Calculated lengths of the marked lake trout emphasize the differences in length between fish caught in the 4½- and 2½-inch-mesh nets. The differences increase in size with each year of life (table 21, fig. 21). Undoubtedly, the small (average length at capture, 10.0 inches), slender lake trout of age-group II captured in large-mesh nets were caught by their teeth or by other en-

tanglement in the twine. The size of the mesh in the net could scarcely have been the determining factor in their capture. In fact, the small representation from age-group II in the sample (that from age-group III was six times as large) indicates that the fish in this age group were too small to be caught systematically in commercial nets of any mesh size used. Evidently, too, these

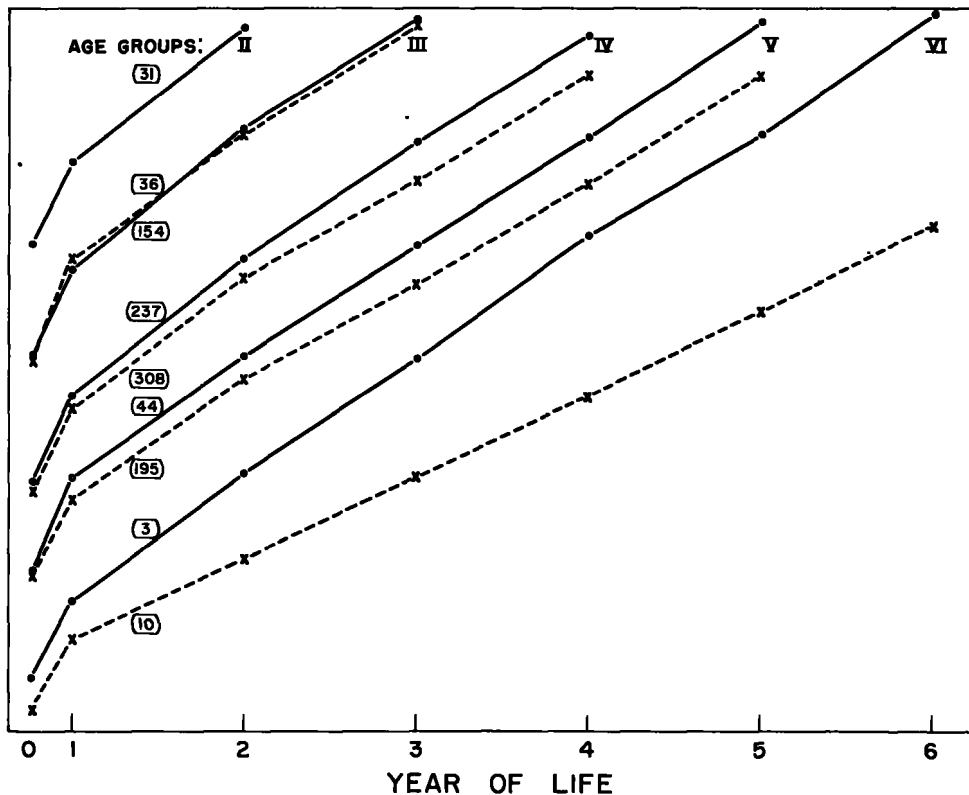


FIGURE 21.—Calculated lengths of marked lake trout (year classes combined) caught in large- and small-mesh gill nets. For each age group the calculated lengths of the fish caught in $4\frac{1}{2}$ -inch-mesh nets are connected by a solid line and those of fish caught in $2\frac{1}{2}$ -inch-mesh nets by a broken line. As all age groups represented in the sample are shown in the same graph, the curves do not have a common base, hence none is shown. Consult table 22 for values (inches of length) of points on the curves. The numbers of fish taken by each net are shown in parenthetical boxes.

lake trout were the smaller individuals of age-group II. Their mean calculated lengths were all smaller than those for the same years of life of the fish in age-groups III, IV, or V caught in either type of net (with the exception of the calculated length for the second year of age-group V caught in the small-mesh nets which was just 0.3 inch shorter than the one for age-group II). Nets of both sizes of mesh took fish of approximately the same size from age-group III (larger-mesh nets captured only slightly larger fish). The difference in the calculated lengths of fish caught by large- and small-mesh nets increased gradually, as the fish advanced in age, from 0.1 inch in the third year of life of age-group III to 0.9 inch in the fourth year of age-group IV, 1.3 inches in the fifth year of age-group V, and 5.0 inches in the sixth year of age-group VI.

The large discrepancies in the older age groups between the calculated growth histories of fish caught in $2\frac{1}{2}$ - and $4\frac{1}{2}$ -inch-mesh nets leave some

uncertainty as to the true rate of growth. Possibly the samples from small-mesh nets give better estimates of the growth rates for the younger age groups and the fish from large-mesh nets may provide better estimates for the older age groups. Because of the different selectivities shown by the gill nets of these two mesh sizes, the marked and unmarked lake trout caught in nets of each mesh size were studied separately.

The growth rates of marked and unmarked lake trout of the same year classes (1944-46) caught by $4\frac{1}{2}$ -inch-mesh nets in northern Lake Michigan were closely similar. However, with but one exception, sizes equal at formation of the first annulus, the calculated lengths of the unmarked fish were somewhat lower, ranging from 0.2 inch at formation of the O-mark to 1.2 inches at the sixth annulus. The average annual increment of growth in length after the first year was 2.8 inches for the marked and 2.5 inches for the unmarked fish. The calculated lengths of the unmarked

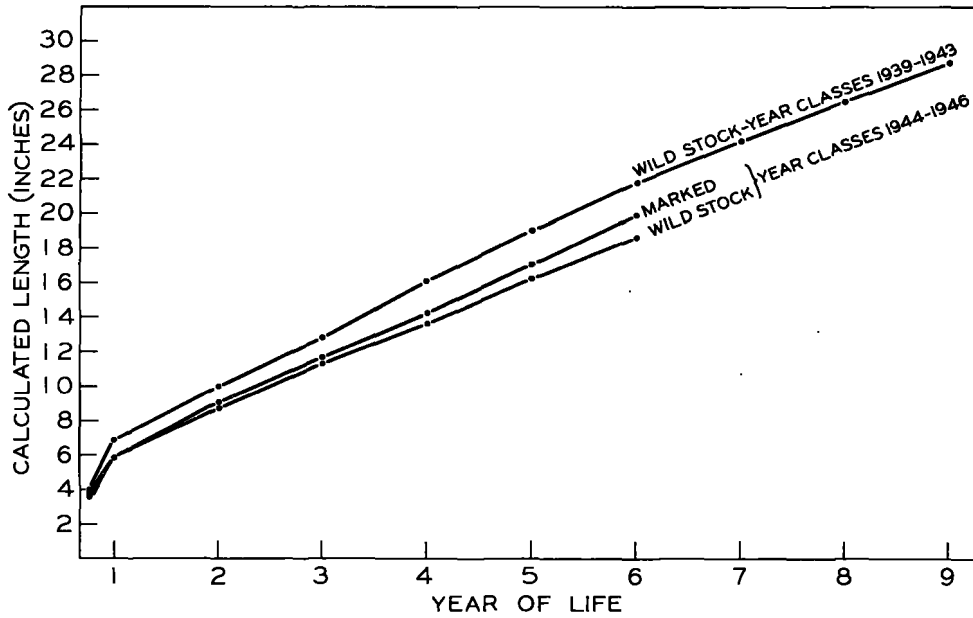


FIGURE 22.—Calculated lengths (sums of mean increments of growth in inches) of marked and unmarked lake trout of year classes 1944–46, and of the older year classes (1938–43) from the wild stock, caught by 4½-inch-mesh nets in northern Lake Michigan, areas 1–6.

lake trout (year classes 1944–46) caught by 2½-inch-mesh nets in northern Lake Michigan were also lower than those of marked lake trout caught in the same nets. In fact, the differences between their calculated lengths ranged from 0.4 inch at formation of the first annulus to 1.1 inches at the fifth annulus. The average difference was 0.2 inch greater than the average difference between the groups of marked and unmarked lake trout caught in large-mesh nets. The average annual increment of growth in length for the fish from small-mesh nets was 2.4 inches for both marked

and unmarked lake trout but the marked fish were already 0.4 inch longer than the unmarked fish at formation of the first annulus (table 22, fig. 22). Although marked and unmarked lake trout of the same year classes caught by small-mesh nets were somewhat smaller than those caught in the large-mesh nets, the calculated lengths of the unmarked fish retained about the same relative position below those of the marked fish that the unmarked fish had to the marked fish caught in large-mesh nets.

TABLE 22.—Calculated lengths (sums of mean increments of growth in inches) of marked and unmarked lake trout of year classes 1944–46 caught in Lake Michigan

[Increments of growth in parentheses]

Locality of capture and group of lake trout	Mesh of nets (inches)	Number of fish	Calculated lengths at year of life						Average increment of growth	
			0	1	2	3	4	5		6
Areas 1-6:										
Marked.....	4½	565	3.8	5.9	9.1	11.7	14.2	16.9	19.8	(2.8)
Unmarked.....			3.0	5.9	(3.2)	(2.6)	(2.5)	(2.7)	(2.9)	
Differences in calculated lengths.....			0.2	0.0	0.4	0.4	0.6	0.7	1.2	
Areas 1-6:										
Marked.....	2½	738	3.7	5.6	8.6	10.9	13.3	15.8	17.8	(2.4)
Unmarked.....			3.2	5.2	(3.0)	(2.3)	(2.4)	(2.5)	(2.0)	
Differences in calculated lengths.....			0.5	0.4	0.8	0.7	0.7	1.1	0.8	
Area 8:										
Unmarked.....	2½	76	2.5	4.6	6.9	9.1	11.1	13.2	14.8	(2.0)
Differences in calculated lengths of unmarked fish.....							(2.3)	(2.2)	(2.0)	
Areas 1-6 and area 8.....	2½		0.7	0.6	0.9	1.1	1.5	1.5	2.2	

The discrepancies might have been explained on the basis of annual fluctuations of growth, had not the calculated lengths from fish of all the age groups within each year class of unmarked lake trout varied consistently about a lower mean than those of the marked fish. Evidently, the larger size of marked lake trout over unmarked fish of the same year class is a real rather than apparent difference, which suggests that the marked fish may have derived a certain advantage from the hatchery environment during their first summer that carried over into later life.

The lake trout of year classes 1944-46 from area 8, caught in small-mesh nets, were decidedly smaller than the northern wild stock caught in these nets. The average calculated length of the southern fish at the first annulus was only 4.6 inches and the average annual increase in length to the sixth year of life was 2.0 inches (table 22; fig. 23) compared with a calculated length of 5.2 inches at the first annulus and an annual increase of 2.4 inches for the northern fish.

A major difference between samples of marked lake trout from 2½- and 4½-inch-mesh nets was the near absence of Lee's phenomenon in the data for the fish taken by the latter gear (fig. 24). These fish were subject to little or no selectivity from the nets, for few of the marked lake trout grew large enough to exceed the catching potential of the large-mesh nets.

Another factor in bringing about apparent decline, even cessation, of the growth of marked

lake trout with increase in age is believed to be destruction by sea lampreys of the most rapidly growing fish. Lengths, at capture, of marked lake trout in age-group V were little greater than those of fish a year younger; and lengths of fish in age-group VI were actually smaller than those in age-group V. A high percentage of the larger specimens in age-groups V and VI (28 percent of those caught in 1951) bore scars or open wounds made by lampreys. Smaller fish were unscarred; hence it is thought that lamprey predation is most severe among larger lake trout 14 or more inches long. It is possible, nevertheless, that small lake trout which have been attacked by lampreys die immediately so they do not come into the nets with wounds as do the larger fish. Hall and Elliott (1954) found also an increase of scarring with increase in length of the fish for the white sucker (*Catostomus commersoni*). They showed that incidence of scarring was consistently greater among suckers more than 10 inches long than among smaller fish and near 100 percent for fish 19 to 20 inches long. Thus the larger fish of the younger age groups and nearly all in the older age groups were being eliminated leaving only small, slow growing individuals.

Wild and hatchery lake trout of the same year classes were subject to the same selectivity by the nets and the same predation by lampreys. The marked lake trout and the wild stock of year classes 1944-46 were comparatively free from attacks by lampreys until they were about 14

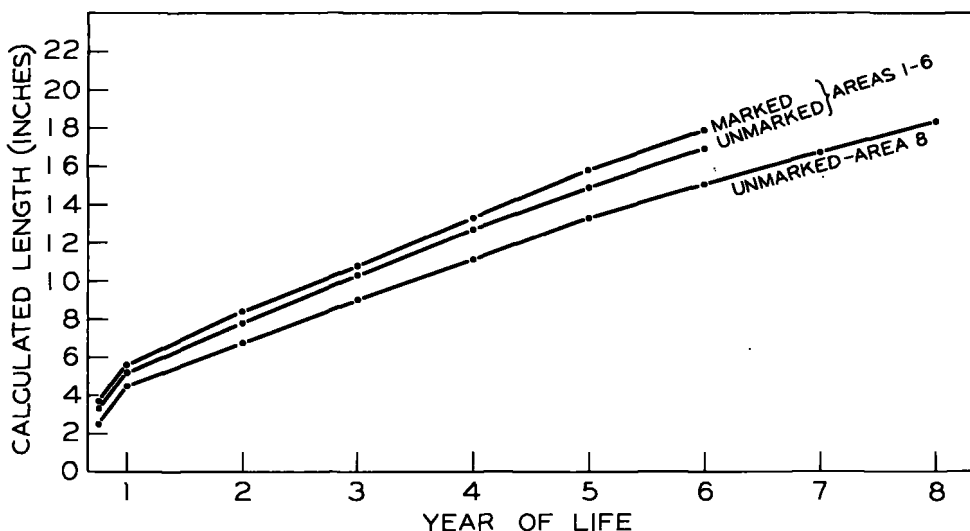


FIGURE 23.—Calculated lengths (sums of mean increments of growth in inches) of marked and unmarked lake trout (year classes 1944-46) caught in 2½-inch-mesh nets.

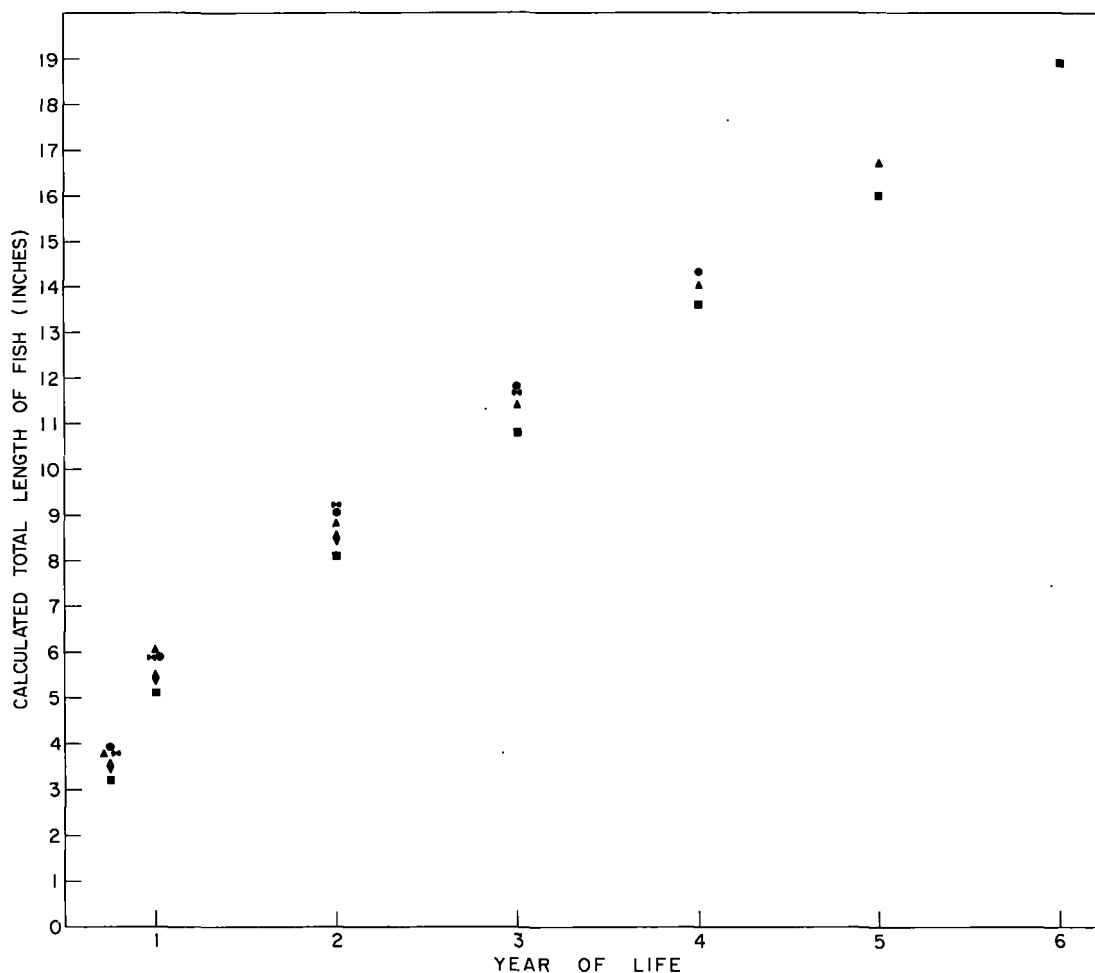


FIGURE 24.—Calculated lengths of age groups of marked lake trout caught in 4½-inch-mesh nets (year classes combined). Symbols: diamonds, age-group II; dumb-bells, age-group III; dots, age-group IV; triangles, age-group V; squares age-group VI.

inches long, during their fourth year of life. Fish from earlier year classes were subject to the selectivity of large-mesh nets for a longer period of time than the marked fish, but to a lower level of lamprey infestation because they were caught before the lampreys had made appreciable inroads into the lake-trout population in their areas of the lake.

The best estimates available of the growth of lake trout in the lake before sea lampreys entered it in large numbers are from data provided by the wild stock from the earlier year classes. In the northern part of the lake, areas 4, 5, and 6, sixteen individuals of year classes 1939–43 were caught by large-mesh nets in 1947. These fish were considerably larger at each year of life than the surviving fish of year classes 1944–46 caught in the same nets from 1947 to 1951. The average

calculated length of the lake trout in the earlier year classes at formation of the first annulus was 6.9 inches and the average annual increase in length to the sixth annulus was 3.0 inches compared with 5.9 inches at the first annulus and an annual gain of 2.8 inches for the marked fish of year classes 1944–46 (tables 22 and 23, fig. 22).

The early year classes of lake trout that lived in southern Lake Michigan were represented by two groups, both captured in 1947 by large-mesh nets. The larger sample of 97 fish (82 of which were of year classes 1939–43) was taken in area 7 off Montague, Michigan (Van Oosten 1950). The other group contained 17 lake trout of the same year classes from the collections of fish with deformed fins caught in area 8 off South Haven, Mich. The average calculated lengths of the two groups differed little from the second to the

TABLE 23.—Calculated lengths (sums of mean increments of growth in inches) of unmarked lake trout caught by 4½-inch-mesh gill nets in 1947 in Lake Michigan

[Year classes 1939-43 combined]

Locality of capture	Number of fish	Calculated lengths at years of age										Average increment of growth to sixth annulus
		0	1	2	3	4	5	6	7	8	9	
Areas 4-6.....	16	4.0	6.9	10.0	12.8	16.1	19.0	21.8	24.2	26.4	28.7	3.0
Area 7: Off Montague, Mich.....	82		5.1	(3.1)	(2.8)	(3.3)	(2.9)	(2.8)				
Area 8: Off South Haven, Mich.....	17	3.6	6.1	8.7	12.1	15.3	18.3	20.9	23.1	24.7		3.1
				(3.0)	(3.4)	(3.2)	(3.0)	(2.6)				
Areas 7 and 8 combined (from 3rd to 8th years)	99			9.0	12.1	15.4	18.7	21.2	23.6	26.3		3.0
				(2.9)	(3.1)	(3.3)	(3.3)	(2.5)				
				8.8	12.1	15.3	18.4	21.0	23.2	25.0		3.0
				(2.7)	(3.3)	(3.2)	(3.1)	(2.6)				

seventh annulus. Differences at the eighth annulus were due to the small number of measurements (6 for area 7 and only 1 for area 8). As explained earlier, the calculated length at the first annulus for lake trout caught in area 7 (as published), was not based on the same criteria as the data on the O-mark and the first annulus treated in this paper. For this reason, the calculated lengths of the fish from areas 7 and 8 were combined only from the second to the eighth annulus. The mean calculated length at the first annulus of the fish from area 8 was 6.1 inches and the average annual increase in length of the combined groups was 3.0 inches (table 23). Comparison cannot be made of these figures with like figures from lake trout of year classes 1944-46 from the southern areas of the lake as none of those fish were caught in large-mesh nets. The calculated lengths for the early year classes, however, were very much larger than those for the fish of year classes 1944-46 caught in small-mesh nets (table 22).

Selective destruction of the more rapidly growing individuals by sea lampreys and by nets of the commercial fishery leads to a decrease of growth rate with increase of age which would not exist within a stock not subject to such selective mortality. It is a natural consequence of continued selective destruction of large fish, that each older age group should be composed of slower-growing fish than the younger age groups.

Because the combined effects of biased sampling and selective destruction of the marked lake trout by lampreys cannot be measured, it must be recognized that the "normal" growth of lake trout in Lake Michigan probably was not determined precisely. However, the use of summations of the mean increments of growth in length to describe general growth tends to lessen the effects of selective mortality and thus to yield curves

more representative of the true rate of growth than otherwise could be obtained from these data.

A third cause for discrepancies in estimates of growth of lake trout in Lake Michigan, not, however, affecting area estimates, is geographic differences in size and growth. Lake trout inhabiting the northern part of the lake were larger at each year of life than those in the southern part of the lake. This difference in size is apparent in comparisons of fish in the same year classes caught in nets of the same mesh size. Examples: the early year classes (1939-43) caught in 4½-inch-mesh nets (table 23, fig. 25), and the later year classes (1944-46) caught in 2½-inch-mesh nets (table 22, fig. 23). For these and other groups of lake trout from the two parts of the lake, the differences appear to stem principally from a slower growth of the southern fish during their first summer to formation of the first annulus. The southern fish of the early year classes caught in the large-mesh nets, at formation of the first annulus, were 0.8 inch shorter than a similar group of the more northern fish, but the average annual increases in length in later years were identical. Those of the more recent year classes caught in 2½-inch-mesh nets, at formation of the first annulus were 0.6 inch shorter and the average annual increases in length were 0.4 inch less than the annual gains of the unmarked northern fish of the same year classes. The consistency of the discrepancies between the calculated lengths of lake trout from southern and northern Lake Michigan indicates that they represent a true geographical difference of growth between the two populations.

GROWTH IN WEIGHT

Weights were available for only 1,118 of the 1,319 marked lake trout, but these were sufficient

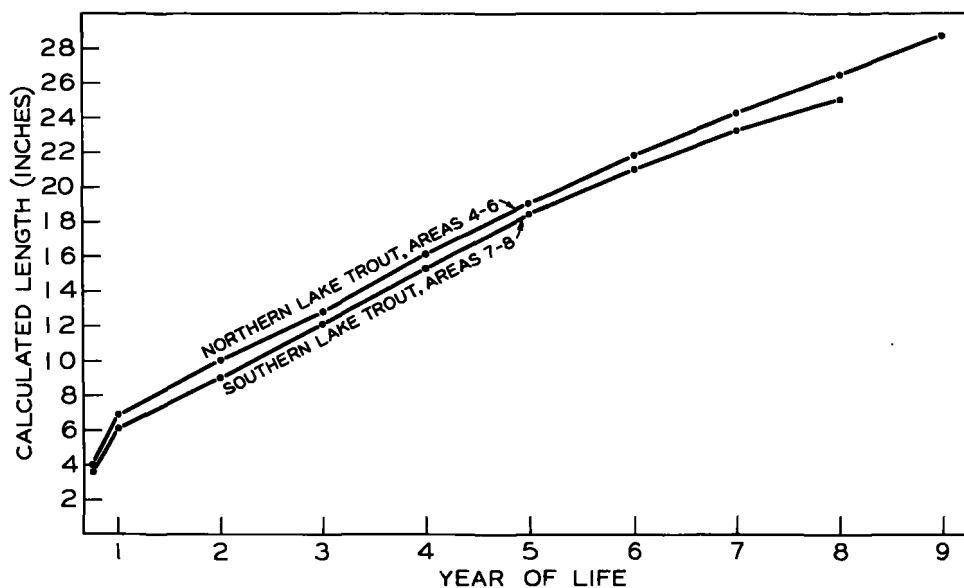


FIGURE 25.—Calculated lengths (sums of mean increments of growth in inches) of unmarked lake trout caught in Lake Michigan by $4\frac{1}{2}$ -inch-mesh nets in 1947. Year classes 1939–43 of the fish from areas 4–6 were combined as were those from areas 7 and 8.

for determination of mean weights at capture of the fish in each age group represented. Further information on growth in weight was obtained by calculating weights corresponding to calculated lengths at the end of the several years of life and at the time the O-mark was formed. These calculated weights were computed by the length-weight equation.

Weights at Capture

The range of weight in all age groups of the marked lake trout was large, as would be expected from fish that differed so greatly in length. Both the average weights and the ranges of weight of the different age groups are presented in table 24. In 9 of the 12 age groups for which data are given in the body of the table, the weight of the heaviest fish was more than 5 times that of the lightest (the advantage was more than 10-fold in age-group IV of the 1945 year class). In the remaining 3 age groups the heaviest trout weighed 2.0 to 4.5 times as much as the lightest.

Despite the great variability in weight, the mean weights of certain age groups of the different year classes were similar. The average weight ranged from 4.3 to 4.4 ounces in age-group II, from 6.6 to 9.7 ounces in age-group III, and from 11.2 to 15.2 ounces in age-group IV. The range of the mean weights was somewhat larger in age-group V (15.2 to 27.4 ounces). Comparable data on

the weights of the fish in age-group VI were not available.

TABLE 24.—Mean weight (ounces), at time of capture, of the year classes of marked lake trout, by age groups

Item	Age group				
	II	III	IV	V	VI
1944 year class:					
Mean weight.....		7.0	15.2	15.2	
Range.....		3.5–32.0	9.1–46.0	10.5–21.2	
Number of fish.....		10	9	11	
1945 year class:					
Mean weight.....	4.4	9.7	11.2	20.5	26.9
Range.....	1.2–8.3	3.9–22.4	4.7–47.8	5.1–48.8	11.5–36.5
Number of fish.....	28	174	523	184	5
1946 year class:					
Mean weight.....	4.3	6.6	14.0	27.4	
Range.....	1.9–8.5	3.7–21.5	6.0–41.0	8.2–50.2	
Number of fish.....	8	38	116	12	
Combined year class:					
Mean weight.....	4.4	9.0	11.8	20.6	26.9
Range.....	1.2–8.5	3.5–32.0	4.7–47.8	5.1–50.2	11.5–36.5
Number of fish.....	36	222	648	207	5

Calculated Weights

The growth in weight of the marked lake trout (as determined by the length-weight equation from the calculated lengths shown in table 20) was slower in the earlier than in the later years of life. Whereas the most rapid growth in length occurred during the first year, growth in weight proceeded slowly through the second year. The weights calculated for the first year of life were typically less than 1 ounce and averaged only 3.0 ounces at the end of the second year. The annual

TABLE 25.—Weights of the marked lake trout at capture and as calculated for the end of each year of life ¹

[Weight in ounces]

Age group	Year planted	Number of specimens		Weight at capture	Calculated weight at end of year of life						
		measured	weighed		0	1	2	3	4	5	6
II	1945	31	28	4.4	0.15	0.57	2.6				
	1946	8	8	4.3	.18	1.10	3.0				
	Mean			4.4	.17	.65	2.6				
III	1944	16	10	7.0	.18	1.16	3.6	8.2			
	1945	190	174	9.7	.23	.85	3.4	7.4			
	1946	49	38	6.6	.20	.85	3.0	5.7			
IV	Mean			9.0	.22	.90	3.4	7.2			
	1944	10	9	15.2	.18	.85	3.2	7.6	13.7		
	1945	555	523	11.2	.22	.94	3.0	6.6	11.7		
V	1946	167	116	14.0	.20	.85	2.8	6.1	12.5		
	Mean			11.8	.20	.90	2.8	6.4	12.0		
	1944	17	11	15.2	.17	.76	2.2	5.0	9.2	14.9	
VI	1945	240	184	20.5	.20	.72	2.6	5.6	10.4	17.9	
	1946	23	12	27.4	.15	.76	2.3	4.7	10.4	19.0	
	Mean			20.6	.20	.72	2.5	5.4	10.2	17.5	
	1945	13	5	26.9	.07	.34	1.2	2.8	5.4	9.5	16.2
Number of specimens					1,319	1,319	1,319	1,280	1,025	293	13
Mean increment of growth in weight					0.21	0.65	2.1	3.4	5.2	7.3	6.7
Weight from summation of increments					.21	.86	3.0	6.4	11.6	18.9	25.6
Mean calculated weight					.21	.86	2.9	6.4	11.3	17.4	16.2
Increments of mean weight					.21	.65	2.0	3.5	4.9	6.1	-1.2

¹ Weights calculated with length-weight formula from calculated lengths shown in table 20.

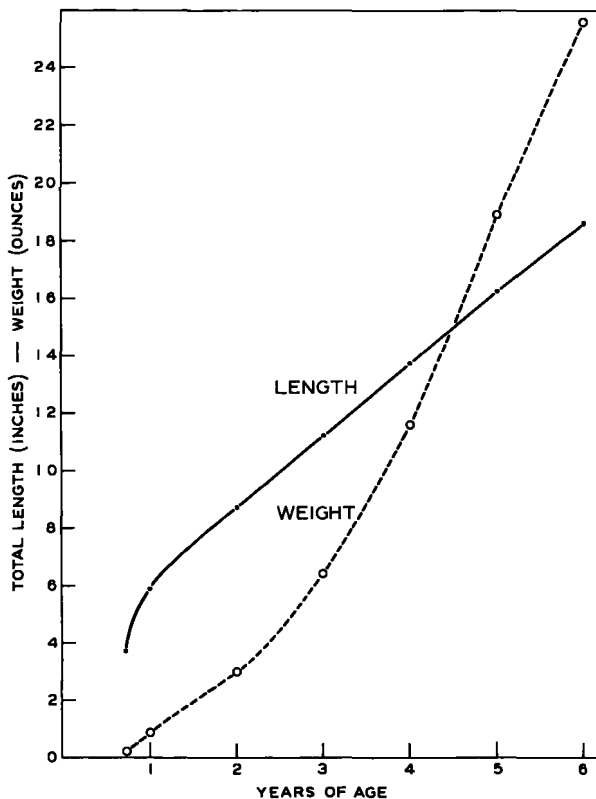


FIGURE 26.—Calculated growth in length and weight of marked lake trout [summation of annual increments of growth].

addition of weight increased sharply from 2.1 ounces in the second year to 3.4, 5.2, 7.3, and 6.7 ounces in succeeding years. The calculated increments of weight of fish in the older age groups (especially age-group VI) would have been larger except for selective mortality of the more rapidly growing lake trout which resulted in reduction of the average length increment (table 25, and fig. 26).

Calculated weights obtained by summation of the mean increments of growth in weight were slightly smaller than weights of the fish at capture for the same reason that the calculated lengths were smaller than the measured lengths. The differences in weight ranged between 0.2 and 2.6 ounces as shown in the following tabulation:

Year of life	2	3	4	5	6
Weight from summation of calculated increments	3.0	6.4	11.6	18.9	25.6
Age group	II	III	IV	V	VI
Weight at capture	4.4	9.0	11.8	20.6	26.9

PROGRESS OF SEASON'S GROWTH

As a first approach to the estimation of the progress of the growth of lake trout during the growing season, tabulations were prepared of the sizes attained by the age groups of the marked fish at capture in each month of the year.

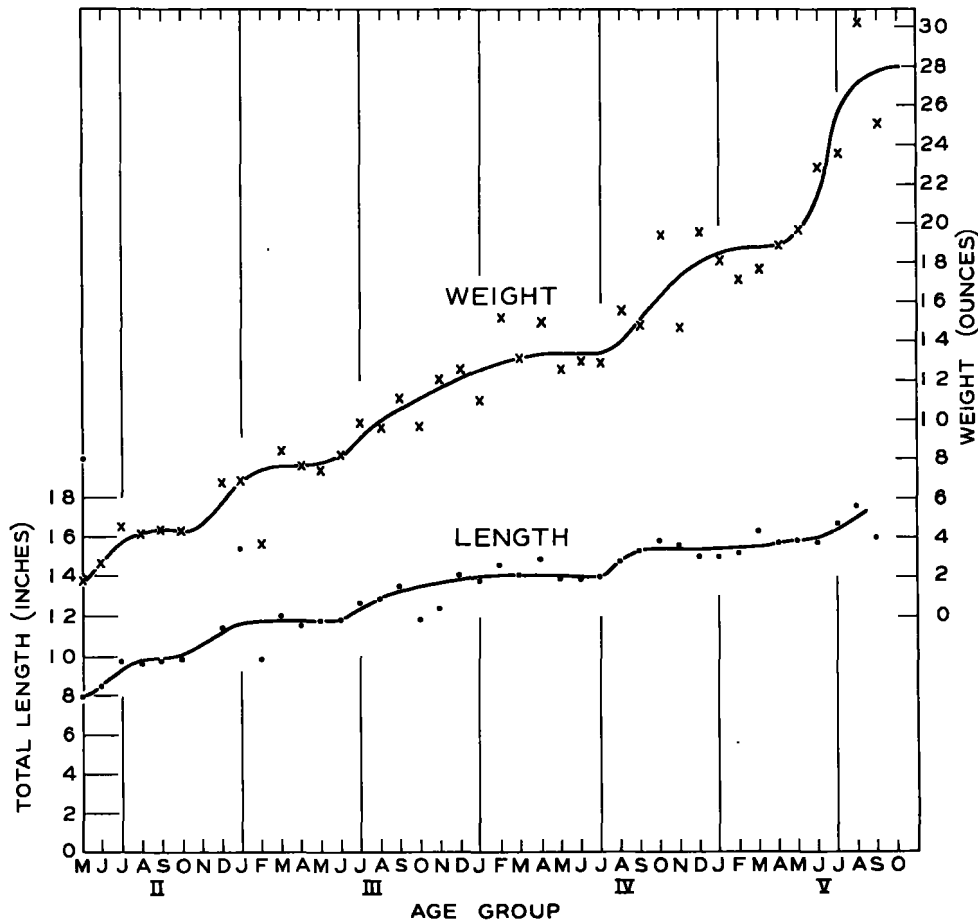


FIGURE 27.—Mean lengths and mean weights of the marked lake trout at time of capture. Year classes 1944–46 combined. [Curves drawn by inspection.]

The average lengths of lake trout of the 1944–46 year classes of the same age group were originally tabulated by semimonthly periods, but as division of the data into shorter time intervals did not provide additional information, the averages of table 26 (see also fig. 27) were based on monthly groupings. Although the month-to-month changes in the average lengths of the age groups were decidedly irregular, the figures do give the general impression that much of the increase in length took place in the late summer and fall. In other words, rapid growth seems to have started about the end of June and to have continued at least through October, possibly longer. The records of average weight of the age groups at capture support a similar interpretation (table 27, fig. 27).

TABLE 26.—Average lengths (inches) of marked lake trout at time of capture

[Data for 1944, 1945, and 1946 year classes combined.¹ Number of specimens in parentheses]

Month	Age group			
	II	III	IV	V
January.....		15.4 (1)	13.8 (27)	15.0 (24)
February.....		9.9 (1)	14.6 (13)	15.2 (6)
March.....		12.0 (2)	14.1 (17)	16.3 (5)
April.....		11.6 (8)	14.9 (80)	15.7 (24)
May.....	8.0 (1)	11.8 (22)	13.9 (156)	15.8 (81)
June.....	8.5 (3)	11.9 (36)	13.9 (120)	15.8 (60)
July.....	9.8 (4)	12.7 (30)	14.0 (183)	16.7 (34)
August.....	9.7 (5)	12.9 (64)	14.8 (109)	17.6 (33)
September.....	9.8 (12)	13.5 (72)	15.3 (13)	16.0 (12)
October.....	9.9 (7)	11.9 (7)	15.9 (6)	
November.....		12.4 (8)	15.6 (4)	
December.....	11.5 (7)	14.1 (4)	15.0 (4)	13.1 (1)
Mean length.....	10.0 (39)	12.8 (255)	14.3 (732)	15.8 (280)

¹ Lengths of the 13 fish in age-group VI omitted because the data are too scattered to be of value in this table.

TABLE 27.—Average weight (ounces) of marked lake trout at time of capture

[Data for 1944, 1945, and 1946 year classes combined.¹ Number of specimens in parentheses]

Month	Age group			
	II	III	IV	V
January		6.9 (1)	11.0 (19)	18.1 (18)
February		3.7 (1)	15.2 (13)	17.1 (4)
March		8.4 (2)	13.1 (16)	17.6 (4)
April		7.7 (1)	15.0 (65)	18.9 (19)
May	1.9 (1)	7.4 (20)	12.7 (155)	19.7 (65)
June	2.6 (3)	8.2 (28)	13.0 (80)	22.8 (38)
July	4.5 (4)	9.9 (25)	12.9 (172)	23.6 (28)
August	4.1 (3)	9.6 (57)	15.5 (102)	30.2 (24)
September	4.3 (12)	11.3 (69)	14.8 (12)	25.0 (7)
October	4.2 (6)	9.6 (5)	19.4 (6)	
November		11.9 (9)	14.7 (4)	
December	6.8 (7)	12.6 (4)	19.6 (4)	
Mean weight	4.6 (36)	9.9 (222)	13.6 (648)	21.9 (207)

¹ Weights of the 13 fish in age-group VI omitted because only 5 fish were weighed and the data are too scattered to be of value in this table.

More dependable data on the progress of the season's growth may be obtained by computation of growth from scale measurements. Examples of the distribution of these increments are contained in the records for the 555 lake trout of age-group IV from the 1945 year class, the largest year class in the collections. Their increments of growth in length were computed by semimonthly periods (table 28).

The amount of growth attained by individual lake trout in any stated time varied widely. By the end of April, the range in the amount of seasonal increment of growth in length was from nil to 1.4 inches. This range continued nearly constant and the mean advanced only slightly (0.14 to 0.40 inch) until the middle of July.²⁵ In the latter part of July the range in lengths of the increments began to broaden and by the end of August the spread was 2.8 inches. In the fore part of August, some lake trout were still just beginning to grow whereas others had been growing since the middle of March or possibly even longer. It was largely because of this wide spread in the time of the onset of growth that the average increment was still only 0.22 inch in the first half of June. Subsequent more rapid increase carried the average to 1.7 inches in the first half of September. Returns of lake trout were so sparse during the remainder of the year that dependable estimates of growth cannot be

²⁵ New growth cannot be recognized on the scales until the first circulus has been formed, a circumstance which probably accounts for the small proportion, at any time, of fish having as little as 0.2 inch calculated growth. The smallest calculated length increment is more often 0.4 inch. Hence the fish usually had grown nearly $\frac{1}{2}$ inch by the time the annulus could be read with confidence.

made from them. It is especially difficult to form a judgment as to the time the season's growth ends. It appears from the data in table 29 that the growth of the fish in age-group IV had not been completed by the end of December, when the average increment (4 fish) was 1.95 inches or 0.64 inch below the figure of 2.59 inches computed for the full season from age-group V of the same year class. (The fish in age-group V that had not yet completed the fifth annulus gave nearly the same estimate of growth in the fourth year, 2.60 inches, as did those on whose scales the fifth annulus was visible, 2.58 inches.)

Records of the percentage of the season's growth completed by age groups of the 1945 year class up to various dates of capture, despite gaps in the data and the small numbers of fish on which certain percentages were based, give evidence of annual differences in the progress of growth and of irregular growth in some years (table 29). These points are well illustrated by the curves in figure 28 which were fitted by inspection to the empirical data.

The data were scanty for the lake trout of the 1945 year class in age-group II. The single trout captured in the first half of June had made no growth. Percentages of growth completed by fish caught later in the season rose quickly to 51 in early August but fluctuated erratically thereafter. Seven fish recovered in December had grown more (percentage, 115) than the "expected" increment for the full season calculated from measurements of the fish in age-group III.

The 4 lake trout of age-group III caught in late April and early May 1948 exhibited no new growth, but those captured during the last half of May had completed 7 percent of the expected growth for the season. The percentage dropped in early June, but thereafter it increased steadily (except in the first half of September) to 94 percent in early October. The single trout caught in December had gained only 79 percent of the expected total increase.

Age-group IV, captured in 1949, seems to have started growing early in the season. Possibly the single lake trout with new growth in January could be dismissed as aberrant, but all semimonthly collections from the latter half of March onward contained some fish that had begun to grow. The advantage of this early start was later lost, however, for the percentage of new growth remained

TABLE 28.—Increment of growth in length (inches) of marked lake trout, age-group IV from the 1945 year class, at semimonthly intervals, carried on through the fifth growing season

Increment of length	January		February		March		April		May		June		July		August		September		October		November		December		Growth increment for full season ¹		
	1-15	16-31	1-15	16-28	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30	1-15	16-31	Without new growth	With new growth	
0.0	4	5	2	9		14	20	33	66	25	23	21	38	6	1												
0.2											2	3	7	2													
0.4		1				1		2	4	2	6	7	8	4	1												
0.6						1	1	2	3	2	2	3	11	10	2												
0.8								2	3	2	1	7	13	14	1												
1.0								2	2		2	8	14	14	1												
1.2											2	5	8	17	3				1			1			1	2	
1.4								1				2	2	5	2									1	2	3	
1.6									1					4	4		1	3	1			1		1	3	5	
1.8														2	1	2						1		1	6	8	
2.0														1							1			9	9	9	
2.2																								10	13	13	
2.4																				1				16	14	14	
2.6																								11	17	17	
2.8																							1	17	10	10	
3.0																	1							17	9	9	
3.2																1								10	5	5	
3.4																								6	5	5	
3.6																								3	1	1	
3.8																								5	5	5	
4.0																								1			
4.2																										1	
4.4																										1	
4.6																										1	
4.8																									1		
Number of fish...	4	6	2	9	0	16	21	40	79	31	36	47	100	57	71	17	4	1	4	2	1	3	4	134	106		
Average.....	0.0	0.06	0.0	0.0		0.06	0.03	0.14	0.13	0.13	0.22	0.35	0.40	0.75	1.05	1.39	1.73	1.65	1.57	2.09	2.16	1.62	1.95	2.60	2.58		

¹ Computed from measurements of scales of age-group V lake trout of the 1945 year class. Data are given separately for fish that had and had not completed the fifth annulus as a demonstration that the preceding season's growth was completed between December and the time of capture of members of the same year class caught the next calendar year.

TABLE 29.—Average percentage of season's growth completed at various dates during the season by age groups of the marked lake trout from the 1945 year class

[The bases for the percentages are the increments of growth for full seasons computed from measurements of the scales of fish of the next higher age groups of the same year class]

Date	Age-group II		Age-group III		Age-group IV		Age-group V		Unweighted average ¹ percentage
	Number of fish	Average percentage	Number of fish	Average percentage	Number of fish	Average percentage	Number of fish	Average percentage	
Jan. 1-15					4	0.0	11	0.0	0.0
16-31					6	2.3	11	.0	1.2
Feb. 1-15					2	.0	3	.0	.0
16-28					9	.0			
Mar. 1-15									
16-31					16	2.3			
Apr. 1-15					21	1.2	1	.0	.6
16-30					40	5.4	18	9.4	4.9
May 1-15			1	0.0	79	5.0	48	8.5	4.5
16-31			3	.0	31	5.0	22	13.4	8.5
June 1-15	1	0.0	17	7.2	36	8.5	32	6.7	4.8
16-30	1	13.3	14	19.1	47	13.5	27	8.0	13.5
July 1-15	2	17.2	9	25.0	100	15.4	14	30.8	22.1
16-31			12	43.2	57	29.0	11	54.9	42.4
Aug. 1-15	4	50.8	21	53.4	71	40.6	24	65.2	52.5
16-31	1	41.8	25	65.7	17	53.7	5	88.9	62.5
Sept. 1-15	1	16.4	42	64.8	4	66.8	8	70.5	54.6
16-30	7	50.4	29	72.9	1	63.7	4	92.4	69.8
Oct. 1-15	7	54.7	2	94.1	4	60.6			69.8
16-31					2	80.7			
Nov. 1-15					1	83.4			
16-30					3	62.6			
Dec. 1-15									
16-31	7	114.9	1	79.3	4	75.3	1	58.0	81.9
Completed growth (inches)		2.56		2.36		2.59		2.24	
Number of fish	31		190		555		240	(?)	

¹ In order that age-group IV, which was represented in nearly all semimonthly periods, would not exert undue influence on the trend only those periods which were represented by one or more other age groups are included.

² Based on the 13 fish in age-group VI.

at 5 from mid-May through June. Beginning with the first half of July, the percentages were consistently smaller than those for age-group V and, with one exception (early September), were also below the percentages for age-group III.

The erratic variation of the percentage of completed growth for age-group IV during September-December can be attributed partially to the small numbers of fish in the samples, but the generally low level (61 to 83 percent; 75 percent for 4 lake trout caught in late December) is further evidence that the seasonal growth was not completed at the end of the calendar year. As the average increment of growth of the 4 lake trout caught the last part of December was only 2.0 inches, the actual amount of growth between December 31 (ages change on January 1) and the completed growth of 2.6 inches at formation of the fifth annulus was 0.6 inch. It was pointed out earlier that the average estimate of the growth of age-group IV for the entire season, calculated from measurements of the scales of lake trout in age-group V taken in 1950, was the same for fish without the fifth annulus as it was for those that had that annulus visible. However, the average increment for 11 lake trout caught the first half

of January, which did not have new growth on their scales, was only 2.3 inches (88.5 percent of the total increment), whereas the average increment for an equal number of lake trout caught the last part of the month was 2.59 inches (100 percent of total increment). Increments for 4 fish taken between the first of February and the 15th of April were low (2.13 inches), but the average increment for 12 fish taken the first half of May (2.63 inches) showed a slight rise over that for January. These few fish, caught January to May, do not furnish definitely reliable information on the end of the growing season, however they do indicate that in certain years lake trout may continue to grow through the winter months.

The 25 lake trout of age group V taken in January and February and a single fish caught in early April had not started to grow. The increment of new growth on the scales of lake trout captured in the last half of April amounted to 9 percent of the expected total increment, but this percentage showed no clear tendency to increase during May and June. A sharp upturn, beginning in July, however, carried the percentage to 92 in late September (with a single exception to the trend in the first half of the month). The single

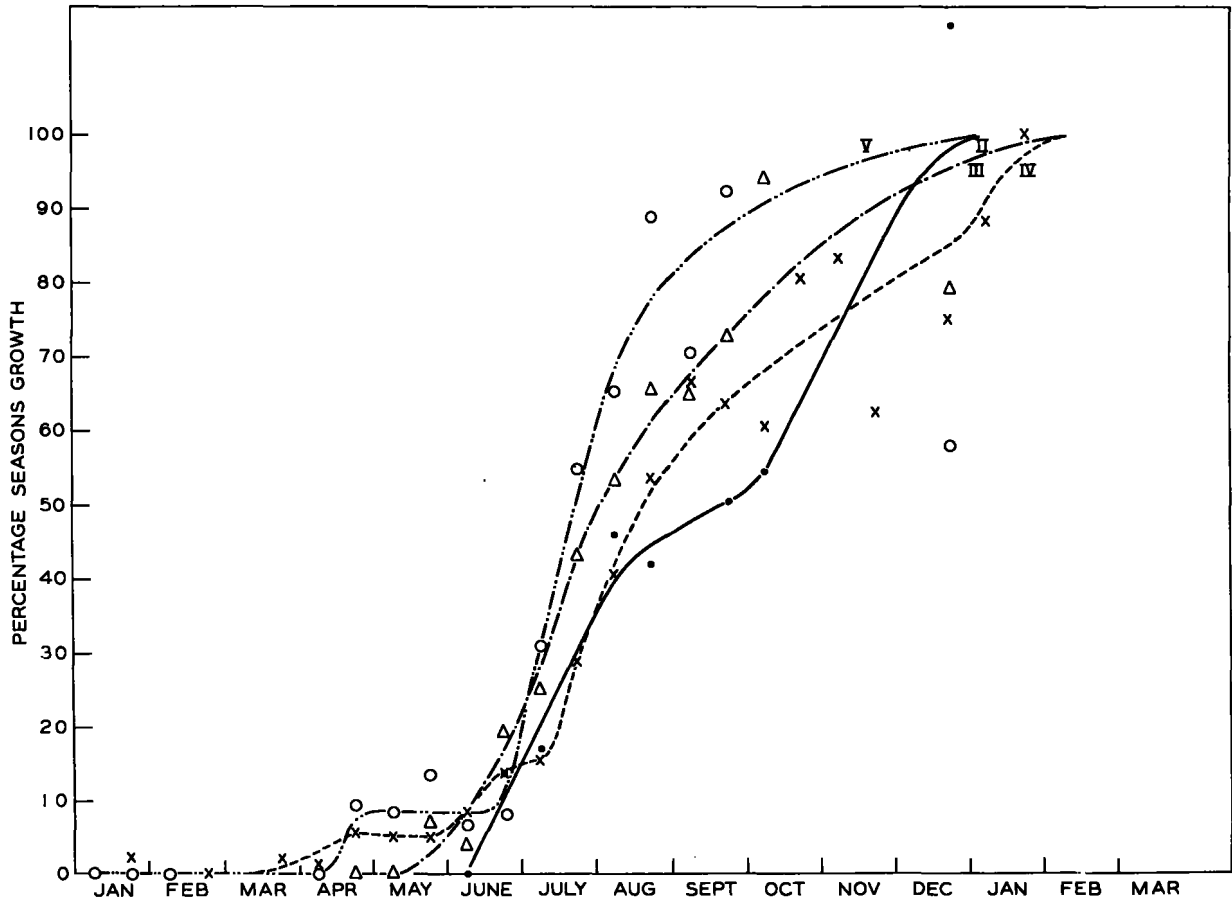


FIGURE 28.—Percentage of season's growth of the marked lake trout from 1945 year class (the bases for the percentages are the increments of the full season computed from measurements of the scales of the next higher age group of the same year class).

lake trout of age-group V caught in December, however, had completed only 58 percent of the expected total growth.

A start of growth followed by a stoppage or near-stoppage as demonstrated for age-group IV in the last half of April through May, and for age-group V in May and June, might be expected to produce irregularities in the scale structure. Nevertheless, examination of the scales of lake trout of age-groups IV and V captured late in the growing season revealed no checks or marks that could be attributed to this stoppage.

Some of the irregularities in the data of table 29 can be attributed to the inadequacy of the samples, but the majority give evidence that the course of the season's growth varies considerably from one calendar year to another. (There is no evidence of a progressive change with age). This year-to-year variation and the uncertainty as to the time

growth ends (data were conflicting even among the best represented age groups) prohibit a general description of seasonal growth of the marked lake trout. Growth may start as early as March or as late as June. Once started, growth may follow a regular course; but in some years it may stop, completely or nearly so, for a period of several weeks. The end of the season as well as the start probably varies from year to year. In some seasons growth may continue into the next calendar year. Because of the variation in the start and finish of the growing season, growth of lake trout in Lake Michigan is likely to occur in at least 9 or 10 months of the year, possibly in even more. The most rapid growth, nevertheless, appears normally to take place in July and August. The percentages at the right of table 29 indicate that nearly half of the total season's growth occurs in these months. The same set of figures shows

that, in general, the lake trout gained about 30 percent of their growth sometime after the middle of September.

The growing season for lake trout in Canadian waters is shorter. Kennedy (1954) found that the lake trout in Great Slave Lake "grow only between late May and the middle of September, with no growth at any other time." Of the seasonal growth of the lake trout in South Bay, Lake Huron, Fry (1953) stated, "The lake trout . . . add about 1 inch to their total growth increment for the year by mid-September. The total for the major year class represented in 1949 (the 1944 year class) . . . was estimated at 1.8 inches. This increment would indicate the rapid growth observed from June to September probably continued at least until mid-October."

SUMMARY

From 1 to 1½ million hatchery-reared lake trout (average length 3.2 inches) were liberated into northeastern Lake Michigan in September of each of the years 1944-46. About 10 percent of these fingerlings were marked by the removal of fins. In the years subsequent to the plantings, 1947-52, fishermen captured 1,747 lake trout with abnormal fins of which only 1,507 were adequately documented. Of the latter group, 102 caught off South Haven, Mich., differed so much from those caught in the northern part of the lake that all, or nearly all, were considered to be unmarked wild lake trout with abnormal fins; hence, they were excluded from the main sample. The scales of the remaining 1,405 fish were studied to determine the validity of age readings from scales and the rate of growth of lake trout in Lake Michigan.

Lake trout scales are small and have concentric circuli. They develop first as platelets adjacent to the anterior end of the lateral line when the fish are about 2 inches long and rapidly cover all the body except the head. Probably young lake trout in Lake Michigan are fully scaled before the end of their first summer.

Even though the scales were rather difficult to interpret, simple criteria for recognition of the annulus were determined. The annulus is generally indicated by wider spacing between circuli outside closely spaced circuli, but this arrangement, usually most clearly seen in the lateral fields, is seldom definite enough to be followed

entirely around the scale. Other indications of an annulus are: a V-shaped pattern in the circuli of the lateral fields, a ridge across the posterior field, also such irregularities as broken or crooked circuli and fine accessory lines. An annulus is usually located by a combination of these criteria.

The annulus was formed on the scales of some lake trout as early as the middle of March, of the majority during June and July, and of a few as late as the middle of August.

In addition to the expected number of annuli for the marked fish, a central check was found within the first annulus which has been designated the "O-mark." The scales of the unmarked, wild-stock lake trout from Lake Michigan examined during this study also carried the central check (O-mark).

Two readings were made of the markings on the scales. The ages read agreed on 96.8 percent of the specimens.

The number of annuli read from the scales agreed with the age of the fish indicated by the deformed fin for 93.9 percent of the lake trout in the sample of presumably marked fish. Most of the disagreements were of 1 year but some were of 2 or more years.

The principal difficulty in the way of determining the accuracy of age readings from the scales of the lake trout from northern Lake Michigan resulted from the presence in the collections of a small percentage of unmarked fish. The exact number of these fish could not be counted but evidence from several lines of investigation led to the conclusion that nearly all the 86 fish, for which the age read from the scales disagreed with that indicated by the deformed fin, were unmarked lake trout. The average lengths of the age groups indicated by the deformed fins of the 86 "unmarked" fish were very different from those of the age groups of the 1,319 "marked" fish (those with agreement between age indicated by the fin and that read from the scales); furthermore, the average length of the 86 fish decreased with increase of age. On the other hand, at ages read from the scales, the growth curve for these 86 fish was similar to that of the 1,319 "bona fide" recoveries. It was concluded, therefore, that the age read from the scales rather than the age indicated by the deformed fin was correct for most fish.

The evidence strongly indicates a high depend-

ability of age readings from lake trout scales. The reader does, nevertheless, need considerable experience with scales from fish of known age to become proficient in recognition of the O-mark and annuli.

The estimate obtained of the relation between weight in ounces and total length of the fish is expressed by the formula:

$$\log W = -2.4698 + 3.1125 \log L$$

The range of total lengths at capture of fish within an age group of marked lake trout was wide. The average length for an age group of one year class, however, was close to those for the same age group of the other two year classes. Lake- and pond-reared fish had attained about the same lengths at 2, 3, and 4 years of age.

The calculated lengths of the fish at various ages prior to capture were computed by direct proportion from the diameters of the annuli. The calculations from 2 scales were averaged. The calculated lengths (sums of the mean increments of growth in length) being lengths of the fish at the end of growing seasons were, as would be expected, somewhat smaller than the mean lengths of the fish of the same age groups at time of capture which was, in most cases, after the beginning of a new growing season.

The lengths calculated from the fish in age-groups III-VI exhibited Lee's phenomenon of gradually decreasing values with increasing age. Most of the discrepancies are explained by selective destruction of the most rapidly growing fish by nets and sea lampreys.

Scars and open wounds made by lampreys were found more often on large than on small lake trout. The destruction of the large, fast-growing fish could account for the small size of the fish remaining in the older age groups which were caught after the population had been materially reduced.

Gill nets of the two sizes of mesh most commonly used in Lake Michigan caught lake trout of greatly different sizes. During the years marked lake trout were caught, the fishermen gradually shifted from use of large- to small-mesh nets. The large-mesh nets caught larger fish than the small-mesh nets and the difference became greater as the fish grew older. It is questionable, therefore, whether a general average gives a true estimate of the growth of these lake trout. The fish caught in the small-mesh nets may give the better esti-

mate of the growth of the younger age groups, whereas those caught in the large-mesh nets may be more representative of the older age groups. Lee's phenomenon, prominent in measurements of the first group, is almost lacking from the measurements of the fish in the latter group.

Summing the increments of growth in length minimizes the effects of biased sampling and selective destruction of the fish.

The weights of the marked lake trout were similar to the lengths in that the weights of individual fish at capture varied greatly within age groups and the mean weights for the age groups at capture were slightly larger than the calculated weights. Although the most rapid gain in length occurred during the first year of life, the gain in weight was least in this year and much greater in later years.

Seasonal growth of the marked lake trout reflected the long period of annulus formation. The growing season was extended and variable. Growth for the three year classes indicated a long period of slow growth in the spring, rapid growth from the end of June through October, and slower growth again on into December. Monthly distribution of the increments of growth in length of the 1945 year class suggested that lake trout may occasionally have a somewhat longer season of growth. The average percentage of growth completed at semimonthly intervals for the separate age groups showed that the growing season varied considerably from one year to the next. Not only the time of the beginning but also of the end of the growing season may vary several weeks, even months. Because of this lack of uniformity in the time of start and finish, growth of lake trout in Lake Michigan may be expected to take place in 9 or 10 months of the year.

As large- and small-mesh nets caught fish of different sizes and the destructiveness of the sea lampreys increased during the years the marked lake trout were in the lake, it was necessary for estimation of the growth in length, to select fish of the same year classes caught in the same calendar years by nets with mesh of the same size. The marked fish (year classes 1944-46) caught in large-mesh nets were slightly larger than the unmarked fish also caught in the northern part of the lake, which suggests that the marked lake trout gained some small advantage from early care in the hatchery. Lake trout caught in large-mesh

nets in northern and southern areas of the lake could not be compared because no fish of year classes 1944-46 were caught in large-mesh nets. Those caught in small-mesh nets were considerably smaller than both marked and unmarked lake trout caught in these nets in northern waters.

Lake trout that had lived in Lake Michigan before the sea lampreys became numerous were larger and had grown at a faster rate than the marked fish. Two samples of lake trout of these early year classes from the southern part of the lake, caught in 1947 by large-mesh nets were so similar they are believed to have been drawn from the same population, but one that differed from the northern population by an important characteristic. Growth during the first summer to formation of the O-mark was much less than for fish in the more northern waters. Subsequent annual growth in length was the same in both areas.

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