LIFE HISTORY OF THE LAKE HERRING (*Leucichthys artedi* Le Sueur) OF LAKE HURON AS REVEALED BY ITS SCALES, WITH A CRITIQUE OF THE SCALE METHOD

By JOHN VAN OOSTEN, Ph.D.

DEPARTMENT OF COMMERCE

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Associate Aquatic Biologist, U. S. Bureau of Fisheries

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ERRATA

Figure 16, p. 353. - In the legend the symbol for the year 1921 should be a continuous line (_____) instead of a broken line (- - -).

Figure 33. - In the legend the word "female" should occur after the length and before the age.

Figure 37, p. 356. - In the legend the symbol for the year 1921 should be a continuous line (_____) instead of a broken line (- - -).

Figure 38, p. 360. - In the legend the symbol to indicate the males should be a continuous line (_____) instead of a broken line (- - -).

Table 39, p. 368. - The footnote references in the body of the table that are indicated by the figure 2 refer to footnote b at the end of the table.

Figure 39, p. 374. - In both sections A and B of the legend the first symbol should be a continuous line (_____) instead of a broken line (- - -).

Figure 40, p. 375. - The first symbol in the legend should be a continuous line (_____) instead of a broken line (- - -).

Figure 41, p. 376. - In the legend the symbol indicating males alone should be a continuous line (_____) instead of a broken line (- - -).

Page 416, first line of last paragraph: "coregonoid" should read "coregonid."

LIFE HISTORY OF THE LAKE HERRING (*LEUCICHTHYS ARTEDI* LE SUEUR) OF LAKE HURON AS REVEALED BY ITS SCALES, WITH A CRITIQUE OF THE SCALE METHOD

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PART II

INTRODUCTION

The most extensive inland fisheries of this country, those of the Great Lakes, had an output in 1922 of more than 102,000,000 pounds, and the gross return to the fishermen was some $6,500,000.[1] Statistics of the Great Lakes fisheries have been collected for United States waters nine times, at intervals varying from three to nine years. In 1893, 1899, and 1903 the whitefish and herring statistics were variously combined in the several lakes with those of other species of fish. The statistics collected in the other years show that on the average 49 per cent of the product has consisted of species of whitefishes and herrings, fishes constituting the family Coregonidæ. Attention has been called often to the depletion of the coregonid fisheries. (See P. Reighard, 1910, and citations for the whitefish.) As the result of an exhaustive study of the history of the coregonid fisheries of the Great Lakes recently completed for the United States Bureau of Fisheries, Dr. Walter Koelz (1926) concludes that, on the whole, these species are diminishing in varying degrees in all the Great Lakes.

Proper measures of conservation or rehabilitation can be formulated only after thorough study of all phases of the biology of the individual species and of the effect of the fishing industry on them. Doctor Koelz has laid the foundation by describing the species and by collecting data on their occurrence and life history and on the fisheries. The present study aims to contribute by other methods to our further knowledge of the biology of the coregonids.

Many investigators in many countries have found it possible to determine the age and rate of growth of fishes by a statistical study of the structure of the scales. The same characters often have permitted the discrimination of local races not otherwise distinguishable. The method is referred to currently as the scale method. The results, embodied in a voluminous literature, have been used in formulating fisheries regulations. The method has been used for determining the age of coregonids by Seligo (1908), Heide (1912), Järvi (1920, 1924), Clemens (1922), Couch (1922), Van Oosten (1923), Prawdin (1925), and Riakhovsky (1925), and divergent views have developed as to its validity. Before applying the method extensively to the coregonids of the Great Lakes, therefore, it has seemed best to test its basic assumptions and its applicability to a coregonid species.

THE PROBLEM

This paper, based on the structure of the scales and on the weights and measurements of a single coregonid species, attempts (1) to determine whether the structural characters of these scales are so clearly recognizable as to permit their use by the scale method; (2) to determine from the same material, if usable, how far the fundamental assumptions underlying the method are warranted (this involves a critical study of

[1] For detailed statistics see Sette (1925 and 1928) and U. S. Tariff Commission, Tariff Information Series No. 36, 1927. For statistics of the Canadian waters see the annual reports of the game and fisheries department of Ontario, Canada. The manuscript for this paper was submitted to the bureau in June, 1927, and has not been revised to include data and reviews of publications that have appeared since January, 1927.

the technique of the method and of the errors involved in its use); and (3) to apply the method, if found valid, in a study of the life history of the species.

Koelz (1929) recognizes 11 species of coregonids in the Great Lakes Basin (10 in the Great Lakes). Preliminary examination of the scales of these species shows them to be so much alike that a method found valid for one species may be applied with confidence to the others. The form selected for this study is the lake herring (*Leucichthys artedi* Le Sueur) of Lake Huron, known also as blueback. (Fig. 15.) Its abundance and cheapness and the accessibility of the extensive Lake Huron fisheries determined the choice. Data on other coregonids of the Great Lakes have been accumulated and will be used in later studies.

MATERIAL

All the lake-herring specimens collected by Doctor Koelz in 1917 and 1919 have been at my disposal, and the scales of all have been studied. In order to have larger series than were needed by Doctor Koelz for systematic purposes, I collected additional material in 1921, 1922, 1923, and 1924 at Bay City, Mich. (see fig. 1), and in 1922 at Oscoda near the mouth of the Au Sable River. Bay City ranks first in the herring industry of Lake Huron, and I believed that with its protected Saginaw Bay it would be more likely to furnish homogeneous material than the more open ports on the lake proper. The Bay City material collected in 1921, 1922, and 1923 was taken by pound nets set at Tobico, about 3 miles west of the mouth of the Saginaw River. The 1924 material was taken from pound nets set on various sand bars (Tobico, Nayanquing, Au Gres, and Gravelly Point) in Saginaw Bay.

The ports at which collections were made, with the dates and numbers of specimens, are given in Table 1. Of the 3,724 lake herring examined, 321 were taken by Doctor Koelz at various ports and 3,403 by me in the region of Bay City and Oscoda.

TABLE 1.—*Ports on Lake Huron at which herring were collected and their scales examined*

Locality	Date	Number taken	Locality	Date	Number taken
Harbor Beach	Dec. 9, 1917	11	Alpena	Sept. 12, 1917	1
Bay City	Oct. 25, 1917	17	Do	Sept. 14, 1917	5
Do	Oct. 26, 27, 1921	292	Do	Sept. 17, 1917	5
Bay City (Tobico)	Oct. 29, 1921	267	Do	Sept. 22, 1917	2
Bay City	Nov. 3, 1921	81	Do	Sept. 24, 1917	4
Do	Nov. 4, 1921	32	Do	Sept. 26, 1917	6
Bay City (Tobico)	Nov. 1, 1922	501	Rogers City	Nov. 15, 1919	19
Do	Nov. 12, 1923	519	Cheboygan	Oct. 14, 1917	2
Do	Nov. 23, 1924	109	St. Ignace	Sept. 29, 1917	7
Do	Nov. 25, 1924	197	Duck Islands	July 17, 1917	70
Do	Nov. 27, 28, 1924	94	Lake Mindemoya	Oct. 22, 1919	11
Bay City (Nayanquing)	Nov. 22, 1924	28	Gore Bay	Nov. 12, 1917	12
Do	Nov. 24, 1924	146	Kagawong	Nov. 10, 1917	2
Do	Nov. 27, 1924	111	Do	do	3
Do	Nov. 28, 1924	3	Tobermory	Oct. 16, 1919	1
Bay City (Au Gres)	Nov. 21, 1924	119	Wiarton	Oct. 2, 1919	3
Bay City (Gravelly Point)	Nov. 30, 1924	367	Do	Nov. 5, 1917	14
Do	Dec. 4, 1924	175	Do	July 29, 1919	6
East Tawas	Oct. 22, 1917	25	Killarney	Dec. 3, 1919	14
Oscoda	Nov 2, 1922	362	Blind River	Oct. 12, 1919	41
Alpena	Aug. 13, 1917	11		Nov. 8, 1917	6
Do	Sept. 5, 1917	1	Total		3, 724
Do	Sept. 8, 1917	9			
Do	Sept. 10, 1917	13			

ACKNOWLEDGMENTS

This study was carried on in the zoological laboratory of the University of Michigan. I am indebted to the authorities of the university for the use of rooms and equipment and to Prof. Jacob Reighard, until recently director of the zoological laboratory, for critical supervision of my work.

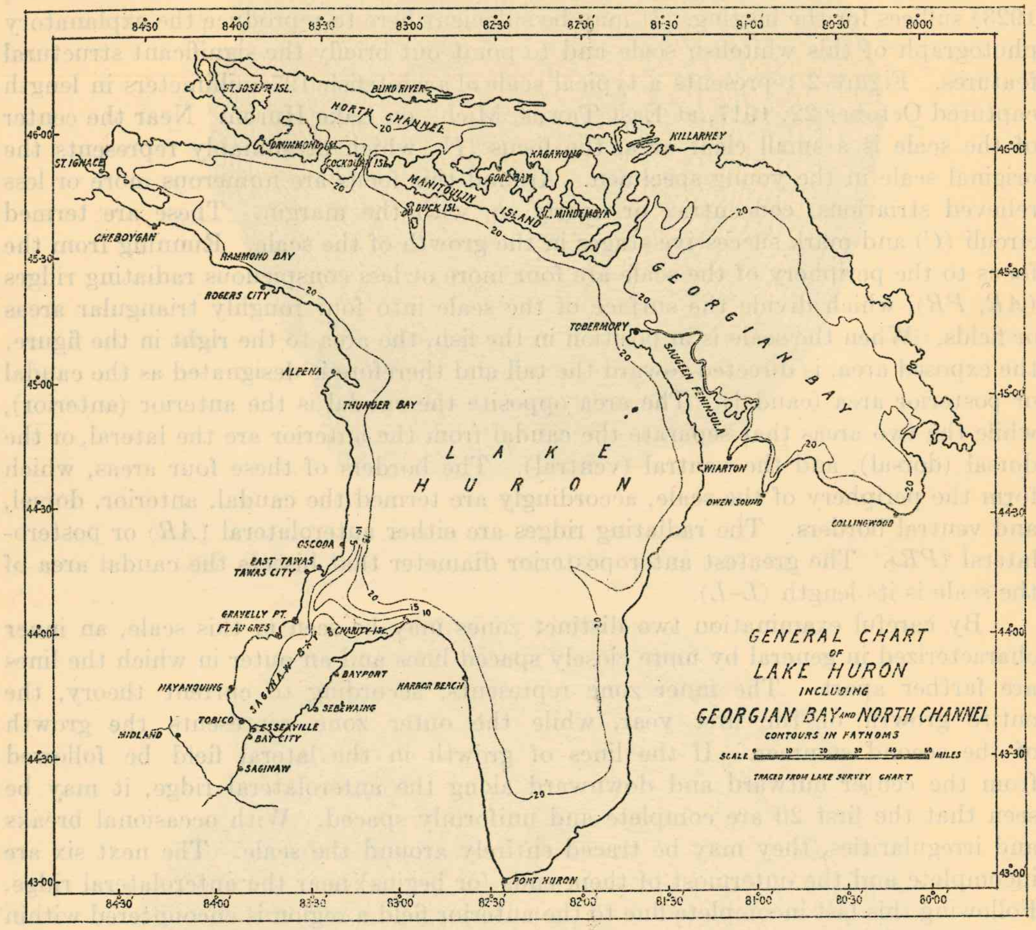

FIG. 1.—Lake Huron

I am indebted, also, to Dr. Walter Koelz, whose material, field, and laboratory data on the coregonids have always been at my disposal; to Dr. Charles Townsend and Miss Ida Mellen, of the New York Aquarium, for valuable whitefish material and for cooperation in experimental work; to Prof. John C. Merriam, of the Carnegie Institution, for encouragement and a donation toward the furtherance of the research; and to Messrs. W. P. Kavanaugh, Norman Macaulay (manager of the Booth Fisheries Co.), R. McCoy, and B. Trombley for the facilities placed at my disposal while working in their fish houses at Bay City, Mich.

GENERAL CONSIDERATIONS

DESCRIPTION OF COREGONID SCALES

TYPICAL SCALES

In their general features the scales of coregonid species are so much alike that the detailed description of a typical whitefish scale published elsewhere (Van Oosten, 1923) suffices for the herring. It may be sufficient here to reproduce the explanatory photograph of this whitefish scale and to point out briefly the significant structural features. Figure 2 represents a typical scale of a whitefish 197 millimeters in length captured October 22, 1917, at East Tawas, Mich., on Lake Huron. Near the center of the scale is a small clear area, the focus (*F*), which presumably represents the original scale in the young specimen. Around this focus are numerous more or less relieved striations, concentric, or nearly so, with the margin. These are termed circuli (*C*) and mark successive stages in the growth of the scale. Running from the focus to the periphery of the scale are four more or less conspicuous radiating ridges (*AR*, *PR*), which divide the surface of the scale into four roughly triangular areas or fields. When the scale is in position in the fish, the area to the right in the figure, the exposed area, is directed toward the tail and therefore is designated as the caudal or posterior area (caudal). The area opposite the caudal is the anterior (anterior), while the two areas that separate the caudal from the anterior are the lateral, or the dorsal (dorsal), and the ventral (ventral). The borders of these four areas, which form the periphery of the scale, accordingly are termed the caudal, anterior, dorsal, and ventral borders. The radiating ridges are either anterolateral (*AR*) or posterolateral (*PR*). The greatest anteroposterior diameter that bisects the caudal area of the scale is its length (*L–L*).

By careful examination two distinct zones may be seen in this scale, an inner characterized in general by more closely spaced lines and an outer in which the lines are farther apart. The inner zone represents, according to current theory, the entire growth of the first year, while the outer zone represents the growth of the second summer. If the lines of growth in the lateral field be followed from the center outward and downward along the anterolateral ridge, it may be seen that the first 20 are complete and uniformly spaced. With occasional breaks and irregularities, they may be traced entirely around the scale. The next six are incomplete and the outermost of them ends (or begins) near the anterolateral ridge. Following this last incomplete line to the anterior field a region is encountered within which the individual circuli can no longer be traced with certainty, for they are less distinct, much broken, anastomosed, and closer together. This zone of faint, approximated, and much broken circuli, when contrasted with the preceding and succeeding areas of strong, complete, and widely spaced circuli, often stands out as a rather sharply defined band. This band may be traced around the whole scale and is, perhaps, better defined in the posterior field, where it appears as a lighter zone with very little detail. This band, representing retarded growth, is here called the annulus (*A*).

When the scale resumes its rapid growth, a complete circulus is formed again, which, in the process of uniting, as it were, the incomplete lines, bends sharply at the anterolateral ridge. This circulus is considered the limit of the annulus it incloses and is employed so in the measurements of scales.

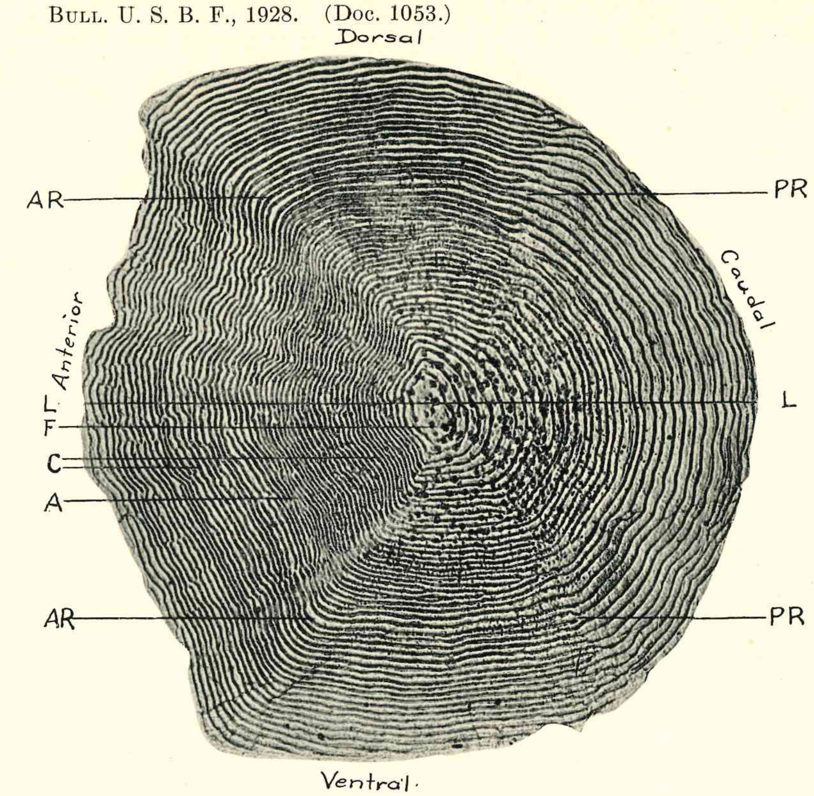

FIG. 2.—Typical scale of Lake Huron whitefish (*Coregonus clupeaformis*, Mitchill) from East Tawas, Mich. Length of fish, 197 millimeters; captured October 22, 1917. *L–L*, length of scale; *F*, focus; *C*, circuli; *A*, annulus of first winter; *AR*, anterolateral ridges; *PR*, posterolateral ridges; dorsal, ventral, anterior, and caudal border and area. ×25

FIG. 3.—Scale of Lake Huron herring (*L. artedi*) taken October 22, 1919, at Duck Isle (Lake Huron). Length, 232 millimeters. Female. Age VI (?). Scale shows a regenerated focus

FIG. 4.—Scale of Lake Huron herring (*L. artedi*) taken October 22, 1919, at Duck Isle (Lake Huron). Length, 232 millimeters. Female. Age VI (?). Scale shows a rotated nucleus or central area

FIG. 5.—Scale of Lake Huron herring (*L. artedi*) taken November 1, 1922, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 58829. Length, 262 millimeters. Mature male. Age VI. Scale shows near its focus a small scar, presumably a repaired injury, and at its margin a large clean-cut scar, presumably not a repaired injury, with obscure circuli and well-defined typical annuli

BULL. U. S. B. F., 1928. (Doc. 1053.)

FIG. 6.—Scale of Lake Huron herring (*L. artedi*) taken November 1, 1922, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 58557. Length, 239 millimeters. Weight, 5.25 ounces. Mature male. Age V (determined from other scales). Scale shows accessory annuli in the second, third, and probably in the fifth summer's growth zone.

FIG. 7.—Scale of Lake Huron herring (*L. artedi*) taken October 27, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54329. Length, 219 millimeters. Male. Age III. Scale shows a wide double annulus in the second year

FIG. 8.—Scale of Lake Huron herring (*L. artedi*) taken October 27, 1921, at Bay City, Mich. (Saginaw Bay). Length, 227 millimeters. Mature female. Age V. Note the distinctness of the first annulus. Compare with Figures 9 and 10

FIG. 9.—Scale from the same individual of which scales are shown in Figure 8. Note the indistinctness of the first annulus. Compare with Figures 8 and 10

FIG. 10.—Scale from the same individual of which scales are shown in Figures 8 and 9. All trace of the first annulus has disappeared. Compare with Figures 8 and 9

FIG. 11.—Scale of Lake Huron herring (*L. artedi*) taken September 17, 1917, at Alpena, Mich. University of Michigan Museum No. 52220. Length, 108 millimeters. Immature. Age I. No completed annulus shown on scale

IRREGULARITIES IN SCALE STRUCTURE

Various irregularities may occur in the structure of coregonid scales.

1. The normally small, clear, well-defined focus may be replaced by an expanded central area, devoid of circuli, rough or granular in appearance and irregular in outline, the relative size of which depends upon the recency of its formation. (Fig. 3). Scales with such expanded centers are termed "regenerated scales," because they have replaced those that are lost (Ryder 1884, Scott 1912, Creaser 1926).[2]

2. The first circulus, that which limits the normal focus, may assume various characteristics. It may be complete and entirely separate from other circuli (figs. 6, 8, etc.); it may be incomplete and continuous with other circuli, forming a spiral (fig. 9), or incomplete, with one half missing, so that it resembles a horseshoe.

3. Occasionally a condition is found that may be interpreted by assuming that young scales sometimes become dislocated and rotate in their scale pockets. As later growth is normal in direction, there results the appearance of a large scale with a smaller one inset, the two with foci in different positions and main axes at different angles. (Fig. 4.)

4. Small scars or patches commonly found on scales presumably are the repaired injuries of what was formerly the margin of the scale. These scars, like the expanded centers of regenerated scales, are irregular in form, granular in appearance, and entirely devoid of circuli or annuli. (Fig. 5 near focus.) Other patches clear, clean-cut, and with obscure circuli occur very rarely. (Fig. 5 at margin.) These apparently are not repaired injuries, as the lower layers in these patches of the scale appear normal with well-defined and typically formed annuli, continuous with those of adjacent areas.

5. With respect to the annuli, various irregularities appear. Their circuli are not always approximated. The divergence of the circuli is sometimes apparent in one lateral field only. Approximated circuli often appear between two annuli, so as to form "accessory annuli." Especially is this the case during the years with large growth increments, when the scales show more clearly a retardation in growth at a temporarily unfavorable time. In the scales of some fish these "accessory annuli" simulate the true annulus so closely as to make an accurate age determination impossible. (Fig. 6.) In such cases the fish are discarded unless other more easily read scales can be found on them. Very rarely two annuli form in the place of one (fig. 7), so as to produce a wide, double annulus. This may be interpreted as due to a resumption of growth following its retardation caused by some unusual circumstances in the life of the individual, such as an injury, disease, starvation, etc. Still more exceptional is the case in which an annulus fails to form on all the scales of the same fish. The first annulus of the scale shown in Figure 8 is very distinct and unquestionably a true annulus. Figure 9 shows a scale of the same specimen, in which the first annulus is less distinct but recognizable. A third scale (fig. 10) of this same fish shows no trace of the first annulus. That all three scales actually belonged to the same individual and that, therefore, no error occurred in technique, such as would accidentally introduce a stray scale into the scale sample of the individual, can be

[2] According to Taylor (1916), Dahl (1910) was the first to explain correctly the significance of abnormally large foci in scales. However, Reighard (1906) published a photograph of a regenerated scale of a whitefish and designated it as an "atypical" scale "probably formed after the fish had grown to some size and in place of scales that had been lost [p. 51]."

determined readily by a comparative study of the finer structures of these scales. This is the only example of a disagreement in the number of annuli of easily read scales of the same fish I have found in my material.

These irregularities in the structure of scales do not invalidate necessarily the scale method but emphasize the necessity of examining several scales from each individual.

SCALE METHOD AND ITS APPLICATION

By a study of the scales we may determine the age of a fish in years, the approximate length attained by it at the end of each year of its life, and its rate of growth for each year of life. The age in years is found by counting the annuli. The length at the end of each year of life is computed from a series of measurements of a scale of a fish of known length. Given the total length of a scale, the length included in its annulus of year X, and the length of the fish from which the scale is taken, the length attained by the fish at the end of year X is determined by the use of the following formula, in which the third term is the unknown:

$$\frac{\text{Length of scale included in annulus of year X}}{\text{Total length of scale}} = \frac{\text{Length of fish at end of year X}}{\text{Length of fish at time of capture}}$$

Repeating this formula for the annulus of each year, the length attained by the fish at the end of each successive year of life is computed. From these lengths the rate of growth for each year is obtained by a simple subtraction. The assumptions upon which this formula rests are discussed in later sections.

METHODS OF MEASUREMENTS AND COUNTS

BODY MEASUREMENTS

Many of the fish used by me were preserved in formalin, transferred to 70 per cent alcohol, and brought to the laboratory before they were measured or scales removed from them. Others were measured in the field while fresh and discarded after removal of scales for study. The method employed in measuring fish in the field previous to 1924 consisted in laying a steel tape along the curvature of the body and reading, to the nearest millimeter, the distance from the tip of the snout to the caudal margin of the last perforate scale of the lateral line.[3] In making measurements in the laboratory it seemed best to get the length, not along the curvature of the body but, in the usual way, parallel to the long axis of the body, and between verticals from that axis through the tip of the snout and the posterior margin of the last perforate scale. The fish was straightened, if need be, laid on its right side in a wooden tray, with its snout lightly touching a pin driven into the tray. The measurement was made with the steel tape in a straight line between this pin and another stuck into the tray just behind the last perforate lateral-line scale. The field measurements obtained before 1924 thus exceeded those made in the laboratory, for two reasons: They were made along the curvature of the body instead of in a direct line and they were made on fresh fish not shrunk by preservatives. To obtain the true length of the fresh fish along its axis it is necessary to correct the field measurements, which are too high

[3] In 1924 and thereafter length measurements were made in the field, not along the curvature of the body, but in a direct line—the steel tape was held parallel with the long axis of the body. No corrections were made for these fish.

because measured along the body curvature. It is necessary to correct the laboratory measurements to those of fresh fish by making allowance for shrinkage in the preservatives.

TABLE 2.—*Errors in the measurements of length of Bay City herring, due to use of the field method and due to shrinkage of the body in formalin*

	Millimeters
Average length of 182 herring preserved in 4 per cent formalin and measured Nov. 28, 1921, by field method	238.28
Average length of the same 182 herring preserved in 4 per cent formalin and remeasured Nov. 28, 1921, by laboratory method	232.98
Difference due to method of measurement	5.30
Average length of 182 fresh herring measured Oct. 26 and 27, 1921, by field method	242.24
Average length of the same 182 herring preserved in 4 per cent formalin and remeasured Nov. 28, 1921, by field method	238.28
Difference after shrinkage in formalin	−3.96
Average length of 199 herring preserved Oct. 29, 1921, in 4 per cent formalin and measured Nov. 28, 1921, by field method	238.21
Average length of the same 199 herring preserved Oct. 29, 1921, in 4 per cent formalin and remeasured Dec. 2, 1921, by field method	239.54
Difference due to error in measurements made by field method	±1.33
Coefficient for correcting lengths of fish measured by the field method	.978
Coefficient for correcting lengths of fish preserved in formalin	1.016

To obtain a coefficient of correction for the length of fish measured along the body curvature 182 preserved herring were measured on the same day by this method and by the laboratory method. The difference between the averages, 238.28 for the field method and 232.98 for the laboratory method (Table 2), was found to be 5.30 millimeters. This involves an error of about +0.022 millimeter for each millimeter of the field measurement. The coefficient of curvature for correcting field measurements is therefore $\frac{1.00}{1.022}$, or 0.978. To obtain a coefficient for shrinkage in preservation 182 fresh herring were measured by the field method and remeasured by the same method after being a month in 4 per cent formalin. The difference of the averages was 3.96 millimeters. (Table 2.) To learn whether this difference is due to the errors involved in the method of measurement, 199 fish that had been in formalin for about 30 days were measured and then remeasured after 4 days. The difference between the two averages was found to be 1.33 millimeters. (Table 2.) Thus, a fish of 242 millimeters apparently shrinks 3.96 ±1.33 millimeters through the action of formalin, or 0.016 millimeter per millimeter of body length. A shrinkage coefficient of 1.016, therefore, was used for all preserved fish.

Errors due to shrinkage or body curvature generally have been ignored in life-history work. According to Sæmundsson (1913), Schmidt reports an average shrinkage of 0.5 centimeter in the length of fish (plaice?) upon death. Williamson (1914) observed no significant shrinkage in the length of the marine herring preserved in formalin. Johansen (1915) corrected his plaice lengths, as follows: 0.5 centimeter for shrinkage at death and 1.0 centimeter when the specimen had begun to putrefy, had been salted, or been left to dry.

In the lake herring several other measurements besides total length were employed. *H* represents the length of the head as measured from the tip of the snout to the most distant point on the margin of the bony suboperculum, excluding the soft opercular membrane. H_1 represents the length of the head as measured from the tip of the snout to the most anterior point of the body proper on the projected lateral line and just posterior to the supra-clavicle of the shoulder girdle. Ordinary straight calipers were used for both measurements. To find the point on the body proper for the H_1 measurement the point of the caliper is inserted as far as possible under the soft, posteriorly directed flap of the supraclavicle. This point of the body is usually more dorsal than the one chosen on the suboperculum for H and is more constant in position. The H head measurements were made by Doctor Koelz for taxonomic purposes. The H_1 head measurements were made later by the writer, as they represent more nearly the true head lengths as included in the length measurements of the body. H_1 measurements are more often parallel with the long axis of the body than the H measurements. The head lengths were not corrected for shrinkage. The distance between the caliper points was measured on a steel millimeter tape. T and T_1 represent the length of the body proper, excluding the head and tail. They were obtained by substracting the head from the body length (K), as follows: $T=K-H$; $T_1=K-H_1$.

The weights of all fish were recorded to the nearest ¼ ounce and were taken with a sealed "Chatillon improved circular spring balance." It is assumed that the readings of the balance were accurate. After it had been used for this work it was damaged, unfortunately, before its error could be determined. The herring collected at Bay City, Mich., in 1921, 1922, and 1924 were weighed on shore while fresh. In order to determine whether the preservation of a herring in formalin and alcohol materially alters its weight the herring collected and weighed November 1, 1922, were weighed again individually in March, 1923, after having been hardened in formalin and transferred to alcohol. Before weighing the preserved fish they were piled in a tray to allow the excess alcohol to drip off. The 499 herring averaged 5.17 ounces before preservation and 4.96 ounces after preservation, a loss in average weight of 0.21 ounce. As the weights were read fairly accurately to only ¼ ounce the error involved in the weight of each individual should not have exceeded ±0.125 ounce, and average weights obtained by reweighing identical material should differ by less than ±0.125 ounce. The above averages obtained by weighing before and after preservation differ by 0.21 ounce, or about 4 per cent. There seems, therefore, to have been some loss of weight in preservation. Järvi (1920) found that specimens of *Coregonus albula* increased in weight after preservation in formalin. The average increase for the six specimens employed amounted to 0.5 gram.

SCALE MEASUREMENTS AND COUNTS

All scales were removed from the left side of the body and whenever possible from the area situated midway between the dorsal fin and the lateral line. This area was chosen after a careful examination had shown that its scales were less variable in shape and size, when compared one with another, than those of other parts of the body. To compare the body-scale ratio of different fish corresponding scales were thought to be possibly essential in order to eliminate the errors due to the variability of scales from different body regions. (See p. 311.) In the marine herring Lea (1910) located corresponding scales by means of their position on a definite myomere of a definite scale row. He found that, the caudal extremity excepted, only one scale is superimposed upon a myomere. In the coregonids the scales do not follow the myomeres so closely. I found, by enumerating both the myomeres

and the scales superimposed upon them for portions of different scale rows on different parts of the body, that the number of myomeres is usually less than the number of the scales superimposed upon them. My corresponding or X scales were selected, therefore, with reference to their general position on the body and not with reference to any particular myomere. They were taken from the fourth longitudinal row above the lateral line from the vertical drawn through the base of the first ray of the dorsal fin.

In the field a dozen or more scales were removed from each fish with forceps and preserved in the standard scale envelopes furnished by the Bureau of Fisheries. The fish were not preserved. The following data were then entered upon the face of each envelope, if required: Species, locality, date, length, weight, sex, stage of sex organs, gear, and collector. When ready to mount, three or four of the dried scales of each specimen were scrubbed clean in water. By use of a binocular microscope care was taken that only typical and good scales were selected. The scales were cleaned best with a small brush made of the stout ends of shoemaker's bristles tied to a stick. The scale was held in place during the scrubbing by the blunt end of a teasing needle, which was also employed to remove the more adhesive pigment cells or dirt. When the three or four scales were cleaned, warm glycerin-gelatin solution was placed on a clean glass slide in amount deemed necessary to cover completely the scales placed in it. If the gelatin and the pure glycerin are mixed in such proportion [4] that a small amount stiffens immediately upon cooling, and if a liberal amount of the solution is used, no evaporation occurs under the cover glass and the mounts may be kept permanently without sealing. Some of the photographs shown are of scales that had been mounted for two years. A little carbolic acid must be added to the glycerin-gelatin solution to insure its preservation. All scales were mounted with the circuli or rough side up and with the caudal area toward the lower edge of the slide.

The scale to be studied was projected upon the ground glass of an apparatus constructed on the principle of a photomicrographic camera (Van Oosten, 1923). All measurements of scales were made on this image, projected at a magnification of 19. On exploring the illuminated field covered by a scale image so magnified, I found, by the use of a stage micrometer, that the magnification is everywhere uniform—there is no discoverable optical distortion.

In measuring the projected scale, a wooden ruler was placed along the diameter that bisects the caudal area of the scale (L–L, fig. 2) and readings were taken (to the nearest millimeter) at the center of the focus, at each annulus in both the anterior and posterior area, and at the anterior margin of the scale. More accurate measurement was not found possible. I found, by scratching a line drawn parallel with the long axis of the body on a longitudinal series of consecutive scales in situ, that the line on all the scales followed the anteroposterior diameter defined above. This diameter, therefore, gives more easily comparable measurements than any other. The measurements were made use of in computing the lengths of fish by the formula given on page 272. All computations were made with a slide rule or with a Monroe calculating machine. The circuli of the anterior area were enumerated along the

[4] It was found by long experimentation that the following formula gave the best results: Dissolve 8 ounces gelatin (WH, No. 1866, Germany) in 850 cubic centimeters distilled water and add 250 cubic centimeters glycerin and a few drops carbolic acid.

edge of the ruler, all those that were separated being considered as complete circuli even though they were connected with others a short distance from the ruler.

Scale counts were made along the lateral line on the left side of the body. I enumerated the perforated scales only, which excluded, therefore, the small, irregularly placed scales at the extreme caudal end of the fish. Scale pockets were counted for the lateral-line scales that were lost.

The age of a fish is usually indicated by a Roman numeral, representing the year of life in which the fish was caught. Thus, a IV-year fish is one that, having hatched in the spring, has passed its third winter following hatching; has, therefore, three complete annuli on its scales and is somewhere in its fourth year.

GENERAL HISTORICAL REVIEW

The early scale investigators were concerned principally with the development, the structure, and the chemical composition of scales and with their relation to taxonomy. Thus, they paved the way to a correct appreciation of the relief structures in scales, upon which the scale method rests. The following historical review sketches briefly the trend of thought among these early investigators relative to the correlation of relief structures of scales and their growth. More comprehensive reviews of the scale literature of this period may be found in the publications of Baudelot (1873), Thomson (1904), and Taylor (1916).

After the invention of the microscope, fish scales became one of the interesting objects for study. Fabricius d'Aquapendente (1618, 1621, 1625), Borellus (1656), and Hooke (1667) wrote brief descriptions of the microscopic appearance of fish scales.

The first record relative to the growth of scales is found in one of the letters of Leeuwenhoek (1686), dated July 25, 1684, in which he, describing the microscopic appearance of an eel scale, writes "although all the Scales [of an individual] are not of the same shape, I have yet observed, in many of them as I judged, the same number of Circular lines. From whence I conclude that every year the Scale encreased one Circular line; and by consequence, the number of these Circular lines, being seven; the Fish must have been seven years old." (Turrell, 1911.) His illustration shows that Leeuwenhoek actually referred to the growth zones of the scale. In a letter written May 22, 1716, and published in 1719, Leeuwenhoek describes his method of determining, from its scales, the age of a carp 42¼ inches long and 33¼ inches in circumference at its thickest. He cut the scale obliquely to count the age rings. The scale having 40 rings, the author concluded that the carp was 40 years old. In this letter Leeuwenhoek postulated scale growth as being due to the development of a new scale underneath the old one, which it exceeds in size and to which it adheres and is gradually closely welded. One such new scale is formed each year, so that by enumerating the superimposed scales one can determine the age of the fish. It is clear from his illustration and from his method of sectioning that in this case Leeuwenhoek did not refer to the growth zones but to the lamellæ of the scale.

Réaumur (1718) believed that the concentric lines indicated "different degrees of growth in scales, just as the analogous markings indicate the growth of shells."

Without giving the reference, Lea (1919) quotes Pastor Hederström, a Swede (1759), as follows: "Anyone taking the trouble to examine a vertebra from a boiled

fish will observe certain rings thereon. And as many rings as there may be, so many years will be the age of the fish."

Kuntzmann (1829) maintained that no relation existed between concentric lines on scales and age, as the scales of old carp possess no more of these ridges than those of young carp. Similarly, Blanchard (1866) stated that the concentric striæ are as numerous in very small as in very large fish of the same species. Agassiz (1834), however, believed that the concentric lines are the reflexed edges of the lamellæ and increase in number with the growth of the scale. Mandl (1839) claimed that the formation of these lines is linked closely with the peripheral growth of the superior layer of the scale, while Williamson (1851) asserted that these ridges are not lines of growth "but the result of a peculiar arrangement of the superficial tissue of the scale."

Vogt (1842) discovered that scales do not appear in salmon until the third month after hatching, and that the concentric lines are relatively few in number in very young fish but very numerous in adult fish.

Steenstrup (1861) is apparently the first to state specifically that the scales of osseous fishes persist during the entire life of the fish and grow with the growth of the animal.

Baudelot (1873) made a comparative study of scales, employing a dozen species of fish. He noted, among other things, the variation in the number and character of the concentric ridges with the species and with the individuals of a species. He observed that these lines remained fairly constant in number with scales taken from the same region of the body of a fish, but that they increased in number in the older individuals of a species, the number of ridges increasing proportionally with the age of the fish and the size of the scales. He discovered, further, that the concentric ridges varied in their degree of separation and regularity, so that concentric zones were visible on the scale surface. He believed that the cause of this phenomenon was very unstable, but lacking sufficient data left the matter undetermined.

It was left for Hintze (1888) to link Baudelot's "zones" with Leeuwenhoek's first theory of age determination. Hintze was enabled to correlate the two by his knowledge of the age and life history of the carp, upon which he worked. Carp of commercial ponds were employed. Due to the presence of accessory annuli, however, Hintze made an error of one year in his interpretations, which error caused the temporary abandonment of his theory. His work is considered more in detail in a later section (p. 294).

Hintze's theory had at least one adherent, Victor Burda, for Max von dem Born writes (1894, p. 58) "Nach Burda kann man das Alter der Karpfen an den Jahresringen erkennen, welche auf den Schuppen sichtbar sind, wenn man diese in Spiritus legt, und von Schlamme befreit; ich habe mich von der Richtigkeit dieser Mitteilung durch den Augenschein überzeugt."

Fritsch (1893, p. 89) enumerated the circuli (Anwachsringe) in the scales of salmon of known ages and of various lengths (34 millimeters to 90 centimeters) and concluded: "Genaue Verfolgung dieser Zunahme der Anwachsringe der Schuppe mit zunehmendem Alter dürfte einen Anhaltspunkt geben nach der Zahl der Anwachsringe bei grossen Lachsen das Alter zu bestimmen. Bei Salmlingen, von denen ich voraussetzte, dass sie schnell wachsen, fand ich die Anwachsringe weiter von einander entfernt und in geringerer Zahl im Verhältniss zur Gesammtlänge des Körpers." According to Arwidsson (1910), Hofer (1895), however, refutes Fritsch's conclusion that the age of a salmon can be ascertained from the number of concentric ridges on its scales.

Petersen (1895) referred to the zones on eel scales as "growth streaks which possibly correspond in number fairly exactly to the years passed."

Smitt (1895, p. 957), in delineating and describing a marine herring scale, writes: "In the striature the growth rings of the scale also appear as concentric lines." The accompanying figure indicates clearly that by "growth rings" the author referred to the annuli.

It was not until 1898 that the scale method of age determination was tested critically. In that year Hoffbauer published a preliminary paper, in which he set forth the true character of the annuli, supporting his views by experimental evidences. These are discussed elsewhere (p. 294).

Thus far I have traced the development of the age hypothesis based on the structures of scales from its inception in 1686 to the end of the nineteenth century. During this period all the fundamental structural phenomena utilized in the scale method were discovered and described; but the exact relation of these structures to the life history of the individual remained undetermined, in spite of the fact that, peculiarly enough, the first presentation of the theory was in all probability the correct one. In 1898 the correct hypothesis was rediscovered and critically tested by Hoffbauer, and the second period of scale study was ushered in. During this second period the scale method was established firmly, elaborated greatly, and applied extensively. It need be said here only that publications appeared in England, Scotland, Norway, Denmark, Sweden, Russia, Holland, Germany, France, America, and other countries. In these studies more or less elaborate life histories based on scales have been worked out for the whitefishes, salmon, trout, marine herring, halibut, plaice, flounder, sole, smelt, mackerel, muttonfish, sardine, eel, hake, haddock, cod, squeteague, perches, and other fishes. The literature of this period is too voluminous to review. The more important papers will be considered under the various subtopics to which they refer.

Part I—CRITIQUE OF SCALE THEORY AND METHOD

ASSUMPTIONS OF THE METHOD

The soundness of the scale method of determining the length of a fish at successive years of its life and its annual growth increments depends on the validity of the following propositions:

1. That the scales remain constant in number and [retain their] identity throughout the life of the fish.

2. That the annual increment in the length (or some other dimension which must then be used) of the scale maintains, throughout the life of the fish, a constant ratio with the annual increment in body length.

3. That the annuli are formed yearly and at the same time each year [or that some other discoverable relation exists between their formation and increment of time].

Incidentally the following questions are raised, but the validity of the scale method of computation is not affected by them:

4. Whether the annuli represent periods of retarded or arrested growth of the scale?

5. Whether the growth of the fish in length is retarded or arrested at the time of formation of the annuli?

6. What factors are responsible for the arrest of or retardation of growth in fish and scales? (Van Oosten, 1923.)

The last three questions I have attempted to answer in another place (Van Oosten, 1923). It remains to discuss the first three questions.

IDENTITY OF SCALES THROUGHOUT LIFE

Were scales commonly or regularly shed and replaced by others they could not be made use of in life-history studies. It is a tenet of the method that they retain their identity throughout life, that only a few are lost accidentally and replaced. The many life histories unraveled by the scale method are, in themselves perhaps, proof enough that identity persists; but some of the well-established facts in proof of identity are these: (1) That the nuclear area or central part of the scales of old fish of a species is structurally identical with the scales of young fish (Snyder; see p. 300 following). (2) That regenerated scales, which replace those accidentally lost, have a central portion of quite a different type from that of normal scales. (The characters of regenerated scales are distinctive and generally easily recognized. Scott (1912) and Creaser (1926) established this experimentally, and I have extracted normal scales from carp and found them replaced by typical regenerated scales. I have also found regenerated scales covering the repaired injuries of several herring.) (3) That scales increase in size as long as the fish grows.

CONSTANCY IN NUMBER OF SCALES THROUGHOUT LIFE

If scales of typical teleosts, their number remaining constant, were in contact by their edges they must grow in proportion to the body, else the surface would not be always covered; the relation between scale length and body length would be mechanical; but as these scales overlap, they may or may not grow in length in proportion to the body's length. The question of whether they do or do not is one of physiological growth correlation and may be answered only by observation.

The number of scales in the lateral line is made use of in discriminating species, and it is well known that it varies within the species. The question is whether the individual differences in scale number arose when the scales were first laid down and have continued since then, or whether the scales increase in number during the life of the fish. Do the fish that were large at the time of scale formation develop more scales at that time than smaller fish, and does their number remain constant? If the number of scales (for example, in the lateral line), increases with age, they can not grow in proportion to the body's growth, for it has been shown by Lea (1919) that when a new scale is formed in place of one accidentally lost the growth rate of surrounding scales is retarded.

That the size of the scales varies with their number is shown by the fact that of 45 lake herring 240 millimeters in length, 25 had 80 or less (average=77.9) scales in their lateral line, while 20 had 81 or more (average=82.8) scales in the lateral line. The average length of the scales of the former group was found to be 5.16 millimeters, while that of the scales of the latter was 5.05 millimeters, or 0.11 millimeter less.

If the number of scales in the horizontal rows is less in the adults than in the juveniles whose scalation is complete, the ratio of the body-scale growth would decrease with age, as the scales would grow relatively faster than the body. When an adult fish loses a scale it is replaced by a "regenerated" scale, and the number of scales is not altered; but there appears some evidence that scales may be crowded out and covered by others. Both Brown (1904) and Thomson (1904) discovered minute scales under and between the large ones in species of Gadidæ. The former author concluded from this fact that scales are shed after spawning and are replaced by the small underlying scales, while the latter stated that these juvenile scales, which do not possess many lines of growth, are crowded out and covered by the larger ones and finally disappear. Thomson's interpretation is based partly on his belief "that the exact number of scales in a row on the fish has been regarded as sufficiently constant for use in the determination of species [p. 58]." He states further that Klaatsch found the same thing to occur in the trout. Klaatsch found that "between such large scales as already partly cover one another, small scales are very frequently found which are in the earliest stages of development. In older animals such an irregularity does not occur." And "As in Elasmobranchs, new scales originate in the trout between the well-developed scales; thus one finds lying between the older scales of the trout even in later stages quite young scale foundations. This irregularity in the early development soon ceases in the trout [p. 58]."

In the lake herring the presence of minute scales and scales strikingly smaller than the neighboring or contiguous, well-developed scales is not uncommon. These minute scales usually are covered by the normal ones; but the small scales are not, as Klaatsch and Thomson say of their material, "juvenile." They are abnormal, in that they are stunted in growth; but they possess as many annuli as the normal contiguous scales and are as old.

These facts indicate that all the scales formed during the first year of life do not necessarily grow proportionately with the body of the fish, and that in some instances the number of normal scales in a horizontal row is reduced as the adult stage is attained by the fish. Whether or not the abnormal minute scales occur generally, their existence in some forms throws doubt on the assumption that the number of scales remains constant with age. Especially is this true when it is known that this assumption has never been supported by critical data.

To test the question of constancy in the number of scales throughout life, I have enumerated the scales in the lateral line of the lake herring (*Leucichthys artedi*) collected at Bay City, Mich., October 26, 27, and 29, 1921, November 1, 1922, and November 12, 1923. The fish of October 26 and 27, 1921, were taken in different pound nets set in Saginaw Bay. Each of the remaining collections forms a unit, as each represents the partial catch of 1 pound net. These unit collections were taken from the same fishing grounds in Saginaw Bay about 3 miles west of the mouth of Saginaw River. All the herring were taken on or near their spawning ground and were nearly ready to spawn. There can hardly be any question, therefore, as to the homogeneity of the material taken in the same haul. As individual herring are not known to return to the same spawning ground each year, the possibility exists that the fish collected in different years may belong to different races, even though taken on the same spawning grounds.

Two methods suggest themselves by which we may try to determine the constancy in the number of scales throughout life. We may compare either the scale-number averages of the several age groups (fish of the same age) taken in one and the same haul, or the averages of the age groups taken in different years but belonging to the same year class (fish hatched at the same time). In the first case we compare fish of different ages, hatched in different years, but taken at the same time; in the second case we compare fish of different ages, hatched at the same time, and taken in successive years.[5] In the first case we must assume that the number of scales remains constant with the year classes, in the latter we must determine that all the collections consist of homogeneous material. By both methods we assume either that scale number does not vary with sex or size in an age group, or, if so, that both sexes and all sizes are represented in correct proportions.

TABLE 3.—*Average number of scales in the lateral line of males and females for different size groups of Bay City lake herring of various ages* [1]

Size groups, millimeters	Oct. 29, 1921, age group IV					Nov. 1, 1922, age group IV				
	Average scale number			Average size		Average scale number			Average size	
	Male	Female	Male and female	Male	Female	Male	Female	Male and female	Male	Female
211–220	77.00 (1)	75.75 (4)	76.00 (5)	216 (1)	218 (4)					
221–230	79.36 (39)	81.04 (26)	80.03 (65)	226 (39)	227 (26)	76.35 (20)	77.60 (15)	76.89 (35)	227 (20)	227 (15)
231–240	81.08 (25)	81.94 (16)	81.41 (41)	234 (25)	235 (16)	77.94 (53)	79.09 (22)	78.28 (75)	236 (53)	236 (22)
241–250	82.60 (5)	82.40 (10)	82.47 (15)	260 (5)	266 (10)	79.22 (32)	79.78 (9)	79.31 (42)	244 (32)	244 (9)
251+						78.00 (5)	80.80 (5)	79.40 (10)	257 (5)	262 (5)
Grand average	80.17 (70)	81.16 (56)		232 (70)	236 (56)	78.03 (110)	78.94 (51)		238 (110)	237 (51)

Size groups, millimeters	Nov. 12, 1923, age group IV					Size groups, millimeters	Average scale number of all 1921 herring, age group III			Average scale number of all 1923 herring, age group V		
	Average scale number			Average size								
	Male	Female	Male and female	Male	Female		Male	Female	Male and female	Male	Female	Male and female
211–220						Under 226	77.83 (18)	79.53 (17)	78.66 (35)			
221–230						Over 226	82.08 (12)	79.73 (15)	80.78 (27)			
231–240	80.41 (27)	79.74 (19)	80.13 (46)	238 (27)	236 (19)	Grand average	79.53 (30)	79.63 (32)				
241–250	81.43 (49)	81.96 (23)	81.60 (72)	246 (49)	245 (23)	Under 251				81.36 (25)	80.30 (10)	81.06 (35)
251+	81.75 (16)	83.00 (11)	82.26 (27)	254 (16)	253 (11)	Over 251				82.80 (25)	81.27 (11)	82.33 (36)
Grand average	81.18 (92)	81.38 (53)		245 (92)	244 (53)	Grand average				82.08 (50)	80.81 (21)	

[1] Numbers in parentheses indicate the number of specimens employed.

In connection with the last-mentioned assumptions Table 3 is significant. In this table is given the average number of scales in the lateral line of males and females

[5] It is not feasible to arrange the fish according to size groups instead of age groups on the assumption that the small fish are also the young fish. This we know is not strictly true. Further, the fact that the smaller fish of an age group have fewer lateral-line scales than the larger fish of that age group (see p. 283) introduces an error in the size-group method, which tends to reduce the average scale number of the small fish below that of fish of equal size but of younger age.

for different size groups of Bay City lake herring of various ages. A detailed examination of those averages that include a sufficiently large number of specimens shows that, with four exceptions, the averages of the females are higher than those of the males. The averages are higher for the males of the smallest size group of the 4-year fish and of both size groups of the 5-year herring of 1923 and of the larger size group of the 3-year fish of 1921. It is to be noted, however, that the 4-year males of 1923 average somewhat more in length than the females of this group. The larger averages in the scale number of females can be correlated with size in the 4-year fish of 1921 but not in the same aged fish of the other two collections. When the grand averages of the scale number of the males and females are compared it may be seen that those of the females are slightly higher in every age group except the fifth of 1923, irrespective of the average size of the females. If the differences between the mean scale number of the two sexes of a size group are compared for all age groups, it is found that the differences vary from 0.53 to 1.70 in those cases where the averages of the females are the higher and from 0.20 to 2.35 in those cases where the averages of the males are the higher. When the differences between the grand averages of the two sexes are compared (fifth year of the 1923 fish with a difference of 1.27 excepted), it is found that they vary from 0.10 to 0.99 and that their mean approximates 0.55. If these differences in the average scale numbers need be considered, I may state that they lie well within the limits of personal error in scale counts, as I shall show later (p. 283), and therefore have no significance. The number of scales in the lateral line, then, is shown not to vary with the sexes.

Further examination of the averages of Table 3 shows that the larger individuals of both sexes of an age group possess, on the average, a greater number of scales in the lateral line than the smaller. The scale number increases consistently with size. The differences between the average number of scales of the small and large males of an age group vary from 1.34 to 4.25; of the females from 0.20 to 3.26. The range in the differences between the grand averages (male and female) of an age group extends from 1.27 to 2.44. The mean of these differences is approximately 2.09. The difference between the scale number of the small and large herring of an age group is therefore about 3.8 times as great, on the average, as that between the sexes.

Are these differences significant or are they due to errors in scale counts? To answer this question I reenumerated the lateral-line scales of most of the 4-year herring collected October 29, 1921, and of a random sample of the 1922 herring. The 1922 collection was selected for the recount because a large percentage of its individuals had lost many of the lateral-line scales, and inasmuch as scale pockets are overlooked more easily than scales the discrepancy between two enumerations in these fish should represent the maximum. No counts were taken when the scales of the caudal region were lost.

The results of this recount are summarized in Table 4. It will be noticed that averages were made at various stages of the recount to indicate the trend or direction of the personal error with the increase in the number of variates. In both series the discrepancy decreased as more individuals were employed.

TABLE 4.—*Comparison of duplicate scale counts with the original for various numbers of herring taken October 29, 1921, and November 1, 1922, at Bay City, Mich.*

Date	Number of individuals selected at random	Average scale count		Difference between original and duplicate counts
		Original	Duplicate	
Oct. 29, 1921	52	80.58	79.69	+0.89
Do	113	80.71	80.29	+.42
Nov. 1, 1922	18	78.22	79.88	−1.66
Do	39	78.36	79.95	−1.59
Do	63	78.52	79.54	−1.02

The duplicate scale count for 113 herring of the 1921 collection averaged only 0.42 less than the original, while that for 63 herring of the 1922 collection averaged 1.02 more than the original. As was expected, on account of the large number of scales missing in the lateral line the personal error in the counts for the latter collection exceeded that involved in the counts for the former.

Table 4 seems now definitely to answer our inquiry. The range (0.10 to 0.99) in the differences as well as the mean (0.55) of the differences between the grand averages of the scale number of the two sexes (p. 282) may be accounted for very well by the personal factor involved in the scale count; but the range (1.27 to 2.44) in the differences and the mean (2.09) of these differences of the two size groups (p. 282) can not be so accounted for, as they greatly exceed the personal errors involved. Neither is it probable that random sampling can account for these large differences, inasmuch as the greatest difference obtained between any two scale counts of one and the same series, as given in Table 4, amounted to 0.60 (80.29 to 79.69), which means that the greatest difference due to random sampling amounted to approximately 1.20. The consistent difference between the average scale number of small and large fish of an age group is apparently, then, significant; the large herring have the greater number of scales in the lateral line.

The greater number of scales in the large fish may be accounted for in one of two ways: (1) The scale number can be determined more accurately for large fish than for the small, due especially to the larger size of the lateral-line scales at the caudal extremity in the former, or (2) the large fish of an age group were always large in their year class and consequently needed and always had more scales than the small individuals.

The data already accumulated for the 4-year herring collected in 1921 and referred to above (p. 282) may be employed to determine the status of the first proposition. The fish were divided into two size groups, and the averages of the duplicate scale counts of each size group were compared with those of the original counts. Sixty-two herring 231 millimeters or less in length were found to have an average of 80.08 in the first scale enumeration and 80.02 in the second, a difference of 0.06. Fifty-one individuals 232 millimeters or more in length were found to have an average of 81.39 in the first count and 80.63 in the second, a discrepancy of 0.76. These data indicate that scale enumeration is as accurate for the small as for the large fish considered.

Table 5 has been constructed to test the postulate that the fish with the larger number of scales were always large. Each age group of the two collections employed was divided into two size groups. The lengths, in millimeters, attained by the individuals at the end of their first year of life, as computed from the scales, were then averaged according to these size groups. It may be seen from the table that the large fish of each age group were also the large fish of their year class at the end of the first year of life. Thus, the average size of those fish of age group III, taken in 1922, that were less than 230 millimeters long (average length 222 millimeters) was 137 millimeters at the end of the first year of life, while the average size of these fish of the same group that exceeded 230 millimeters in length (average 236 millimeters) was 142 millimeters at the end of the first year of life. Similar differences appear in Table 5 in the other age groups. This presumably explains why the large fish of an age group possess more scales than the small ones. The fish were longer during their first year of life, and more scales were laid down in the longitudinal rows.

are scales laid down at certain age or certain size

TABLE 5.—*Average calculated length, in millimeters, at end of the first year of life of Bay City lake herring of different size groups within an age group* [1]

	Herring collected Nov. 1, 1922, age group—						Herring collected Nov. 12, 1923, age group—					
	III		IV		V		III		IV		V	
	Under 230	Over 230	Under 237	Over 237	Under 240	Over 240	Under 234	Over 234	Under 243	Over 243	Under 251	Over 251
Average length of fish of each size group	222	236	229	243	233	249	225	241	236	250	243	259
Average length at end of year 1, based on scales	137(75)	142(73)	121(130)	123(115)	110(45)	118(50)	139(79)	144(91)	130(121)	135(119)	113(47)	126(43)

[1] Numbers in parentheses indicate the numbers of specimens employed.

See statement page 337 ?

The data indicate for the lake herring (1) that the number of scales in the lateral line does not vary with the sexes and (2) that the number of scales in the lateral line is greatest, on the average, in the large individuals of an age group, due to the fact that these fish were also the large individuals of their year class at the time of scale formation.[6] In our discussion of scale constancy, therefore, an allowance must be made for the deviations due to personal errors and to the size of the fish as well as to random sampling.

If we find, when comparing the means of the scale number of the age groups of a collection with one another, that they remain constant with the year classes, then we can conclude also that in all probability they remain constant with age. I have constructed Table 6, therefore, in which these averages for each age group of each collection are shown. In order to determine whether the differences between the averages are significant, I computed the probable error of the extreme means according to the formula, $P.E._{M}=\frac{0.6745\sigma}{\sqrt{n}}$, in which σ = standard deviation and n = the number of variates, and then determined the probable error of the differences between the means according to the formula, $P.E._{M1-M2}=\sqrt{(P.E._{M1})^2+(P.E._{M2})^2}$, the difference

[6] It may be suggested here that these facts, as well as the one relative to the discrepancy in scale counts, may have special significance in studies considering the variation of meristic characters in fish. Hubbs (1922), for example, accepted a difference of 0.40 between the average scale number of two year classes of *Notropis atherinoides* as significant.

between the two means being considered significant if it is at least five times its probable error.

TABLE 6.—*Average number of scales in the lateral line of herring collected October 26, 27, and 29, 1921, November 1, 1922, and November 12, 1923, at Bay City, Mich., for each age group* [1]

Date	Average number of scales in lateral line of herring in year					
	III	IV	V	VI	VII	VIII
Oct. 26 and 27, 1921	77.92 (12)	79.45 (66)	80.81 (80)	79.72 (29)	81.25 (4)	81.67 (3)
Oct. 29, 1921 (from one net)	79.98 (50)	80.61 (126)	81.02 (61)	81.55 (22)	80.00 (6)	----------
Grand average of all 1921 fish	79.58 (62)	80.21 (192)	80.90 (141)	80.51 (51)	80.50 (10)	----------
Nov. 1, 1922 (from one net)	78.05 (83)	78.34 (163)	78.20 (76)	77.38 (8)	----------	----------
Nov. 12, 1923 (from one net)	80.71 (56)	81.26 (151)	81.70 (71)	81.73 (11)	80.00 (2)	----------

[1] The number of specimens upon which each average is based is given in parentheses. Eighteen fish of age group II, taken Nov. 2, 1922, at Oscoda, Mich., about 70 miles north of Bay City, had an average scale number of 80.39, while 10 fish of this age group taken in different years and at different localities on Lake Huron had an average of 80.80. The grand average of the 28 fish was 80.54.

The two 1921 collections have been grouped together, as it is probable from a study of Table 7 (containing the frequency distribution of the scales in the lateral line) that both groups belong to the same population. The mean of the scale numbers as well as the mode and range are virtually identical in the two collections. This homogeneity is further evident when we compare statistically the two 4-year groups, for example, which involve the greatest number of specimens. The difference (1.16) between the two averages was computed to be 2.79 times its probable error. The differences [range = 0.21 − 1.83 (2.06); average = 1.11 (1.30)] of the other age groups of the 1921 collections also may be accounted for by personal errors or by random sampling (see Table 4, p. 283), or possibly by the persistently though trifle larger average lengths (1 to 3 millimeters) of the fish taken October 29.

It is seen from Table 6 that the grand average of the 1921 age groups, though lowest in year III, does not increase consistently with each higher age group. Computations show that the probable error of the mean of the 3-year fish is 0.3191, of the 6-year group 0.3203, of the difference between the means 0.4521, and that the difference, 0.9291,[7] between the averages of these two age groups of 1921 equals 2.06 times its probable error and is therefore not significant. The differences between the averages of the 1922 fish are even less than those of the 1921 herring. Here, also, an increase in scale number can not be correlated with a higher age group. In the 1923 herring, however, as in the 1921 fish of October 29, the average increases slightly with each older year class. As the difference between the extreme means of the October 29 specimens is greater and the number of individuals included in these means is larger than that of the 1923 fish, the averages of the 1921 herring are preferred for statistical treatment. Computations show that the probable error of the mean of the third and sixth age group of this collection is 0.3318 and 0.4562, respectively, that the probable error of the differences between the two means is 0.5641, and that the difference, 1.57, is 2.78 times its probable error. The difference between the extreme averages (III and VI) of the 1923 herring is only 1.02. The footnote of

[7] In the table the averages are given to the second decimal place.

Table 6 shows that the average scale number (80.54) of the 2-year fish is in general not strikingly different from the averages of the older fish.

A comparison of the differences between the means of these year classes with those due to personal errors (Table 4) or to size of the fish (Table 3) leads us to the same conclusion as that obtained by the application of statistical methods; namely, that the number of scales in the lateral line remains constant with the year classes studied and consequently with age.

If, now, the average scale number remains constant with the year classes, we should expect to find insignificant differences between the averages in Table 6 of the same age groups taken in different years. We find that the differences between the averages of the 1921 and 1923 fish, which vary from 0.80 to 1.22 (average = 1.05), are unquestionably insignificant, but that the differences between the averages of the 1922 and 1923 fish, which vary from 2.66 to 4.35 (average = 3.36), are much greater.

TABLE 7.—*Frequency distribution of scales in the lateral line of Bay City herring*

Date	Scale number																															Number of individuals
	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	Mean	
Oct. 26, 27, 1921	0	0	1	0	5	5	6	9	9	19	12	16	24	15	23	16	10	6	9	5	2	1	0	0	1	--	--	--	--	--	80.03	194
Oct. 29, 1921	0	0	0	1	1	3	6	8	13	19	26	23	34	25	17	26	21	22	10	5	1	4	0	0	0	--	--	--	--	--	80.65	265
1921 combined	0	0	1	1	6	8	12	17	22	38	38	39	58	40	40	42	31	28	19	10	3	5	0	0	1	--	--	--	--	--	80.39	459
Nov. 1, 1922	2	1	2	4	11	12	20	22	26	38	32	31	47	26	24	11	6	8	5	1	1	0	0	0	0	--	--	--	--	--	78.21	330
Nov. 12, 1923	0	0	0	0	1	2	8	7	14	12	22	25	23	38	35	32	27	13	6	11	9	2	1	0	0	0	0	2	0	1	81.27	291

Table 7, showing the frequency distribution of scales in the lateral line, likewise indicates that the 1921 and 1923 material belong to the same population, whereas the 1922 fish probably belong to another, in so far as scale number is concerned. I am inclined to believe, in spite of the fact that the difference between original and duplicate scale counts diminished with an increase in the number of variates (Table 4), that the averages of the 1922 fish were low because, as stated on page 282, a large percentage of these individuals had lost many of their lateral-line scales, and scale pockets are overlooked more easily in counting than scales. This belief is supported by the fact that the 1922 averages are persistently low, irrespective of the year class involved. The large differences between the scale averages of the 1922 and 1923 age groups, as given above, therefore should not be considered as evidences for the variability of the number of lateral-line scales with the year classes.

Whether the 1922 herring are actually different or whether the difference is due to inaccurate scale count, it is at least clear that the 1922 collection can not be compared in its scale number with the others on the assumption that all the collections form a unit.[8] In studying the scale averages of the different age groups belonging to the same year class, only the 3-year fish of 1921 and the 5-year fish of 1923 may be compared with confidence. The sixth age group of the 1923 collection includes too few specimens to permit valid comparision with the fourth age group of the 1921 collection.

[8] If such an assumption be held, then it is clear the data of Table 6 show that neither a decrease nor an increase in scale number with age occurs, as the averages of all year classes decrease in the 1922 and increase in the 1923 age groups.

Applying the statistical formulas, I found the probable error of the mean of the 3-year fish of October 29, 1921, to be 0.3318; that of the 5-year herring of 1923 to be 0.2421. The probable error of the difference between the means equaled 0.8344, which is contained 2.06 times in the difference, 1.72. The difference, 1.12, between the fourth age group of the October 29, 1921, collection and the sixth age group of the 1923 collection was found to equal 1.08 times its probable error. Thus, the little evidence a comparison of the averages of different age groups that belong to the same year class produces confirms the conclusion previously arrived at that scale number remains constant with age. This conclusion, of course, involves only the herring 3 years of age and older, although it would apply undoubtedly to the juveniles, also, which, unfortunately, are unprocurable at the present time. (See footnote, Table 6.)

Throughout the preceding discussion we assumed that all sizes were represented in correct proportions in each age group. This assumption, however, probably is not warranted. (See p. 334.) The third age groups, at least, probably include a disproportionate number of the larger individuals, and this would tend to raise the averages of the scale number above the more representative values. The average (80.54) of the 2-year fish suggests, however, that the averages of the 3-year fish are not very much too high, if any.

In this section an attempt has been made to learn whether the number of scales of a fish remains constant throughout life. If the number of scales increased or decreased with age, the growth rate of the individual scales would vary accordingly and they would not grow in direct proportion with the body. Further, there is evidence that in at least some individuals of certain species the number of normal scales is reduced as the adult stage is reached. Herring of the same year class and of different year classes were compared. These methods rest upon the assumption either that scale number does not vary with the sex or the size of a fish of an age group or, if so, that both sexes and all sizes are represented in correct proportions in each age group of the samples. Data were obtained that indicated that the number of scales in the lateral line did vary with the size of a fish but not with the sex. It was ascertained further that the greater number of scales in the large fish of an age group could not be attributed to an error in scale count whereby some of the scales of the smaller individuals were overlooked, but very probably was due to the fact that the large individuals of an age group were also the large individuals of their year class at the time of scale formation, so that more scales were laid down in the longitudinal rows. A comparative study of the average scale numbers of the various age groups of the three collections considered indicated that the number of scales in the lateral line remained constant with the year classes and with the age groups (III and older) studied.

see page 284

ANNULI AND NUMBER OF YEARS OF LIFE

That the annuli of scales are truly "year marks" has been conceded in the past by most of the investigators who employed the scale method. In many instances the basis for the acceptance of this assumption has been the fact that the scale method actually worked in practice. Masterman (1913) states it as follows: "In studying the average sizes, average weights, and seasonal occurrence of the different age groups and numerous other statistical relations the age data obtained from the scales give a rational and consistent result throughout." The more recent literature, however, shows a tendency that views with some skepticism certain phases of the scale theory. One or more of the assumptions (p. 278) of the scale method, which were taken for granted by most of the investigators of some years ago, are now being subjected to a more critical examination. Further, whereas previously an assumption found valid for one species of fish was accepted in many cases without investigation as valid for another, now the tendency exists to consider each species on its own merits. These present tendencies justify a reconsideration of the whole scale theory, but especially of the assumption that annuli are age marks—the keystone of the theory. In this section, then, an attempt has been made to review all the criticisms that have been directed against the age hypothesis and the nature and extent of all the evidences, direct and indirect, that support or contradict the hypothesis.

CRITICISMS

Brown (1904) comes to the conclusion that the concentric rings (circuli) on gadoid scales do not represent annual increments because (1)[9] scales obtained from different parts of the body show 90, 60, or 30 rings, according to the part selected and (2) because the scales are shed immediately after spawning. Tims (1906) concurred with Brown and found further (3) that he could not detect a regular alternation of narrow and broad zones on the scales of Gadidæ after the first annulus (a photograph of a scale of a cod 2½ feet long showed no year rings), and (4) that in clupeoid scales the annuli varied in number in scales removed from the same situation from the same fish. This same variation in the number of annuli was found in the marine herring by Buchanan-Wollaston (1924) and Hodgson (1925), in the eel by Gemzoë (1908), in the Atlantic salmon (rarely) by Calderwood (1911), and in the lake herring (rarely) by the writer (p. 271). In the haddock, Thompson (1923) found that all scales of a fish show the same number of annuli, "with the exception of those, which, lying on the head and the bases of the fins, were as many as two years short and are evidently much later in being developed [p. 16]." Both Buchanan-Wollaston and Hodgson discovered that certain symmetrical scales taken from the region between the dorsal fin and the tail, above the lateral line, often were found to show a less number of rings than the scales from the anterior part of the body. Either the former scales cease to develop after three or four years or the latter become "ringy." Hodgson (1925) writes, "The generally accepted theory that all the scales of a fish exhibit the same number of rings is erroneous. This, of course, does not mean that in a complete suit of scales a widely different number of rings can be found, but, rather, that in certain areas, on larger fish, the number of rings may be less than the modal number for that particular herring [p. 3]." The scales of Gemzoë's 65 centimeter eel showed from 1 to 6 annual rings, the number varying with the areas on the body.

Gemzoë (1908) claimed (5) that the scales of the eel first appear after the second year of life, while Schneider (1909) asserted that the scales of the eel (*Unguilla vulgaris* Flem.) form in either the third, fourth (usually), or fifth summer. "Als

[9] The criticisms are numbered consecutively.

absolut sicheres Merkmal für das Alter eines Aalindividuums an Jahren können also die Zuwachszonen der Schuppen nicht dienen, was in anbetracht des sehr unregelmässigen Entwicklungsganges * * * zu erwarten war." Hornyold (1922) concludes, similarly, that in the eel, scales first appear not at a definite age but at a definite size (6 inches) of the fish; and further, that the difference between the number of zones of the otolith and the scale varies during the life of the eel according to the faster or slower development of the various zones of the scale. The differences varied from 4 to 10, in general the greater discrepancies occurring in the larger eels. In the yellow eels of the Sarthe, however, the author (Hornyold, 1926) finds much smaller discrepancies between the otoliths and scales (difference of 2 or 3 zones), which discrepancies do not increase with the age of the fish. Wundsch's (1916) tables show that the otoliths of his eels generally form three more zones than do the scales, although the difference in the number of zones varies from 2 to 6. Ehrenbaum (1912) believed that mackerel scales form during the second year of life, while Meek (1916) stated that as the marine herring spawn in August the first winter is not registered on their scales. According to Molander (1918), the spring herring (marine) hatched in the spring and the winter herring hatched in late summer or early fall (September) form an annulus in the first winter of life, but the autumn herring hatched in October–November do not form an annulus until the second winter of life. It is possible that individuals among the winter herring that hatch late do not form a ring the first winter, while those among the autumn herring that hatch early do form a first winter's ring. At any rate, the following condition generally obtains: A 2-year-old spring herring has its second annulus at the margin of the scale, a 2-year-old winter herring has its second annulus within a nearly completed summer growth zone, and a 2-year-old autumn herring has one annulus and a completed summer growth zone at the margin.

Arwidsson (1910) studied a series (148 fish) of young salmon (*Salmo salar*) 2 to 26 months of age and found (6) that the first annulus was completed in September in a 62-millimeter fish 6 months old. In December, at the age of 9 months, several other individuals greater than 60 millimeters in length completed the first annulus. In May, the fourteenth month, none of the fish under 61 millimeters in length had completed the first annulus, but by July all fish showed on their scales seven or more circuli outside the first year mark. In September (eighteenth month) two individuals had already formed 5 to 6 circuli outside the second annulus, while none of the 21 or 26 months old individuals had completed this year ring. The author concludes that the first annulus does not appear at a definite time nor at a definite age but at a definite length of the fish—namely, 60 millimeters.

Rich's (1920) results parallel somewhat those of Arwidsson. If I understand the former correctly, it is possible for the Pacific chinook salmon to show, in the second spring of life, one, two, or three checks on their scales. The yearling fish, migrating in the spring, may show a "primary check" in addition to a winter ring. Migrating fry taken in the estuaries after May may show a "primary" and a "migratory" check. Presumably the early migrants of such fry would, in addition, have formed a winter ring in the sea. The three kinds of checks can not always be distinguished, while in some instances the migratory check is the winter band (Rich, p. 49). The primary check (presumably always the first to form) may occur any time early in life; the migratory check formed in the estuary may occur anytime after the 1st of June in the fry, while the first annulus may form as early as August. The new growth (not the "intermediate" growth of the estuary), outside the first winter rings, may begin any time between August and the May following.

Schneider (1910) presented some evidence to show (7) that the fall marine herring may possibly form two annuli each year, as Damas (1909) had found to be true in the cod (*Gadus virens*). Lee (1920) asserted that normally in the haddock the approximated circuli of the annulus formed some time during the period July–September, to which were added one or two wide sclerites in September or October and additional narrow sclerites in the winter months. H. Thompson (1923) found that the Skagerag haddock usually formed a false ring in the first year at a body length of approximately 11 centimeters, when the fish descended to the bottom and encountered new environmental conditions. Nall (1925) reports that marking experiments have shown that a considerable number of sea trout in the estuary of the Beauly and Ness Rivers feed freely on sprats in midwinter, with the result that these trout put on a rapid growth, represented by a series of widely spaced rings on the scales. To such fish the ordinary rules for age determination can not be applied. Jacot (1920) believed that in the mullets an annulus is the result of a long northward migration in the spring, which may be completed in two stages, and therefore concluded that some fish may form two annuli in a year at times.

Several authors contend (8) that at times one or more annuli fail to form on the scales, for individuals have been found that apparently were far too large for their age, as determined from the scales. Examples of this were found among the Pacific herring by W. Thompson (1917), among the shad by Roule (1920) and Leim (1924), among the haddock by H. Thompson (1923, 1924) and Saemundsson (1925), and among the sea trout by Nall (1926).

(9) In certain waters some species form no annuli at all on their scales, while other species do. Schneider (1910) found definite growth zones in the scales of all the African species of fish examined by him, except in a small form of Gobius(?) from Madagascar. Paget informed Lee (1920) that no annuli are evident in the scales of Egyptian species. Godby (1925) reports that the offspring of certain *Salmo salar* introduced into New Zealand waters showed no winter band on their scales, whereas the young of introduced Quinnat salmon did form an annulus.

As has been pointed out by many authors, much of the confusion in the reading of scales is due (10) to the formation of accessory or secondary rings (see fig. 6), which are difficult to distinguish from the annuli (see W. Thompson, 1926, p. 54), (11) to the indistinctness of certain annuli (Leim, 1924, p. 76), and (12) to the crowded condition of annuli in scales of old fish or of small size. (13) Regenerated scales may introduce errors in age determinations, as these scales sometimes may simulate closely the normal scales, as in the marine herring (Schneider, 1910); or the regenerated area representing the first year's growth may be so small that it is easily overlooked, as, for example, in the scales of the Atlantic salmon (Milne, 1915).

Prof. D'Arcy Thompson (1914; Sherriff, 1922) does not believe that the annuli in the scales of the marine herring are invariably year rings. He can not understand Hjort's and Lea's conclusions, based on scale studies, that (14) one year class dominated the fisheries for five years in succession, because there must be

great fluctuations in the annual birth rate; and this would not allow a smooth curve, as Hjort obtains, when the specimens are arranged according to their year class and the percentage of individuals in each. "* * * an increase of birth rate or a diminution of natural mortality such as would cause the race of 10-year-old herring to outnumber all the rest put together from 4 years old to 15, is very hard, indeed, to imagine [1914]." "That 4-year herring normally show four rings we all believe, but if in a hundred herring, mostly four-ringed, I find a few with three and a few with five rings, am I bound to believe that these are younger and older fish mixed up with the 4-year-olds; or may they not be merely variants or abnormal members of the stock? There is room for doubt * * * [Sherriff, 1922]." Thompson (1914) refers to Miss Massy's (1914) experiments, which showed that 3-year-old oysters reared in an aquarium had formed from two to seven rings in their shells. Experiments on the formation of rings in oyster shells showed that the variations from the mean in the number of rings in an age group appear to follow the laws of chance, the mathematical laws that govern the phenomena of variation. As (15) the samples of herring showed a similar variation about a mode (unimodal) as the oysters, the critic believed that each sample comprised not different age groups but one homogeneous age group with a variable number of rings. Thompson points out that in the haddock, cod, and plaice the size groups fall into several groups; normally the size-frequency curves of these species are multimodal, not unimodal.

Under Thompson's direction, Miss Sherriff (1922), a mathematician, attempts to ascertain by mathematical analysis whether a sample of herring of a single shoal is a homogeneous age group and whether "ringiness" is or is not a measure of age. She concludes that the analysis favors the hypothesis of a homogeneous age group, but that further studies must be made to definitely solve the problem.

Birtwistle and Lewis (1923) and Lea (1924) discuss Miss Sherriff's criticisms. The former authors point out that both symmetrical and asymmetrical curves may come from the "laws of chance;" that asymmetrical curves may go along with homogeneity or with heterogeneity, and that asymmetrical curves may even be the results of several symmetrical curves combined. They construct an age-length frequency curve for 389 plaice and point out that it is difficult to deduce from the resulting asymmetrical curve that the plaice are heterogeneous with respect to age. If the age were in doubt, we might argue that all the plaice were two years and that the number of rings on their scales varied, as Sherriff does in the herring; but in plaice, experiments have shown that age estimation is a fact. "How are we going to reconcile these two positions, namely, that we can construct a curve from a sample of herrings, which suggests that variations in length and scale rings are due to chance and do not indicate age, and at the same time we can construct a similar type of curve from a sample of plaice in which we do definitely know that the variations in length and otolith rings do indicate four different age groups [p. 79]?"

Lea's paper is a direct reply to Miss Sherriff's. Analyzing Sherriff's and Thompson's statements, Lea writes:

> It would appear, therefore, that there can be no doubt that Prof. D'Arcy Thompson considers the conformity between the empirical curves of frequency and the theoretical curves of variation to be a criterion in deciding whether a sample of herrings contains one single year group or several. To my mind it appears somewhat singular that he has made no attempt to demonstrate the justi-

fication of an assumption which is of fundamental importance for the biological valuation of the results of the mathematical analysis * * *. The investigation [Lea's] has been an attempt to decide the following question: Is it possible that herrings of several age groups may form a shoal, for which the curves of frequency with regard to length as well as to age have such a shape that there may be adjusted theoretical curves of variation with considerable "probability of fit" [p. 6] ?

From a consideration of hypothetical and actual samples Lea concludes:

From the above it will be seen that empirical curves of frequency, of which the similarity to theoretical curves of probability or variation can not be doubted, may arise from and represent processes which have nothing to do with variation and variability in the sense given to these terms by Prof. D'Arcy Thompson. The curve of frequency for the length of the herrings in a random sample may easily show sufficient degree of similarity to a theoretical curve of variation, even though the individuals in the sample belong to several age groups, and the curve of frequency for the number of rings on the scales may also have a form, which is so like a theoretical curve of variation that it might be mistaken for one, without this fact arguing against the assumption that the rings are annual rings and that consequently the curve of frequency represents the distribution of age in the shoal from which the sample comes.

But if that is so, the results of Miss Sherriff's analyses justify the conclusion that the rings on the scales are annual rings as little as they justify the assumption of the contrary. The method does not carry us any further towards the solution of this problem, in one or the other direction. It is not a method for an investigation to determine the nature of the scale rings, as it does not suit the problem to be solved.

The problem concerning the rings on the scales of the herrings is *per se* a problem concerning the rate of formation of rings in the course of time.

A general criticism of the age hypothesis, which probably did not receive due consideration by the critics in the past, is (16) the scarcity of convincing experimental evidences. Such data are lacking even now for most of the species of fish whose scales have been employed for age determinations. The experimental data are probably adequate only in the case of the carp, the Pacific and Atlantic salmon, and the whitefish, while they are fragmentary in about a half dozen other species of fish. It is partly due to this factor, "it has never been proved," that Prof. D'Arcy Thompson persists in his attacks on the age hypothesis in fishes in general (1917) and in the marine herring in particular.

Most of the 16 criticisms listed above are specific—that is, they involve only the particular species referred to. It is not improbable, however, that had a critical study accompanied each new investigation some of the valid criticisms would now have a much wider application. Further, all the criticisms do not have the same importance; it is now definitely known that some are untrue [2 and 7 (Jacot, 1920)], or, though acknowledged as being generally true, do not disprove necessarily the age hypothesis (1, 9, 14, 15, and 16); some are questionable, supported by no definite data (8) or supported by controvertible data [3 and 6 (Arwidsson, 1910); 7 and 15 (Sherriff, 1922)]; and some, though valid, apply to exceptional cases only (4 and 13) or permit corrections (5) or make age determinations doubtful in the species of fish involved or in certain individuals only [4 (marine herring, eel), 5, 6 (Rich, 1920), 10, 11, and 12].

INDIRECT EVIDENCES

The indirect evidences that were believed to support the age hypothesis are as follows: (1) By following the growth history of the marginal portion of the scales of fish collected at intervals throughout a part of a year, or for a longer period, it was

ascertained that an annulus formed during a certain definite period of the year (Lea, 1911; Fraser, 1916 and 1917; Clark, 1925; Hodgson, 1925; and many others). (2) In a fixed, homogeneous fish population a dominant age group, as determined by scales, persistently preponderates in all the representative samples of a series taken in the same locality and in the same year but on different dates (Lea, 1910). (3) An unusually abundant year class may persist in the commercial catches for two or more years, and in each successive year the dominant group will show one additional annulus on their scales (Lea, 1910; Hjort, 1914). (4) Fluctuations in the fisheries have been definitely correlated in several cases with the scarcity or abundance of a particular year class, as ascertained by the scales (Hjort, 1914; Järvi, 1920; Storrow, 1922). (5) The interval between the periodic "big spawning runs" in certain species of Pacific salmon coincides with the number of years (as determined by the scales) required for the attainment of sexual maturity by most of the individuals of a year class (McMurrich, 1912, p. 5; Gilbert, 1914, p. 56). (6) Norwegian herring recognized in the commercial catches of 1910 to 1915 by their abnormal scales (the third summer zone was narrower than the fourth) each successive year showed an additional annulus on their scales (Lea, 1919). (7) The well-known fact that the lengths calculated from scales have nearly the same average value as the corresponding average length of directly measured fish whose approximate age is known points to the correctness of the age hypothesis. (See Gilbert, 1914, p. 64; Thompson, 1917, p. 61.) (8) Life-history data acquired by the scale method have, in many species, been found to agree with similar data obtained for these species by other methods, such as the frequency curves first employed by Petersen (1891 and 1895; Thomson, 1904). (9) Immature fish are the young fish. The fact that the scales of these fish show them to be young fish lends support to the accuracy of the scale method (H. Thompson, 1924). (10) Mathematical tests based on the theory of probabilities show that, on the average, the age method by scales is correct in salmon, herring, and gadoids for at least the first two or three years of life (Lee, 1920).

So far as I know, the last statement is the only one of the 10 evidences listed above whose supporting data have been challenged. (See Sherriff, 1922.) The other statements, though supported by accurate even though at times fragmentary data, have not always been accepted as evidences in favor of the age hypothesis. For example, evidences 3, 4, and 6 in the herring did not convince D'Arcy Thompson (1914), but the prolonged dominance of one year class was used by him as an argument against the age hypothesis. (See p. 290.)

DIRECT OR EXPERIMENTAL EVIDENCES

Because of the general lack of emphasis on the direct evidences, many excellent opportunities to obtain good experimental data were disregarded by investigators engaged in studying the rates of growth of fish in the field and laboratory. In some instances the experimenters made no reference at all to the number of growth zones or annuli on the scales, but, fortunately accompanied their reports with clear photomicrographs of the scales; in others the number of annuli or growth zones was mentioned in a casual way only. In this section the papers are reviewed in chronological order under two major subdivisions, the first to include the evidences obtained from fish reared in artificial ponds of commercial institutions or of hatcheries and in

These proofs show approximate correctness of ring theory. A considerable variation in the rings would not be detected.

aquaria, the second to include those acquired from marking experiments conducted in the field.

Hintze (1888), who for some reason seldom is mentioned in reviews, contributed the first bit of experimental evidence toward the determination of age by the scales. He examined carp of known age and announced that the age of this species can be determined quite accurately from the structure of the scales. At the same time Hintze illustrated his method by diagrammatic sketches (reproduced by Walter, 1901) which left no doubt that he referred to the annuli of scales. His sketches represented scales of carp in their first, second, third, and fourth year. From these sketches it becomes quite evident, however, that the author's interpretation of the scales was only partly correct. His scale of the carp in its first summer correctly shows no age rings. The scale of the carp in its second year shows two annuli of approximated and incompleted circuli and three zones of relatively widely separated circuli. The scale of the 3-year fish shows three annuli and four zones of growth, while that of the 4-year individual shows four annuli and five broad zones. It is apparent that Hintze erred in his interpretation of the scales of the 2-year fish. According to Walter (1901), Hintze's difficulties were due to the fact that he did not examine carefully the differences between the finer structures of normal and abnormal scales nor the characteristics of a true annulus. His erroneous interpretation was due to the accessory annuli so common on the scales of carp reared in ponds.

In his preliminary paper Hoffbauer (1898) describes very carefully the finer structures of carp scales and presents two sketches. In a later paper (1900) the correct method of age determination is more clearly elucidated and convincingly established for carp 3 years of age and younger. Hoffbauer based his conclusions on his knowledge of the life history of many carp bred and reared in ponds for commercial purposes. To verify his assumptions supplemental evidences were adduced from carp subjected to experimental conditions. As Hoffbauer's works form the foundation upon which all later scale studies have been built and his experimental evidences carry more conviction than many subsequently produced, I shall review his work more in detail.

Hoffbauer observed that the scales of the pond carp grew with the body. He noticed that during the warm months of the year, when the fish grew most rapidly, the marginal concentric ridges of the scales stood out in bold relief and were well separated, but as winter approached they became more closely approximated and began to diverge and break in the lateral fields. This condition at the margin persisted throughout the winter when the carp were in a state of hibernation and all body growth had ceased. With the resumption of growth in the spring the widely separated circuli reappeared at the margin. The mark thus left on the scales he correlated with a retardation in growth and concluded that the number of such marks gave a correct index to the age of the fish. He successfully applied his hypothesis to many pond carp whose ages and life histories were known.

In order to verify this hypothesis the author subjected normal carp to various environmental conditions. He considers, first, a carp in its third summer which had been undernourished all its life and consequently had grown very slowly. He observed that (1) the circuli were more closely approximated and more uniform throughout the entire scales than those of normal scales, (2) the annuli were less marked than in normal scales but were recognizable by the usual characters of an annulus, (3) the number of the circuli in each growth zone, and (4) the distances separating the annuli fell below the normal.

He considered next a series of scales taken periodically from carp reared in pond and aquarium and observed that the rate of growth of the scales, the number of circuli, and the distances between the circuli varied directly with the rate of increase in body weight. The aquarium fish grew more slowly than those of the pond. Further, to eliminate racial differences he took two carp of the same brood and of equal weights and placed one in an aquarium and the other in a pond, at the same time removing a few scales from each fish. At a later date more scales were removed and compared with those first taken. Those from the pond specimen showed an increase in scale surface with widely separated circuli, while those of the aquarium fish showed little increase in scale surface and closely spaced circuli. He ascribed the difference in growth to the richer supply of plankton food in the pond water.

That other factors may be involved in scale growth he illustrated by the following: The water in a pond containing carp was accidentally allowed to evaporate. Some time after renewing the water supply in this partly dried pond the scales of a surviving carp were examined. It was found that the abnormal condition was registered on the scales by the formation of dark, closely approximated circuli, the normal condition by clear, widely separated circuli. It was assumed that the carp were unable to acquire their customary food. Again, an individual was found to be greatly emaciated, and on examination a swelling was located in its anal region. Hoffbauer found that the scales indicated very clearly when the growth processes were first disturbed.

The oldest carp examined were at the end of their third year. The author believed that the reading of the scales from carp older than three years became increasingly difficult with age as the transparency of the scales diminished with their increased thickness and size, rendering the circuli, especially those of the first year, less distinguishable. He also found that all the scales of a fish were not equally reliable for age determination, as some developed more or less sharply defined accessory annuli. However, if a large number of scales were examined some would register the true age.

In later papers Hoffbauer (1901, 1904, 1905, and 1906) supplied further evidences to support his hypothesis. He extended his observations on the carp and applied his method to several other species of fish (*Carassius carassius*, *Micropterus salmoides*, *Perca lucioperca*, Esox and Salmo).

Reibisch (1899) attempted to apply Hoffbauer's method to the scales of the marine plaice (*Pleuronectes platessa*) but failed. At Professor Hensen's suggestion, Reibisch then turned to the otoliths, or "ear stones," and discovered the year rings in these structures.

The observations of Hoffbauer were repeated, and his conclusions were examined critically by Walter (1901), who studied the scales of the carp in commercial ponds. He granted the general truth of Hoffbauer's hypothesis but maintained that unless the finer structures of a scale were known age determinations would be erroneous in a large percentage of cases. Thus, for example, of 24 determinations that he made 13 were found to be incorrect. He found that Hoffbauer's criteria for a true annulus could not be relied upon with certainty and therefore proceeded to search for other criteria. In doing so he discovered the fundamental principle underlying the method, later devised by Dahl and Lea, of calculating the length of a fish for each year of its life by the proportionate width of the bands on its scales. Walter found that the relative width of a year zone on a scale expressed to a certain degree the relative intensity of body growth, designated in terms of length and height.

As Walter's paper is seldom referred to and his highly significant contribution to the scale method seems to have been overlooked, I quote him verbatim (p. 108):

> Im Durchmesser des Vorder- und Hinter-feldes musz also das Längenwachstum, in demjenigen der Seitenfelder das Höhenwachstum sich widerspiegeln. Die Verhältnisse der einzelnen Jahresfelder und der verschiedenen Teile desselben Jahresfeldes zu einander werden uns deshalb ein getreues Spiegelbild des betreffenden Wachstums geben. Unter normalen Verhältnissen und bei rationeller Zuchtmethode ist der Längen- und Höhenzuwachs im zweiten Lebensjahre weitaus am gröszten, deshalb musz auch das zweite Jahresfeld der Schuppe die gröszte Breite besitzen. Von da ab nimmt bei über-wiegendem Breitenwachstum das Längen- und Höhenwachstum beständig ab, mit ihm auch die Breite der folgenden Jahresfelder der Schuppe. Wir können also bereits aus der relativen Breite der einzelnen Jahresfelder bis zu einem gewissen Grade auf die Intensität des Wachstums innerhalb der verschiedenen Jahre schliessen, und ganz besonders ist das der Fall beim ersten und zweiten Jahresfelde, in welchen ja nur das Längen- und Höhenwachstum zum Ausdruck gelangt.

Walter emphasized the fact that the growth of a scale in length is correlated with the growth of the body in length and not, as Hoffbauer stated, with the growth of the body designated in terms of weight.

Thomson (1904) recorded some observations on the scales of a young whiting (*Gadus merlangus*) held captive from May, 1902, to July, 1903 (age, 1 year and 4 or 5 months). The specimen grew from 10 or 20 millimeters (0.4 to 0.8 of an inch) to a length of 8½ inches. It was "fed regularly from the hand." No winter ring was recognizable in its scales at the time of death. Thomson attributed this absence of an annulus to the fact that the fish was supplied with food regularly.

Johnston (1905) presents photographs of scales taken from hatchery salmon (*Salmo salar*) 1, 2, and 3 years of age. After describing the scales of the 1-year salmon and comparing them with the scales of the 2-year fish he observed that "the growth of the first year is easily distinguished" in the latter and that "the new season's addition is marked by a wider separation of the lines at the periphery of the scale." In the scales of the 3-year salmon retained in a fresh-water pond "the growth of the first and second years can be made out, but the lines of the latter are not so easily distinguished from those of the third year." In a second experiment Johnston (1907) again found that artificially reared salmon 2 years old had completed two annuli on their scales.

Salomon (1908) found two distinct summer growth zones in the jawbones of an artificially reared and well-nourished river trout (Huche) 0.90 kilogram in weight and 1½ years of age.

Dahl (1910) studied hatchery salmon and trout of known age and known life history and concluded, as Johnston, that "the markings on their scales corresponded exactly with the seasons during which the fish have lived," and that the age determined from the scales agreed with the known life of each individual. Dahl's specimens hatched in five different years ranged from 1 to 3 years in age.

Menzies (1912) found it impossible to estimate the age from the scales of an Atlantic salmon hatched in April, 1905, and regularly fed in a pond until its death in August, 1911, when it weighed 4 pounds and 3 ounces. Although the fish had spawned in January, 1910, and in March, 1911, no spawning marks were found on its scales.

Mohr (1916) examined the scales of 28 perch pike (*Lucioperca sandra* Cuv.), which, reared in a pond from eggs laid in April, 1915, were killed November 13, 1915. The fish averaged 9.3 centimeters in length and 4 grams in weight and their scales showed no annuli.

In August, 1914, Storrow (1916) placed a European wrasse (*Labrus bergylta*), 2 to 3 centimeters long, in an aquarium and found that by May 24, 1916, when 8 centimeters long, this fish had formed two broad growth zones on its scales. The new growth of 1916 had not yet started.

Cutler's (1918) experiments on 85 flounders and 52 plaice, though carried on primarily to determine "the conditions necessary to the production of these annual rings [p. 471]," give some direct evidence on the formation of annuli. The experiments were continued from July, 1915, to October, 1916, and scales were taken in July, 1915, and January, May, and October, 1916. The curves representing the scale growth of the fish (ages 2¾ to 4½ years, as determined by scales) in the control tank during the experimental period show distinct minima (annuli) and maxima (broad zones) growth rings and closely follow the temperature changes of the seasons. Even the fish in two of the experimental tanks ("abundant" and "scanty") formed distinct minima and maxima rings, which corresponded to winter and summer temperature conditions, respectively.

Fraser (1918), on examining scales taken January 29, 1917, from four artificially reared sockeye salmon hatched in the spring of 1913, reports that, "although there is much sameness in the rate of growth indicated throughout, it is possible in almost every perfect scale to make out the winter check somewhat readily."

To test Reibisch's otolith method, Williamson (1918) examined the otoliths of two plaice of known age, the one 4.5 centimeters long and 14 months old, the other 11.5 centimeters long and 2 years and 8 months old. The latter individual did not show more rings than a specimen of the same size, which Reibisch believed was 11 months old. Williamson concludes, therefore, that Reibisch's claim that one ring of an otolith stands for one year of life rests on no substantial basis. "His assumptions are unsupported by any satisfactory argument. His paper appears to be a special pleading for the one-ring, one-year hypothesis, not an attempt to discover if age markings actually exist." Williamson considers the number of prominent rings on the otoliths to be a measure of the size of the fish.

Rich (1920) studied several series of scales from chinook-salmon fry and yearlings of known ages and found that, "Compared with the scales of wild fish, those from hatchery specimens show an irregular growth. There are frequent minor checks, indicated by narrower rings; but, as a rule, the true winter check is less well marked [p. 9]."

Peart (1922) observed that annual growth is not nearly as well differentiated on the scales of artificially fed trout as on those of the wild fishes. The former scales are read with some uncertainty, the doubtful area being confined to the first two or three years of life, the years of sexual immaturity. Peart ascribes this "vagueness of artificial scales" to the attempts of the breeders to make their fish grow continuously.

How many rings would have been found if the fish's age had been unknown?

In a previous paper (Van Oosten, 1923) I have shown that scale age and fish age agreed in whitefish 8 and 9 years of age—the oldest fish yet recorded in which the number of annuli was demonstrated to agree with the years of life of the fish.

My conclusions were based on a study of the scales of 27 whitefish (*Coregonus clupeaformis*) hatched and reared in the New York Aquarium. The fish were hatched in January, 1913, and died (or were killed) at intervals between August 13, 1920, and January 3, 1922—a period of 16 months. The fish received had died (been killed) during every month of the year except November. It was shown that the first eight specimens received, which ranged from 7 years and 7 months to 8 years and 2 months in age possessed scales with seven completed annuli and various amounts of marginal growth. The eighth annulus was first completely formed in the specimen killed April 28, 1921, at the age of 8 years and 3 months. The fish received after April, 1921, whose ages varied from 8 years and 4 months to 9 years, showed eight completed annuli and various amounts of marginal growth on their scales. Five photomicrographs of scales taken from fish killed in different months were published. I concluded that the annuli in whitefish scales are "of the same number as that of the winters of the fish's life, if we exclude the first one in which the fish was hatched."

In October, 1919, Dannevig (1925) placed 150 codlings, 8 to 12 centimeters long and presumably about 6½ months old, in a hatchery pond and studied the scales of 61 of these caught at irregular intervals until May 23, 1922. The fish were fed only from May to the middle of December in each year. In October, 1919, small sclerites were situated at the edge of the scales of all fish. In the following March, May, and June the smaller fish still showed small sclerites at the margin of the scales, but the larger specimens showed large sclerites. The fish taken in December, 1920, March and April, 1921, had large sclerites at the edge of their scales and two minimum-growth zones situated at a considerable distance from the margin, although the December specimen was only about 20½ months of age. The specimens taken October, 1921, showed small sclerites at the edge of their scales, while those taken May, 1922, showed three minimum-growth zones and a large marginal growth of wide sclerites. It is unfortunate that the more critical data of winter specimens were not obtained.

The experiment, as far as it goes, probably confirms the age hypothesis. Dannevig concludes that in the majority of individuals the zones with minimum sclerites are autumn zones and tell how many autumns the fish lived. "The greatest difficulties appear when dealing with the slow-growing individuals, the lack of large sclerites makes the resting zones to intermerge, being often only separated by a few medium-sized sclerites. On the other hand, such medium sclerites might appear in the middle of a resting zone; in such cases we may erroneously be inclined to count two zones. This is the case especially when dealing with the medium-sized material from May and June, 1920."

H. Thompson (1926) attempted to show experimentally the effect of regulated and plentiful food supply on the general metabolism of haddock, codling, whiting, and saithe introduced into tanks at various times during the period 1922–1925. The

average temperature of the aquarium water was the same as that of the water in the sea, but abundant food was supplied continuously. The haddock and whiting lived well to the end of the third year; the codling did not do well after the beginning of the third summer, nor the saithe after the completion of the second autumn. Growth was continuous throughout the year, the maximum occurring from May to October, the minimum in March. In all cases where fish were transferred to the aquarium during the season of greatest growth a false winter mark appeared on the scales. Thompson concludes that abundant proof was obtained of the unfailing formation of normal winter markings on each occasion that the fish passed through one or two winters in captivity, although growth did not actually cease, as occurs in the sea. The annulus was a slighter check in the aquarium than in the sea fish.

Creaser (1926, p. 37) writes: "A series of bluegills (*Helioperca incisor*), sunfishes (*Eupomotis gibbosus*), and large-mouthed basses (*Aplites salmoides*) collected in February had scales with margins like those of late fall. When these fishes began to grow in the laboratory a typical annulus was formed by the resumption of scale growth. This production of an annulus after a period of growth cessation has also been shown for the green sunfish (*Apomotis cyanellus*)." (Work on the green sunfish was done by a student of Prof. Frank Smith, University of Illinois.)

Johnston (1905 and 1907) is probably the first to test successfully the age hypothesis by marking wild fish in the field. Atlantic salmon were marked during the period April 25 to June 6, 1905, when, as young fish (smolts), they were migrating to the sea. The first marked grilse of this experiment was recaptured June 1, 1906, and subsequently many other marked specimens were taken (Johnston, 1908 and 1910). Mr. Johnston published photographs of scales taken from marked salmon that had returned after a sojourn of 1, 2, 2½, 2¾, and 3 years in the sea. In all recaptured fish the number of broad summer (sea) growth zones on the scales corresponded with that of the summer seasons the fish were known to have spent in the sea. Johnston's results were confirmed by the work of Hutton (1909 and 1910), Malloch (1910), Milne (1913), Menzies (1913), and others who reported on scales taken from marked Atlantic salmon.

Gilbert (1913) refers to a marking experiment performed in the midwinter of 1910–11 in California on some yearlings of the Pacific coho salmon. "In the spawning run of the winter of 1911–12 several of these returned to the same stream as mature male grilse, with scales clearly in agreement with their known age, having formed a single summer band outside the close-ringed nuclear area and a marginal narrowing for the fall growth [p. 17]."

Winge (1915) found that the marked cod studied by him formed one or two minimum growth zones on their scales, depending on the interval between marking and recapture. The minimum zones formed in March.

Fraser (1921) reports the capture of a Pacific coho salmon on October 11, 1917, and of a Pacific spring salmon on January 9, 1918, both of which had been marked as fry on March 24 or 25, 1915. The scales of both specimens corresponded perfectly with the known age of the fish.

The California Fish and Game Commission made several experimental plantings of marked Pacific salmon. In 1919 one specimen was captured from a lot of 3,500 quinnat salmon hatched in the winter of 1914–15 and marked on February 15, 1916.

Five broad growth zones were plainly evident on the scales of the captured fish (Snyder, 1922, p. 107). Three king salmon hatched in the winter of 1916–17 and marked in the fall of 1917 were captured in the summer of 1920 and according to Snyder (1921) had formed three annuli and an incompleted fourth summer's growth zone on their scales, although, judging from the photomicrographs of the scales, Snyder's conclusion is not wholly convincing, as well-defined accessory checks also appear. The 1919 experiment, however, was the most successful (Snyder, 1922, 1923, and 1924). Of 25,000 king salmon hatched in February, 1919, and marked in November, 1919, 23 were taken in the fall of 1921, 23 during the period June 7 to November 15, 1922, and 12 during the period June 8 to November 15, 1923. Snyder describes in detail and illustrates the structural features of the scales of the marked fish caught in 1921 and later compares these scales with those removed from the marked individuals taken in 1922 and 1923. In the 3-year (1921) specimens the normal fresh-water nuclear area as well as the second annulus are sharply defined. A large third-year growth is situated at the margin. In the second growth zone, however, appear two accessory checks, one near the first, the other near the second annulus. These checks were characteristic of the scales of 17 of the 23 salmon caught. The scales of the remaining marked fish differed only "in a minor degree from the others by having a more or less well-defined check about halfway between" the other two accessory checks. The author associates these accessory or minor checks with the feeding habits of the salmon. Besides indicating that the scales of the marked fish captured in 1921 interpret their age and life history quite accurately, the author compares the nuclear area of these scales with the scales of the yearlings preserved at the time of marking and finds that the two structures are identical. His photomicrographs illustrate this.

The scales of the marked salmon taken in 1922 showed one more annulus than those of the specimens taken the previous year. Not only this, but the minor checks found between the first and second annuli in the 1921 fish were also evident in the 1922 specimens. The 1922 scales could be identified, therefore, not only by the scales of the preserved yearlings but also by those taken in 1921. So, also, the scales of all the marked specimens taken in 1923 showed the same peculiar anatomic features found in the scales of the previously captured fish with the 1919 mark. They also showed one more annulus than those taken in 1922. The fish were in their fifth year.

Nall (1925 and 1927) reports on the recapture of 11 marked sea trout. In every case a reading of the scales of the recaptured fish confirmed the first reading and agreed with the known history of the fish, although in every case except one less than one year intervened between the marking and the recapture.

Sund (1925) published photographs of two scales from each of four saithe, one scale having been removed from the fish at the time of marking in the summer of 1921, the other at the time of recapture in the summer of 1922. The English summary of Sund's article does not state whether the scales correspond with the known history of the fish, but the photographs indicate that the two smaller individuals (53 and 57 centimeters) had, at the time of recapture, added one annulus and part of the 1922 summer's growth to their scales, while all the scales of the larger fish (80 and 90 centimeters) are undecipherable.

The above review indicates that the large majority of the experiments on the scales of fishes favor, as far as they go, the age hypothesis. It is a question, however, in certain cases at least, in how far the interpretation of the scales of the experimental fish was influenced by the known history of the specimens. We know, for example, that Hintze's interpretation rested entirely upon such knowledge. Or, again, in the case of Fraser's (1918) or Snyder's (1921) 4-year-old salmon it appears dubious, as judged from the photomicrographs of the scales, whether one wholly ignorant of the fish's history could interpret correctly its scale with absolute certainty. The failure of an annulus to form so as to be recognizable was in every case (Thomson, 1904; Menzies, 1912; Peart 1922) ascribed to an abundant supply of food.

CORRELATION BETWEEN GROWTH OF BODY AND SCALE

HISTORICAL

Walter (1901) first announced that the relative length and width of a growth zone on a scale expressed to a certain degree the relative intensity of body growth, designated in terms of length and height. (See quotation, p. 296.) He measured the shortest diameter included in each growth zone of 20 scales from each of three races of commercial pond carp in their third year. As the growth history (that is, the average weight, height, and length) for each year of life of these races was known, Walter was able to compare the average length of each growth zone on the scales with the average weight, length, and height of the fish for corresponding years and discover that the growth of scales is correlated with the length and height of the fish and not with its weight. Expressing the average weights of carp for the first three years of life in the form of a ratio, he obtained the values 1:10:30 as against the values 1:1.5:0.67, which express for corresponding years the ratio of the average widths of the zones on the scales. (The author should have employed the ratio of the average diameters; namely, 1:2.5:3.2.) However, as a rapidly growing race of carp attains a length of 7 to 15 centimeters the first year, 25 to 35 centimeters the second, 35 to 45 centimeters the third, and 45 to 50 centimeters the fourth year, it is seen that the ratio of the growth zones on the scales coincides more nearly with the length than with the weight of the fish.

Thomson (1904) and Seligo (1908) measured each growth zone along the anterior radius but did not compute lengths from their measurements, although the latter did base his conclusion relative to the rate of growth of the species directly on the relative width of each growth zone. Dahl (1907) asserted that the rate of growth could be seen from the width of the zones on scales and illustrated by means of diagrams how one may distinguish autumn from spring herring by the comparatively large first year's growth zone on the scales of the former.

The first critical and significant contribution to the subject under consideration is that of Lea (1910), who investigated whether "the scale of herring might not be used merely for determining the age of * * * but also for demonstrating how the particular individual's growth had occurred during the earlier growth periods * * * to what extent the different individual scales mutually accorded with each other in their mode of growth, and might be assumed to give the true picture of the whole animal" (Hjort, 1910). From this study the scale formula (p. 272) was evolved.

In a second paper Lea (1911) applied his formula and showed that the annulus in the scales of herring formed during the winter months.

Dahl (1910) applied Lea's formula to the scales of the Norway salmon and trout and found that the calculated and empirical measurements agree almost exactly.

Sund (1911) noted a lack of agreement between the actual and calculated length values in the sprat (*Clupea sprattus*) and found what was designated by Lee (1912) as the "phenomenon of apparent change in growth rate." Lee undertook a critical analysis of Lea's data and noticed that for corresponding years the total lengths calculated from the scales of old fish were always lower than those calculated from the scales of young fish; that is, the amount of calculated growth at corresponding ages increases regularly as the scales used are taken from fish of younger age groups. Thus, if the first year's growth increment is calculated from the scales of a 6-year fish it is less than if calculated from scales of a younger fish. This "phenomenon" has been found to characterize the uncorrected length computations of virtually all species of fish studied and up to the present time has not yet been accounted for definitely. Lee's is the first serious attempt to account for this apparent discrepancy in calculated growth rate. Her proffered explanations are discussed in detail on pages 328 to 329.

Lea (1913) answers Miss Lee's paper with a pertinent discussion of his published data and offers other statistics to prove that none of Miss Lee's explanations, except one, can apply to his herring. To get a true picture of the "phenomenon," Lea compared the calculated increments of growth, instead of the computed total lengths, of fish belonging to different age groups but to the same year class and taken by nonselective nets and considered the immature and mature individuals separately. He analyzed the phenomenon as follows: (1) In the immature herring all corresponding calculated annual increments decreased with each older age group employed. (2) In the mature herring the corresponding calculated increments decreased with increased age of the fish used for the first three years of life, increased with increased age for the next four years of life (4 to 7), and apparently remained constant with increased age for the later years of life. Lea found that the decrease in the increments was most pronounced in the period of sexual maturity. He explained this "phenomenon" on the basis that the largest individuals of a year class attain sexual maturity first and then segregate from their own component and congregate with another which consists of individuals sexually mature. Each year, then, the sexually mature individuals of a year class congregate with the older spawning fish that comprise the commercial catches until all the herring of a year class have matured. And, further, the development of the sex products has a retarding influence on the increments of growth.

Hoek (1912) did not see how Lea's explanations could account for Lee's phenomenon and believed that it reflected on the accuracy of the scale method, so that a comparison of calculated growth rates of fish of different year classes is unwarranted.

Delsman (1913) believed that the low values of calculated lengths probably were due to the slight contraction with age of the central, older parts of the scales although he ascribed the "phenomenon" in his herring material to the selective action of nets (1914). He concludes that on the whole the scale method is accurate

except for computations for the third year, which are usually about 1 centimeter too low. The author, therefore, added 1 centimeter to all these calculations.

Fraser (1916, 1917) thought that Lee's "phenomenon" was due to the fact that scales do not appear until the fish has attained a certain length and early body growth, therefore is not represented in the scale. In the salmon, scales first appear at a body length of 1.5 or 2 inches. If 1.5 or 2 inches are taken from the total length and the remainder divided in the same ratio as the growth zones divide the scales, Lee's "phenomenon", so Fraser found, is eliminated from the computations of the salmon.

Meek (1916) compares the actual lengths of the scales of younger herring with the corresponding lengths at each annulus of the scales of older fish and concludes that no shrinkage takes place in the scale. Meek plots the growth of the scales in relation to the length of the herring and finds that, due to the late appearance of the scale, it grows relatively faster than the body, the curve of scale growth crossing that of body growth in the fourth year. The author finds that the selective effect of nets on the young age groups would not explain the "phenomenon" in older fish, and that Lea's explanation relative to the segregation of the sexually mature young fish would not explain the "phenomenon" in his (Meek's) material, which consists largely of immature herring. Meek ascribes to the unequal growth rate of body and scale the fact that his calculated length values are always too low in the first two years, nearly accurate in the third year, and always too high in the fourth year of life.

Mottram (1916) discards Lea's method of computing lengths, for "* * * this method can not be of value unless the length of the fish, before scales are laid down, be taken into account, or unless the fish begins to form scales at a very small size, or unless the figures so obtained are such that they can not possibly be accounted for by the error in this method. Further, this method will be liable to an additional error if the scale-covered part of the fish does not always bear the same relation to the whole length of the fish [p. 45]." Lea's scale method is subjected to another source of error, owing to the fact that there is a wide variation in the relative sizes of the different parts of the scale among scales taken from the same fish. Mottram found, further, that Lee's "phenomenon" is reversed in Dahl's calculated measurements of the trout—that is, the corresponding computed values for any one year of life are larger in the big fish than in the small. In a study of comparative growth rates Mottram, therefore, groups his salmon according to the order of size of the actual scale measurements.

Taylor (1916) first pointed out that the error due to the more rapid growth of the scales than of the body relatively in early life "is probably compensated for by the late appearance of the scales," for he found that this error was negligible in his calculated lengths of the squeteague (*Cynoscion regalis*).

Molander (1918) attempted to ascertain whether the noted irregularities in the relations between herring and scales might not explain the irregularities in calculated growths. He obtained some interesting results:

1. In herring of different ages but of the same length the older have the larger scales. The scales, therefore, have not been developed to the same degree in a rapidly growing herring as in a slowly growing fish.

2. "The growth relation between fish and scales is entirely reversed in the course of years. The relatively greater growth of the herring, to begin with, is accompanied

by a relatively weak growth of the scales, whereas afterwards the slower growth of the herring is accompanied by a relatively stronger increase in the scales. * * *. Broadly speaking, the growth of the fish proves to be relatively stronger during the earlier years, that of the scales relatively stronger during the later." In this connection Molander does not explain the overlapping of scales. As was pointed out by Taylor (1916), scales that do not overlap at first must grow proportionately more rapidly than the body in order to do so.

3. The growth of both the scale and body is undulating—that is, a period of relatively strong growth is followed by one of relatively weak growth or, vice versa, weak and strong growths alternate; but alternating growths in fish and scales do not quite correspond. In the first four years fish and scale growth vary in the same way, but after that it appears that when scales have a strong growth the fish has a weak growth, and vice versa. This "antichronizing undulating growth" heightens the disproportion between the growths of the fish and scales, which is chiefly due to the late formation of scales. Tardy scale formation is also responsible for the lack of synchronism in the undulating growth.

4. Lea's explanation of Lee's "phenomenon" (selection and retardation of growth due to sexual maturation; see p. 302) is open to certain objections. If Lea's conjectures are correct, samples of herring should be predominantly mature or immature, and the lowering of increment values should end with the maturing of the species. But neither of these expectations materialize in the Swedish races of herring. Lee's "phenomenon" is due chiefly to the variability of the body-scale $\left(\frac{L}{V}\right)$ ratio from year to year, and the fault of the scale method is that it can not follow these changes in any particular age group. Another factor that produces irregularities in calculated growths is the admixture, in varying proportions, in each age group of different growth groups (faster or slower growing fish) that have dissimilar scale growths.

5. Uncorrected increments of growth and increments corrected for late scale formation were compared with actual measurements from fish. The uncorrected values were always too low in the first year of life (except in age group I), too high in the second and third years, too low in the fourth year, and alternately too high and too low thereafter up to and including the ninth year. The corrected values were much too high in the first year, too low in the second year, on the whole too high in the third year, and thereafter alternately too low and too high including the ninth year. The alternation of high and low calculated increments is due to the undulating growth of the scales.

Huntsman (1918a), employing four species of fish, made measurements of four scale dimensions and examined scales from six different body areas. He measured the dorsoventral or transverse (V) diameter, the anteroposterior or long (W) diameter, and the anteroposterior dimension of the anterior (X) and posterior (Y) fields. The total length of the fish (L) was used as a standard. In *Clupea harengus* $\frac{L}{V}$ decreases continuously with the increasing length of fish, $\frac{L}{W}$ decreases with growth at first rapidly but later extremely slowly, while $\frac{L}{X}$ decreases rapidly at first, then more slowly,

until it becomes approximately 50 at a body length of about 22 centimeters, when it increases slightly until death. Huntsman finds that in fish of different ages but of the same length the older have the larger scales. The varying proportion of small and large herring in an age group, therefore, would be partly responsible for irregularities in the growth relations between body and scales.

Huntsman finds that the changes in computed values based on X dimensions of herring scales are briefly these: "The length at the first winter period decreases rapidly at first [with age], then remains stationary, and finally increases very slightly. For the second winter period the length decreases at first, remains stationary, and then slowly increases. For the third winter period the length is at first stationary and then slowly increases. For the remaining periods the length increases from the first, but more at the beginning than later [p. 76]."

In *Pomolobus pseudoharengus* (alewife) the body scale ratios show that the posterior field grows at the same rate, relatively, as the whole body after a body length of 3 centimeters is reached, and that at least in the beginning the anterior field and the transverse diameter grow proportionately faster than the whole body. The later increase in the latter shows differences, which apparently are characteristic of the several regions of the body.

In *Tautogolabrus adspersus* (cunner) $\frac{L}{X}$ at first decreases with age and subsequently increases, while similarly in *Pseudopleuronectes americanus* (flounder) $\frac{L}{W}$ decreases at first and finally increases with age.

The lack of correspondence between fish and scale growth will account for a considerable portion of the differences between observed and computed values. There is a "lack of correspondence in growth between the two principal layers of the scale, and even between the parts of one layer. * * * The best diameter for use in length calculations, if no correction is to be made, is the transverse in the Clupeidæ. The posterior field would be preferable, but the indistinctness of the annual rings in that region renders it useless [p. 89]."

In another paper Huntsman (1918) points out that by the use of a "movable curve" cut out of cardboard or wood one can compensate for the differential growth of the scale compared with that of the body and for the difference in the time of origin of the various scales according to size.

Savage (1919) states that three factors may cause the low computed values for the first year of life in the marine herring: (1) Earlier outward migration from the inshore waters of the larger yearlings, which would make the actual length values for 1-year-old fish too high, (2) the variability in the length of the head and tail with age, and (3) the possible variation in the position of the basal line of the scales with growth.

Järvi (1920) compared the calculated with the actual length values for fish (*Coregonus albula*) of the same year class. He found that, in general, each year that intervened between the year of capture and the year for which calculations are made introduced an error of 0.5 centimeter in length calculations. That is, the calculated values will be 0.5, 1, 1.5, 2, 2.5, 3, or 3.5 centimeters too low, depending on whether 1, 2, 3, 4, 5, 6, or 7 years, respectively, intervened. He found the error to vary from

3 per cent (when 1 year intervenes) to 20 per cent (when 7 years intervene). The calculated values were based on the scale radius.

Järvi, however, ignored the fact that the discrepancies were greater in his young fish than in the old for corresponding numbers of intervening years. In his table 18 he considers only the 3-year and older fish. His 2-year fish, for instance, show a deviation of 1.5 centimeters instead of 0.5 centimeter in the calculations of the first year of life.

Järvi later (1924) discovered that the errors in computations varied somewhat with the races of coregonids. The correction of 0.5 centimeter per year, referred to above, applies only to individuals of a slow-growing race (Keitelesee, Pielavesi). In a fast-growing race (Nilakka) the corrective factor must be doubled (1 centimeter per year). And, further, if the anteroposterior diameter of the posterior field is employed, the error in each case is reduced by approximately one-half.

Lee (1920) treated the scale lengths (radii) and fish lengths of different species statistically and concluded that the growth increment of scales is, on the average for each species, a constant proportion of the growth increment of the fish, but that the length of the fish and the length of the scale are not proportional to each other. The "phenomenon of apparent change in growth rate" is partly due to the method of calculation, which ignores late scale formation, and is partly due to the segregation of fish according to size. Lee expresses Fraser's (1916) correction for the former factor in the form of a formula, $L_1 = C + \frac{V_1}{V}(L - C)$, in which C is the length of the fish when scales first appear, L the length of the fish at death, V the scale dimension, L_1 the computed length at the end of the first year, and V_1 the scale dimension to the first annulus.

Rich (1920) concluded, from a study of series of fry and yearlings of the chinook salmon, that "the increase in the number of rings on the scales and the increase in the length of the anterior radii are proportionate to the increase in length of the fish [p. 53]."

Birtwistle (1921) recorded for the herring "the width of the respective summer zones on the scales as percentages of the measured part of the scale—that is, the total distance between the 'base line' and the outer edge of the striated portion of the scale"—and found that the corresponding percentages decreased as older fish were employed, and that it seemed "as if the whole scale shrinks up in the older fish and shrinks the more, the older the fish is."

Miss Sherriff (1922) obtained a formula ($L = AV^2 + BV + C$), which presumably expresses mathematically the growth relation between the body, L, and scales, V, in the marine herring.

H. Thompson (1923, 1924) finds that in the haddock, fish and scales grow very nearly proportionally. The disparity between empirical and calculated sizes is due to the shoaling of better grown young haddock with the less well grown older fish, and to the employment of scales other than the largest (on flank) on the body. "The size of the first platelet is proportionally smaller than that of the fish by about ½ centimeter, which must be added to the calculated first year size. If scales are taken from other parts of the body, where they are even later in appearing (than on the flank), the error may increase to 2½ centimeters [1923]." The author finds (H. Thompson, 1924) that the scales situated below the third dorsal fin are "practically representative throughout of the growth of the fish."

Van Oosten (1923) determined that in the whitefish the diameter of scales grew more nearly proportionally with the body than either the anterior or posterior radius, and that lengths computed from diameter measurements corresponded more nearly with the comparable actual lengths than those calculated from either anterior or posterior radii.

Dunlop (1924) found that in the "stream type" of sockeye salmon "the size of the scale relative to the fish is very small at 3 centimeters. It increases rapidly to 3.5 centimeters and less rapidly from that point. The increase from 3.5 to 10 centimeters is fairly constant. The rate of increase becomes less, and at 11.5 centimeters it stops. From this point the growth of the scale becomes constantly less rapid than that of the fish [p. 157]." He ascertained that computations made for a fish length of about 7.1 centimeters are correct, but those made for fish lengths less than 7.1 centimeters are too low and for fish lengths greater than 7.1 centimeters too high.

Leim (1924) plotted a curve showing the relation between the total diameter of the anterior field of the scales and the length of the shad (*Alosa sapidissima* (Wilson)).

Johansen (1925) states that during the first year the scale of the cunner (*Tautogolabrus adspersus* Walbaum) increases its size almost 8 times, while the fish increases its size almost 20 times. During the second year both scales and fish double in size. Johansen accepts the scale theory for age determinations but does not calculate lengths from scales. He judges the relative growth of the fish by the width of the various zones on the scales.

Watkin (1926), by observing whether the circuli of the first growth zone become approximated with age, concluded that the progressive decrease with age in the breadths of corresponding summer zones in his herring scales was not due to a contraction of the scales but must be due to the segregation of the large fish of a year class, as explained by Lea. Watkin does not compute lengths from scales but makes direct comparison between the actual measurements of the scale zones of the various age groups.

Creaser (1926) concluded that in the sunfish (*Eupomotis gibbosus*) the relation of the posterior, anterior, and total length of the scale to the length of the fish is a complicated one, so that no simple formula can be stated for the calculation of the length at past scale margins or annuli. The posterior field grows "proportionately faster than the fish until the fish is about 60 millimeters long, at which time a direct relation is established between the rate of scale growth and fish growth." The anterior field at first gradually grows more rapidly in proportion than the fish, and the regression line bends upward. "This continues and is increased more at a fish length of about 80 millimeters. As the fish reaches about 120 millimeters in length the scale grows proportionally less than the fish, resulting in a sharp turn of the curve followed by a gradual downward trend. In this manner a characteristic sigmoid curve is formed, showing that the relation of the anterior length of the scale to the length of the fish is a changing one [p. 57]." The regression line, showing the relation between total scale length and fish length, "rises in a straight line to a point corresponding to a length of about 120 millimeters, after which the whole scale grows proportionately less than the fish and the curve bends downward."

"For the calculation from the individual scales it is best to use the ordinary scale formula, adding Fraser's correction, and further altering the computation by the addition of a correction obtained from the average (regression) line. This change can be computed for the various year groups by projecting a line from the average size of the year group in question back to the base line at a point corresponding to the length of the fish when the scale was first laid down. The difference between this line and the actual curve is then added or subtracted, as the case may be, to the length obtained by the use of the corrected scale formula [p. 57]."

Menzies and Macfarlane (1926, 1926a) observed Lee's "phenomenon" in the calculated lengths of salmon, which, though of different ages, belonged to the same year class. They asserted that the discrepancies are greater than might be expected from late scale formation alone. The "phenomenon" does not seem to be due to some obscure phenomenon of scale growth, but rather to some interrelation between smolt size and length of stay in the sea and possibly to some racial differences and variations in the food supply of different spawning tributaries.

Nall (1926, 1926a) makes no corrections in the length computations of sea trout inasmuch as they are fairly accurate. He writes, "It should be noted that the figures in the summary do not confirm Mrs. Williams's (Lee) contention that, unless allowance is made for the length of the fry before scale formation begins, the measurements for the earliest stage of life will show a progressive diminution as larger and larger fish are taken."

To obtain direct experimental evidence on the validity of the scale formula in the laboratory is extremely difficult on account of the small amount of body and scale increments and of the relatively large amount of methodical or personal errors involved. To overcome these difficulties, a large number of individuals must be employed. My attempt to test the formula on the New York Aquarium whitefish was therefore doomed to failure. Only few investigators have grasped the opportunity to obtain such experimental data.

Milne (1913) measured the photographs of scales of two salmon kelts captured, marked, measured, and recaptured, and calculated the length of each fish at the time of its marking. His calculated lengths exceeded the true lengths by one-half inch in the 27-inch salmon and by 6 inches in the 26¼-inch fish. Milne concludes that either the latter scale is abnormal "or that Dahl's system of measurement is not applicable to a fish that has spawned." As the measurements from different scales of the same fish seldom agree exactly, the author believes that it is not safe to rely on one scale alone for the calculated length values.

Winge (1915) compared the growth increments of the body and the anterior radius of the scales of four cod captured, marked, measured, and recaptured. In his ratios, given below, the denominator denotes the percentage the length of the cod, at its marking, was of that at its recapture; the numerator denotes a similar value for the scales. If body and scale had grown in direct proportion to each other, each ratio would have equaled unity.

$$\text{Cod I, } \frac{0.800}{0.727}=1.10. \quad \text{Cod II, } \frac{0.713}{0.721}=0.99.$$

$$\text{Cod III, } \frac{0.830}{0.784}=1.06. \quad \text{Cod IV, } \frac{0.670}{0.652}=1.03.$$

The author concludes that body and scale growth are closely correlated, the discrepancies being due to the fact that the measurements of the live cod are subject to "considerable inaccuracy."

Storrow (1916) brought into the laboratory a young Ballan wrasse (*Labrus bergylta*), 2 to 3 centimeters long, taken from a rock pool at Cullercoats in August, 1914. On May 24, 1916, the fish had attained a length of 8 centimeters and completed two summers' growth. According to calculations from its scales, the specimen had attained a length of 3.7 centimeters at the end of the first year. This measurement agrees fairly well with the observed length when it is remembered that the latter value represented an incomplete growth year. On May 24 no new growth increment had yet appeared on the scales nor had any body growth taken place since the previous January.

In April and May, 1915, several carloads of hatchery reared chinook-salmon fry were planted in a small artificial lake near Seufert, Oreg. Rich (1920) measured a small series of these fry at the time of planting. The average length was 44.6 millimeters. On September 2, 1915, 55 of these salmon were recaptured. Their average length had increased to 80.9 millimeters. Rich found that the sudden change in their growth rate left a primary check on the scales. This enabled him to compute from the scales the length of the fry at the time of the plant. His average estimated length of 47.9 millimeters corresponded very closely with the actual observed length at the time of planting.

Snyder (1923) computed the lengths from the scales of eight salmon marked and liberated as fry and recaptured in their fourth year of life. The calculated lengths indicated that the fish averaged 7.9 centimeters in length at the time of their liberation and 55 centimeters at the end of their third year of life. These estimated lengths compare favorably with the actual, which were found to be 8.5 centimeters for 100 fry and 55 centimeters for 50 marked fish recaptured in their third year of life.

H. Thompson (1926) found that haddock formed a sharp "false ring" when transferred from the sea to the aquarium. By means of this accessory check he was able to compute, from the scales, the length of the fish when introduced into the tanks. Employing scales of 1-year fish he estimated that these haddock averaged 13.7 centimeters in length at the time of transference, which value was 0.2 centimeters too high and thus involved an error of less than 2 per cent. Thompson also presented direct evidence that the first zone of haddock scales did not compress when additional material was laid down. Lengths calculated back to the end of the first year varied as follows: 10 fish gave accurate results, 2 gave results that were slightly too low, and 12 gave values that were from 0.5 to 3 centimeters too high. The author explained the high values on the assumption that some of the haddock were so poor at the end of each year that their scales were absorbed slightly. The experiments showed that for the first three years, at least, the size of haddock scales increased on the average in proportion to that of the fish.

Creaser (1926) gives a table showing, for one blue gill (*Helioperca incisor*), the actual increase in length of scales taken from various parts of the body during an increase of 10 millimeters in the length of a 57 millimeter yearling fish. He concludes that "there is little deviation from the direct proportion (between body and scale growth) during the short scale increment of about 0.2 millimeter." The increments calculated from 22 scales varied from 6 to 11 millimeters and averaged 9.3 millimeters or 0.7 millimeter less than the actual.

From the preceding review it may be noted that most of the papers devoted to a study of the body-scale growth relationship are recent, having appeared since 1918, and involve mainly three species of fish—the marine herring and the Atlantic and Pacific salmon. From this review it is apparent that the question of the validity of growth calculations based on the scales of fishes is still a thorny one, indeed. Not only is there a difference of opinion among investigators employing different species of fish, but also among those employing the same species or even the same material (see Dahl, 1910; Mottram, 1916; Lea, 1913; and Molander, 1918). Most of the investigators agree that discrepancies exist in the calculated growth measurements of the nature described by Miss Lee as the "phenomenon of apparent change in growth rate." But of these investigators, only a few (Lea, Järvi, Menzies and Macfarland, and Nall) have attempted to show that Lee's "phenomenon" is also evident in fish that belong to different age groups but to the same year class. There is also much disagreement as to the causes underlying the discrepancies in computed growth values and as to the efficacy of the various methods employed to eliminate these errors; and yet, peculiarly enough, all the experimental evidences reviewed above show, as far as they go, that calculated and empirical growth measurements agree almost exactly.

DIFFERENTIAL GROWTH OF SCALES OF A LAKE HERRING AND OF THE AREAS OF ONE OF ITS SCALES

In the application of the scale formula (p. 272) to the marine herring (*Clupea harengus*), Lea (1910) found that it is rather immaterial in what direction the measurement dimension of the scale is taken if the center of the scale is clearly established. In Table 8 is given, for a lake herring, the length in millimeters reached by it at the end of each year of its life, as calculated from different scale dimensions of three series of scales, one series representing uniform scales taken from the same area and two consisting of scales taken from different places on the body. The calculated lengths vary considerably with the different scale dimensions in an individual scale. They vary less with the dimensions when the averages of several scales are compared, though the differences are still significant. Comparing for each year the extreme averages based on different dimensions of scales taken from the same area (series A) and expressing the difference in terms of its probable error according to the formula given on page 284, I found that the difference between the averages was as follows: For year I, based on the lateral and anterolateral radii, 18.47 times its probable error; for year II, based on the lateral and anterolateral radii, 16.11 times its probable error; for year III, based on the lateral and anterolateral radii, 7.15 times its probable error; for year IV, based on the lateral and anterolateral radii, 7.69 times its probable error; and for year V, based on the anterior and anterolateral radii, 2.68 times its probable error. The difference between the extreme averages is significant in all years except the fifth. When, however, the scales are taken from different parts of the body (series B), the discrepancy between the averages, though still significant in the early years, is greatly reduced.

TABLE 8.—*Length, in millimeters, reached by a lake herring 255 millimeters long at end of each year of its life, as calculated from different dimensions of scales taken from the same and from various areas of the body. The average is given for each of three series of scales for each year, as well as limits of variations represented by the minimum and maximum lengths shown in parentheses*

Dimension of scale employed	Area from which scales were taken	Number of scales used	Average calculated length, in millimeters, with minimum and maximum lengths in parentheses, for year—				
			I	II	III	IV	V
Anterior radius, focus to anterior margin.	Between lateral line and dorsal fin, series A.	10	(78) 85 (92)	(144) 153 (159)	(181) 193 (204)	(203) 219 (228)	(225) 238 (243)
	Various parts of body, series B.	22	(74) 92 (110)	(138) 151 (179)	(165) 188 (217)	(205) 220 (234)	(233) 240 (247)
	Various parts of body, series C.	10	(81) 98 (117)	(133) 158 (179)	(182) 200 (215)	(219) 224 (231)	(235) 242 (247)
Anterolateral radius along anterolateral ridge from focus.	Between lateral line and dorsal fin, series A.	10	(72) 80 (92)	(141) 148 (155)	(183) 192 (199)	(209) 214 (220)	(232) 235 (241)
	Various parts of body, series B.	22	(74) 90 (109)	(124) 149 (169)	(156) 188 (212)	(200) 218 (239)	(224) 237 (244)
Lateral radius, focus to lateral margin.	Between lateral line and dorsal fin, series A.	10	(98) 104 (111)	(159) 167 (171)	(191) 201 (206)	(217) 222 (226)	(234) 237 (239)
	Various parts of body, series B.	22	(88) 108 (134)	(132) 157 (182)	(154) 190 (214)	(198) 218 (240)	(220) 239 (255)
Total length of scale included in annulus; that is, the diameter.	Various parts of body, series C.	10	(97) 112 (126)	(162) 173 (191)	(197) 207 (216)	(220) 228 (234)	(238) 243 (245)

The calculated lengths also vary with the scales, as indicated by the limits of variation shown in parentheses in Table 8. The variability is much less (as is to be expected) for the uniform scales of series A than for the scales of series B taken from various places on the body.

The above data show that neither the scales of a lake herring nor the parts of one of its scales grow at the same rate, and that growth varies least for scales taken from the same area on the body. To minimize the error in calculations due to the differential growth of scales, I have selected for study that area whose scales varied least in shape and size; namely, the one situated between the dorsal fin and the lateral line. (See p. 274.)

The question now arises: How close is the correspondence between the growth of the selected scales and the body, and which scale dimension must be employed? Previous workers almost invariably have selected the anterior radius of the scale. Their calculated values, when compared with the actual measurements, usually were found to be too low. As the scale hypothesis really assumes a correlation between the increase in the length of the body and the length, not radius, of the scale, it might be possible to eliminate the discrepancy between the calculated and actual values by the employment of diameters instead of anterior radii. The length averages computed from scales of series C, Table 8, and based on anterior radii and diameters, indicate at least that the calculated values are increased considerably by the employment of scale diameters. Also, the variability of the calculated lengths based on the diameter is much less than that of the lengths based on the anterior radii, at least in the specimen considered.

Therefore, I have undertaken a series of measurements of small and large lake herrings to ascertain the degree of correlation in growth of body and of the selected scales and to determine whether the diameter of a scale is a better dimension than the anterior radius from which to calculate length values. In my paper (Van Oosten,

1923) on the New York Aquarium whitefish I stated that for a study of the correspondence in growth of body and scales it is essential to acquire a large amount of homogeneous material collected at the same time and place, and that in order to check the calculated values series of fish of the same year class collected in the same season of different years and in the same locality must be employed. No such whitefish material was at hand at the time of writing, though the material available did lead to certain conclusions. At present much more desirable material is available in the collections of lake herring made at Bay City, Mich., on October 26, 27, and 29, 1921, November 3 and 4, 1921, November 1, 1922, and November 12, 1923. As explained in detail on page 280, the collections of October 29, 1921, November 1, 1922, and November 12, 1923, are presumably homogeneous in character, as each was taken from one pound net and consisted of fish ready to spawn.

AGE VARIATIONS IN THE GROWTH OF THE HEAD

As variations in the body-scale ratios of the different age groups may be due to age variations in the growth of the head, I measured, in addition to the diameter (V) of a scale and the body length (K) measured snout to caudal, the length of the scale-covered portion of the body, excluding the head and tail. The last measurement (T or T_1) was obtained by subtracting the length of the head (H or H_1) from the body length (K).[10] From these measurements I computed the following ratios: H/K, H_1/K, H_1/V, K/V, and T_1/V. The H/K ratios were determined for lake herring collected in 1917 and 1919 at various localities on Lake Huron. The H_1/K, H_1/V, K/V, and T_1/V fractions were computed for 191 herring taken at Bay City, Mich., October 26 and 27, 1921. H_1/V is the difference between K/V and T_1/V. A summary of the data is given in Table 9.

TABLE 9.—*Average for each year of H/K ratios for 177 lake herring collected in 1917 and 1919 at various localities on Lake Huron, and average of H_1/K, K/V, and T_1/V ratios for 191 lake herring collected at Bay City, Mich., October 26 and 27, 1921, to indicate age variations in growth of the head. X and non-X scales were employed in the fractions K/V and T_1/V. The H_1/V ratio is the difference between K/V and T_1/V* [1]

Date and locality	Ratios	Year					
		III	IV	V	VI	VII	VIII
1917 and 1919, Lake Huron	H/K	0.222 (21)	0.226 (46)	0.224 (37)	0.226 (27)	0.224 (26)	0.224 (20)
Oct. 26 and 27, 1921, Bay City, Mich.	H_1/K	.205 (12)	.202 (69)	.202 (81)	.201 (29)		
Do	K/V	46.85 (12)	45.03 (69)	46.09 (81)	45.89 (29)		
Do	T_1/V	37.03 (12)	36.04 (69)	36.69 (81)	36.67 (29)		
Do	H_1/V	9.82 (12)	8.99 (69)	9.40 (81)	9.22 (29)		

[1] Numbers in parentheses indicate the numbers of specimens employed.

The H/K ratios of the 1917 and 1919 herring remain practically constant with the year classes and with age, the difference between the extreme averages being only 0.004. The head of the 3-year fish is the smallest. The H_1/K ratios of the Bay City herring also remain constant with age, the difference between the extreme averages being 0.004. In these fish the head of the 3-year-old is the

[10] For details relative to the methods employed in obtaining K, T, H, H_1, and V see p. 274.

largest. The H_1/V ratios, of course, vary as the H_1/K. In the T_1/V ratios the error due to age variation in head length is eliminated, while in the K/V fractions the head measurement is included. It is to be noted that the K/V ratios vary in the same direction as the T_1/V, but not in the same relative amount. This indicates that the head affects the K/V fractions, but only to an insignificant degree. The age variation in head length can not account for any large or significant variation that may occur in the body-scale (K/V) ratio with age after the third year.

This conclusion may be substantiated by the application of the statistical formula for variability, $c=\frac{\sigma}{M}$, in which c is the coefficient of variability, σ the standard deviation, and M the mean. I applied the formula to the K/V and T_1/V ratios of years III and IV only. The coefficient of variability was found to be 6.29 per cent ± 0.8660 for the K/V ratios of year III, and 6.58 per cent ± 0.9059 for the T_1/V ratios of that year, 8.45 per cent ± 0.4851 for the K/V ratios of year IV, and 8.91 per cent ± 0.5116 for the T_1/V ratios of year IV. It is thus apparent that the K/V ratios are no more variable than the T_1/V, and that head length, therefore, is an unimportant variable in the former ratio.

AGE VARIATIONS IN BODY SCALE (K/V) RATIOS BASED ON SELECTED (X) AND UNSELECTED (NON-X) SCALES OF ADULT LAKE HERRING

In a study of the correlation of body and scale length we may compare the actual measurements of body and scale length directly or the body-scale ratios (K/V) based upon these measurements. Both methods are employed for the lake herring.

To eliminate or minimize the errors due to the variability in the growth of individual scales, I employed for this study corresponding scales (X scale)[11] wherever possible; but as the specified scale is not always available and much time is consumed in locating it, it is not expedient to employ it in life-history work. I therefore computed, for comparative purposes, the K/V ratio based on those scales (non-X) actually used for the computations of fish length. As stated on page 274, these scales were taken from the body area situated between the dorsal fin and the lateral line. Three or four scales of each individual were mounted, but only one of these was measured for the computations of fish length. The two series of ratios, K/V on X and K/V on non-X scales, are given in Table 10 for each year of life of the herring collected at Bay City, Mich.

[11] For method employed to locate this special scale see p. 275.

Table 10.—*Body-scale ratio (K/V) for each age group of Bay City herring, based on diameter (V) of special (X) and of unselected (non-X) scales. The body-scale ratios based on anterior radii (ac) of X scales are given only for fish collected October 29, 1921* [1]

Date	Ratio	Year II	Year III	Year IV	Year V	Year VI	Year VII	Year VIII
Oct. 26, 27, Nov. 3, 4, 1921	K/V on X	----------	49.04 (15)	47.39 (77)	47.18 (76)	47.73 (29)	47.73 (4)	46.23 (3)
Do	K/V on non-X	45.22 (5)	44.68 (38)	43.53 (131)	----------			----------
Oct. 29, 1921	K/V on X	----------	49.79 (27)	49.08 (59)	49.79 (32)	48.92 (15)	46.36 (3)	----------
Do	K/ac on X	----------	99.53 (27)	98.16 (59)	97.45 (32)	93.63 (15)	[2] 86.65 (6)	----------
Do	K/V on non-X	----------	45.82 (27)	44.44 (84)	44.70 (40)	44.01 (13)	43.72 (3)	----------
1921 combined	K/V on X	----------	49.52 (42)	48.12 (136)	47.96 (108)	48.14 (44)	47.14 (7)	46.23 (3)
Do	K/V on non-X	45.22 (5)	45.15 (65)	43.89 (215)	44.70 (40)	44.01 (13)	43.72 (3)	----------
Nov. 1, 1922	K/V on X	----------	51.07 (26)	50.15 (77)	50.65 (28)	----------	----------	----------
Do	K/V on non-X	[2] 47.41 (6)	45.57 (122)	45.71 (168)	44.87 (88)	43.95 (9)	----------	----------
Nov. 12, 1923	K/V on X	----------	49.59 (79)	49.61 (110)	49.90 (42)	48.27 (8)	----------	----------
Do	K/V on non-X	----------	44.76 (91)	45.80 (130)	44.64 (48)	43.25 (7)	44.07 (2)	----------
Grand average	K/V on X	47.59 (4)	49.83 (147)	49.11 (323)	48.84 (178)	48.16 (52)	47.14 (7)	46.23 (3)
Grand average	K/V on non-X	45.84 (8)	45.21 (278)	44.97 (513)	44.77 (176)	43.89 (29)	43.86 (5)	----------

[1] The number of specimens employed is given in parentheses. [2] Ratios based on X and non-X scales combined.

From this table it may be seen that the K/V ratio based on X scales is highest for fish in the third year in all collections but the one of November 12, 1923; that the variability in the averages does not occur consistently in one direction; and that the direction of the fluctuation in the averages is not the same in the different collections for corresponding years. The differences between the extreme averages of a collection, based on a sufficient number of specimens, vary from 0.31 for the 1923 fish to 1.56 for the 1921 fish. The average of the three differences is 0.93. The *K/V* ratios based on non-X scales show similar characteristics. The ratio is not always higher for fish in the third than for those in later years, the fluctuations in the ratios do not occur in one direction, nor is this direction the same in all collections. The differences between the extreme averages based on non-X scales vary from 0.84 in the 1922 fish to 1.38 in the 1921 fish of October 29. The average of the three differences is 1.09. The direction of variation in the ratios based on non-X scales does not always follow that of the ratios based on X scales. The ratios based on X scales vary less with the age groups than those based on non-X scales.

When we arrange the ratios on the basis of year classes instead of age groups only, as shown in Table 11, we again find that the *K/V* ratio is not consistently high or low in the fish of the same age group, and that the fluctuations in *K/V* are fortuitous, occurring in all directions. The differences between the extreme averages based on X scales of a year class vary from 0.63 for the 1919 to 2.53 for the 1918 year class. The average of the three differences is 1.54. The range for these differences for the non-X scales extends from 0.23 in the 1920 to 1.07 in the 1919 year class. The average of the four differences is 0.76. In this table the ratios based on non-X scales vary less with the age groups than those based on X scales.

Table 11.—*K/V ratios based on X scales and on non-X scales of several year classes of Bay City herring collected in fall of the years 1921, 1922, and 1923* [1]

Year class	K/V based on scale	Year II	Year III	Year IV	Year V	Year VI
1917	Non-X	----------	----------	----------	44.70 (40)	43.95 (9)
1918	X	----------	----------	48.12 (136)	50.65 (28)	48.27 (8)
	Non-X	----------	----------	43.89 (215)	44.87 (88)	43.25 (7)
1919	X	----------	49.52 (42)	50.15 (77)	49.90 (42)	----------
	Non-X	----------	45.15 (65)	45.71 (168)	44.64. (48)	----------
1920	X	----------	51.07 (26)	49.61 (110)	----------	----------
	Non-X	45.22 (5)	45.57 (122)	45.80 (130)	----------	----------

[1] The number of specimens employed is shown in parentheses.

It is to be noted in Table 10 that where large numbers of individuals are employed the ratios of two consecutive age groups vary only slightly, and that on the whole a tendency exists for the body-scale ratios to decrease with the older age groups. This suggests that the fortuitous fluctuations in the ratios of each collection may be due to the small number of specimens employed for the averages of some of the age groups. As the corresponding ratios of the various collections are comparable, they may be combined and treated as units. The grand averages are shown at the bottom of Table 10.

We now find that the two series of *K/V* ratios give consistent and comparable results. Both decrease consistently with each older age group. Though the difference between the ratios of any two consecutive age groups is still small, that between the extreme averages is significant. We find that the difference between the grand averages of fish in years III and VI is 1.67 for the ratios based on X scales and 1.32 for the ratios based on non-X scales. These differences can not be accounted for by random sampling; nor can they be due to the personal errors involved in the measurements, as can be seen by referring to the differences given in the last column of Table 12. The *K/V* ratios of fish of several age groups were determined twice; but the same identical scale was not always employed for the two ratio determinations of an individual. This and the fact that only a few specimens were used should make the differences between the two series of ratios represent the maximum. And yet, the differences between the extreme grand averages of Table 10 equal or exceed those of Table 12. The former may then be significant. Another factor might possibly be considered significant here. I found (p. 283) that the big fish of an age group possessed more scales in the lateral line than the small fish. I found, also (p. 279), that the size of the scales varies inversely as their number in the lateral line in an age group, but it is possible that the average size of the scales of the large fish with the greater number of scales is about the same as that of the scales of the small fish with fewer scales. If age groups II and III of Table 10 are represented by the bigger fish of the year class, as I believe (p. 333), and the average size of the scales of these bigger fish is no greater than that of the scales of the smaller, the body-scale (K/V) ratios of these younger fish must then be abnormally high; the body length (K) would be too high, whereas the scale length (V) would be normal for these groups. If this be true, the differences between the extreme grand averages of Table 10 are abnormally high and the percentages of increase in length with age in body and scale coincide more closely than is indicated in this table.

However, computations show that the bigger individuals of age group III possess larger scales, on the average, than the smaller fish. The length of the scales of 40 herring less than 226 millimeters in length, of age group III, taken at Bay City, Mich., in 1921, averaged 4.88 millimeters, that of the scales of 26 fish of this age group 226 millimeters or more in length averaged 5.24 millimeters. Similar values were obtained for the 3-year herring collected at Bay City on November 1, 1922, and at Oscoda, Mich., on November 2, 1922. The scales of 48 herring less than 226 millimeters in length of the former collection averaged 4.80 millimeters long, while those of 88 fish 226 millimeters or more in length averaged 5.15 millimeters; the scales of 71 fish less than 226 millimeters in length of the latter collection averaged 4.87 millimeters long, while those of 72 specimens 226 millimeters or more in length averaged 5.11 millimeters. Combining the above averages we find that the scales of the 159 herring less than 226 millimeters long averaged 4.85 millimeters in length, while those of the 186 fish 226 millimeters or more in length averaged 5.15 millimeters. The K/V ratios of Table 10, therefore, may very well be representative of the younger age groups even though based on the bigger fish, since the lengths of both the body (K) and scale (V) of these bigger fish vary in the same direction. The *K/V* ratios of Table 10 show that at least after the second year of life the percentage of increase in length with age is greater in the scale than in the body of the herring. The preceding data also show that the ratios based on unselected (non-X) scales vary no more with the age groups than those based on selected corresponding (X) scales.

TABLE 12.—*Differences between two series of K/V determinations for several age groups, both made for same individuals but based in part on different scales of these individuals*

Age group	Number of specimens	Average K/V	Duplicate average K/V	Difference between original and duplicate K/V
III	20	46.36	47.97	−1.61
VI	24	43.12	44.70	−1.58
VII	14	42.44	44.21	−1.77

AGE VARIATIONS IN BODY-SCALE K/V RATIOS OF JUVENILE COREGONIDS

The absence of juvenile fish in the Bay City collections is a serious handicap. The trend of the conclusions thus far reached suggests what the relation of the size of the body and scale in the young fish must be. I have at my disposal, however, a miscellaneous collection of juvenile coregonids. Some of these young fish comprise part of the collection made by Prof. T. L. Hankinson during August, 1913, at Whitefish Point, Mich., on Lake Superior (Hankinson, 1914); the others were obtained by A. G. Woolman at Kettle Falls, Minn., on July 26, 1895, and turned over to the Bureau of Fisheries. The data of these juveniles are shown in Table 13. The number of circuli indicate roughly the recency of the formation of the scales. A herring 34 millimeters in length, not included in the table, had not yet formed its scales. The

data suggest that in both the herring and the whitefish scale formation begins at a fish length of approximately 35 to 40 millimeters.

Superficial observation of the whitefish series reveals at once that the body-scale ratio in this species decreases rapidly with an increase in the length of the fish, dropping from 109.87 in the 41-millimeter specimen to 56.20 in the 73-millimeter fish, a decrease of 53.67. The average ratios of the juvenile whitefish and herring are considerably higher than those of the older individuals of the same species. The same is true for the related tullibees, whose ratios likewise decrease with size and with age.

TABLE 13.—*Growth relation between body and scale for juvenile coregonids*

Species and series	Date	Number of scales upon which K/V is based	Length (K), in millimeters	Average K/V	Average length of scale diameter (V) × 41	Average number of circuli formed on scales
COREGONUS CLUPEAFORMIS						
Whitefish Point, Mich., year I:						
1	Aug. 12, 1913	6	41	109.87	15.3	(1)
2	do	10	43	92.79	19.0	3
3	Aug. 19, 1913	8	46	63.08	29.9	4
4	Aug. 12, 1913	11	49	70.74	28.4	4
5	Aug. 19, 1913	6	50	71.84	30.2	5
6	do	5	50	75.00	27.4	4
7	do	10	51	60.78	34.4	6
8	do	7	52	69.00	30.9	4
9	Aug. 12, 1913	9	54	69.62	31.8	5
10	Aug. 19, 1913	9	56	61.72	37.2	6
11	do	7	56	59.48	38.6	6
12	do	7	58	58.86	40.4	6
13	do	7	58	60.05	39.6	6
14	do	4	62	57.38	44.3	7
15	do	6	73	56.20	53.3	12
Average			53	69.09		
Alpena, Mich., year III		47	269	46.78		
Difference between averages				22.31		
LEUCICHTHYS ARTEDI						
Whitefish Point, Mich., year I:						
1	Aug. —, 1913	5	39	95.18	16.8	(1)
2	do	5	40	74.55	22.0	2
3	do	5	40	95.35	17.2	(1)
4	do	6	41	112.07	15.0	(1)
5	do	5	45	123.00	15.0	(1)
Average			41	100.03		
Herring (table 10), year III			229	45.21		
Difference between averages				54.82		
LEUCICHTHYS TULLIBEE						
Kettle Falls, Minn., year I:						
1	July 26, 1895	5	50	46.59	44.0	9
2	do	7	52	47.38	45.0	9
3	do	9	56	45.11	50.9	11
Average			53	46.36		
Kettle Falls, Minn., year II:						
4	July 26, 1895	5	105	42.29	101.8	17
5	do	5	119	36.57	133.4	24
Average			112	39.43		
Difference between averages of I and II				6.93		

[1] Plate.

These data indicate that in the coregonids there is a tremendous difference between the rate of increase in length of the scale and of the body in the early years of life, the scale apparently increasing at a much more rapid rate than the body. In the whitefish this is more clearly shown by graphs (fig. 12). The continuous curve is plotted from the data of the juvenile whitefish and shows, from actual measurements, the length relation between body and scale. The broken line shows the form the curve would take if the body-scale ratio of the 41-millimeter specimen were maintained in all the larger fish.

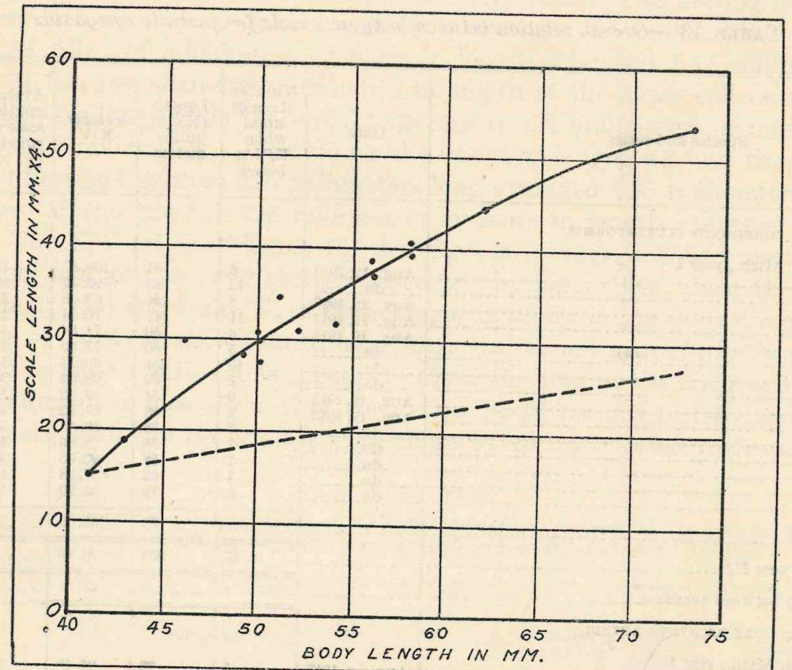

FIG. 12.—Relation between body and scale length in juvenile whitefish (*Coregonus clupeaformis*). The continuous curve is plotted from the body length and scale length data of Table 13. The broken line shows the form the curve would take if scale and body maintained the relation existing at the body length of 41 millimeters

All the K/V data together indicate that the herring scale increases in length at a greater rate than the body throughout life—in early life much faster, in later life (third year and thereafter at least throughout the sixth year) only a little faster.

It may be well to make reference here to Molander's method of studying the relationship of body (L) and scale (V) length (Molander, 1918). This investigator compares the $\frac{L}{V}$ and the $\frac{L-50}{V}$ ratios for each age group (the marine herring studied formed its scales at a body length of 50 millimeters) and assumes that the latter ratios "give the correct picture of the growth relation between fish and scales after the fish has begun to grow scales." The author finds that whereas the $\frac{L}{V}$ ratios decline continuously from the

first to the third year, inclusive, the $\frac{L-50}{V}$ ratios rise during these years. In the fourth year both ratios rise and thereafter vary in the same way. According to Molander, the $\frac{L}{V}$ ratios indicate that the scales grow proportionally quicker than the body during the first three years of life, while the $\frac{L-50}{V}$ ratios indicate that the scales grow proportionally more slowly than the body. The author believes that the trend of the $\frac{L-50}{V}$ fractions would not be altered by a change in the value 50. This, of course, is not true. For example, if we subtract 35 millimeters from the average length values of the whitefish of Table 13 we obtain $\frac{L-35}{V}$ ratios, as follows: For the 53-millimeter fish, 23.4; for the 269-millimeter fish, 40.7—a rise in values occurs. But if we deduct 10 millimeters instead of 35, then the ratios become 53+ and 43+, respectively—a decline in values occurs.

An analysis shows that on the basis of Molander's method of studying body-scale ratios the following relationships obtain:

If $\frac{L-X}{V}$[12] remains constant with increased fish length, $\frac{L}{V}$ must decrease.

If $\frac{L-X}{V}$ decreases, $\frac{L}{V}$ must decrease.

If $\frac{L-X}{V}$ increases, $\frac{L}{V}$ may decrease, remain constant, or increase, depending upon the degree of relative slowness of scale growth.

According to these relationships, if $\frac{L}{V}$ decreases, as is the case in the lake herring, then either the body and scale actually grow in proportion or the scale actually grows faster or more slowly, proportionally, than the body. If $\frac{L}{V}$ remains constant or increases with age, the scales grow more slowly relatively than the body. The $\frac{L}{V}$ fractions do not then express the real growth relationship between body and scale.

In the $\frac{L}{V}$ ratios we study the length relationship between body and scale; in the $\frac{L-50}{V}$ ratios we study the actual growth relationship. According to the first view we say, if the fish at the end of its second year of life has doubled the length reached by it at the end of the first year, then the scale length at the end of the second year must be twice that reached at the end of the first year if body and scale length are to maintain a fixed relationship. The percentage of increase must be the same in body and scale. According to the second view we say if the body growth during the interval between scale formation and the end of the first year is doubled by the end of the second year then the 2-year scale must be twice the size of the 1-year scale if body and scale actually grow in proportion. But in this case the total length of the

[12] X=length of fish at scale formation.

1-year fish is not doubled; the percentage of increase in length is not the same in fish and scale—it is less in the former.

The scale formula, however, is based on the assumption that the lengths of the body and scales maintain a fixed relationship after the first year of life. The formula demands that the body-scale ratio of a fish at death be the same as it was at the time of the completion of each annulus on the scale, irrespective of the actual growth relationship during the first year or during the intervals between the periods of annuli formation. The lengths are calculated back to the periods of annuli formation. To test the scale theory of growth determinations we may then study the $\frac{L}{V}$ ratios,

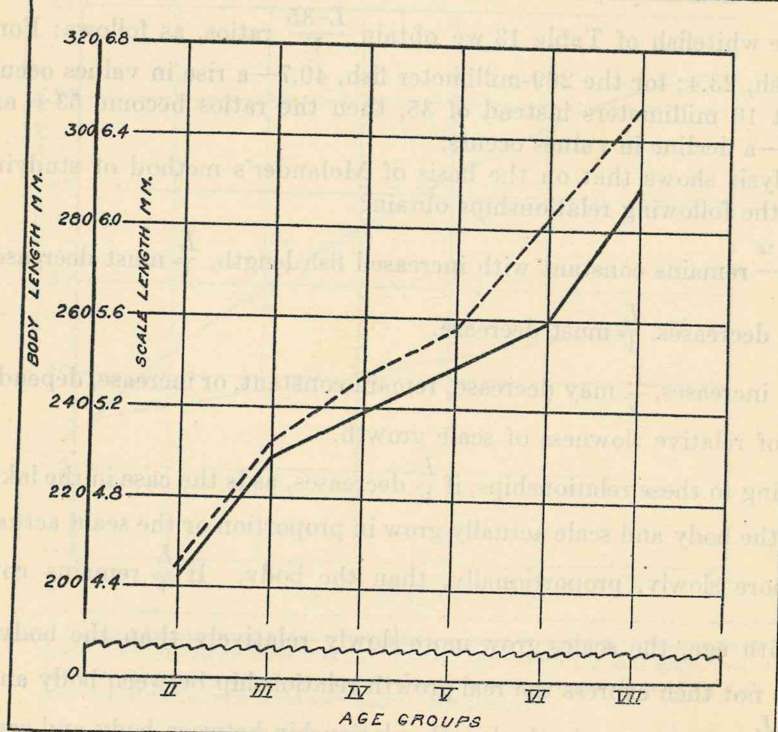

FIG. 13.—Body-scale length relationship of adult lake herring (*Leucichthys artedi*) arranged according to their age. The continuous curve is plotted from the average total lengths of the body, the broken curve from the average total lengths of the scale shown in Table 14

which the theory demands must remain constant with the age groups strictly with those age groups that have completed their last year's growth but have not yet commenced the new year's growth and thus have formed a completed annulus at the margin of their scales. My herring were taken at the end of a growth year, in the fall of the year.

Now, since it has been shown that the body-scale ratios gradually decrease with age in the lake herring (p. 315), we may conclude that the demands of the theory are not fully met—that the percentage of increase in length of the body and of the scale is not the same but that this percentage is greater in the scale. The actual growth increments of the body and scales in the course of time, however, may have increased in direct proportion even though the body-scale length ratios decreased.

AVERAGE LENGTH OF BODY AND SCALE COMPARED FOR CORRESPONDING YEARS

The body-scale length relationship of the adult herring may be shown more clearly perhaps by plotting the average total length of the body and scale for each year of life on the same graph (fig. 13) or by plotting the average size of the scale against the average length of the body, as shown in Figure 14. In both figures the curves are based on non-X scales. The averages employed for Figure 13 are given in Table 14, those employed for Figure 14 are given in Table 15.

TABLE 14.—*Average length of an age group, together with average length of its non-X scales for all Saginaw Bay herring collected in 1921, 1922, 1923, and 1924*

Age group	Number of individuals employed	Body length, in millimeters	Scale length, in millimeters	Age group	Number of individuals employed	Body length, in millimeters	Scale length, in millimeters
II	34	202	4.48	V	525	249	5.57
III	854	229	5.06	VI	111	259	6.02
IV	1,397	239	5.32	VII	20	289	6.54

TABLE 15.—*Average length, in millimeters, of non-X scales at various lengths of body for all Saginaw Bay herring collected in 1921, 1922, 1923, and 1924*

Limits, in millimeters, of size group employed	Average length, in millimeters, of fish of size group	Average length, in millimeters, of scales	Number of specimens employed	Limits, in millimeters, of size group employed	Average length, in millimeters, of fish of size group	Average length, in millimeters, of scales	Number of specimens employed
39–45	41	0.42	5	251–255	253	5.61	176
160–199	190	4.24	27	256–260	258	5.72	78
200–205	203	4.47	38	261–265	263	5.74	54
206–210	208	4.65	31	266–270	269	5.88	37
211–215	213	4.66	68	271–275	273	5.94	28
216–220	218	4.94	140	276–280	278	6.08	26
221–225	223	5.02	247	281–285	283	6.19	21
226–230	228	5.09	370	286–290	288	6.30	13
231–235	233	5.22	479	291–300	295	6.37	26
236–240	238	5.31	425	301–310	305	6.57	19
241–245	243	5.42	356	311–330	318	7.07	16
246–250	248	5.48	258	331–391	351	7.57	15

The curve of Figure 13 based on scale measurements (broken line) rises more rapidly than that based on the length measurements of the body (continuous line) in every year except the seventh. This means that the scale increases its length relatively faster than does the body during every year of life considered except the seventh, when the percentage of increase of the scale is less than that of the body. In Figure 14 the solid line represents the actual relation of the length of the body and scale, as shown in Table 15; the broken line shows what the relation of the length of the body and scale should be if that existing at a body length of 190 millimeters remained constant. It may be seen that the two curves stay close together until a body length of 263 millimeters is reached, when the actual body-scale curve suddenly drops below the theoretical curve and maintains this position. This seems to indicate that after the herring attains a length of approximately 260 millimeters the scale begins to increase in length proportionally more slowly than does the body. This conclusion appears to be corroborated by the curves of Figure 13, where it was shown that after the sixth year, when the herring attained an average length of 259 millimeters, the scale increased in length relatively more slowly than the body.

In Table 10 the average K/V ratios of years VII and VIII were based on so few specimens that no safe conclusion regarding the relative increase in length of body and scale during these years could be drawn from them. For years III to VI, inclusive, the data of this table agree with those of Tables 14 and 15. When all the data are considered together we may conclude that the scale of the lake herring increases in length, on the average, proportionately faster than the body until a body length of approximately 260 millimeters (age VI) is reached, when the percentage of increase in length is less in the scale than in the body.

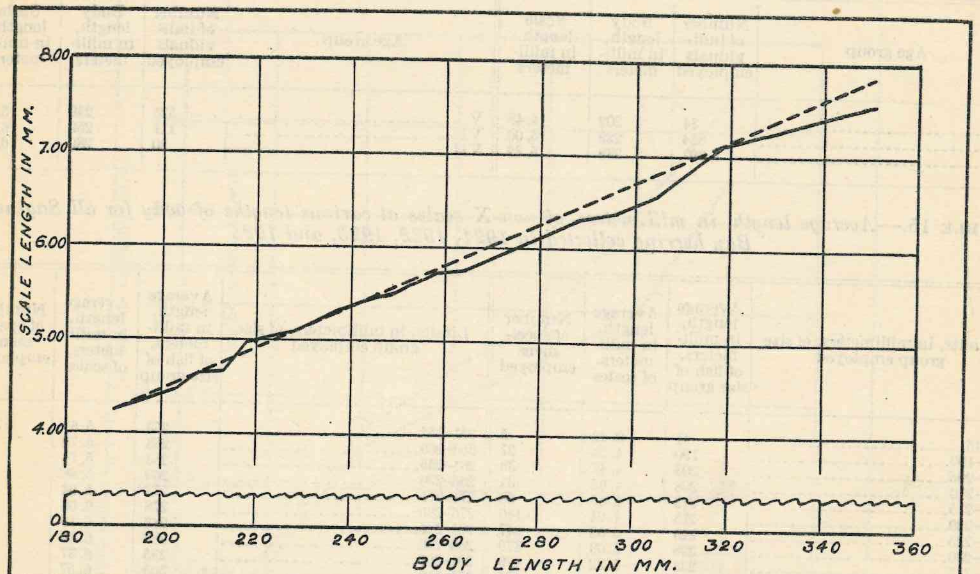

FIG. 14.—Body-scale length relationship of adult lake herring (*Leucichthys artedi*) arranged according to their size. The continuous curve based on the average lengths of body and scale shown in Table 15 represents the actual body-scale length relation; the broken line shows what the relation of the length of the body and scale should be if that existing at a body length of 190 millimeters were maintained

COMPARISON OF COMPUTED LENGTHS BASED ON ANTERIOR RADII AND ON DIAMETERS OF HERRING SCALES

A preliminary study of length computations based on the diameters and the anterior radii of the scales of an adult herring (p. 311) indicated that the former scale dimension would in all probability furnish higher and perhaps more accurate length values than the latter. This section includes other data that indicate that this preliminary conclusion is correct. Two sets of data are available. Two series of body-scale ratios, the one based on the anterior radii (ac) and the other based on the diameters (V) of identical scales, may be compared with each other, and series of length computations based on both the diameter and radius of identical scales may be compared with each other and with the actual length values.

The series of body-scale ratios are included in Table 10. They are based on specially selected (X) scales of the herring taken at Bay City, October 29, 1921. It may be seen that while the K/ac ratios vary in one direction, decreasing consistently with age, the K/V fractions vary only slightly at random. Further, computations show that the difference (0.87) between the extreme averages of K/V (years III and VI) is only 1.22 times its probable error, while that (5.90) between the extreme averages of K/ac (years III and VI) is 3.35 times its probable error. Again, the coefficients of variability of the K/V ratios of years III and VI, for example, are computed to be 6.50 per cent ± 0.5966 and 6.74 per cent ± 0.8300, respectively, while those of K/ac for the same years are calculated to be 9.38 per cent ± 0.8609 and 7.85 per cent ± 0.9666, respectively. These data indicate (1) that the K/V ratios vary less with the age groups than the K/ac; that is, the diameter of a scale increases in length more nearly proportional with the body than the anterior radius, and (2) that the K/V ratios vary less than the K/ac ratios with the individuals of an age group. The diameter of a scale, then, appears to be a better dimension to employ for length computations of growth in the lake herring than the anterior radius.

TABLE 16.—*Measured lengths, at time of capture, of Bay City herring collected in 1921, 1922, and 1923, and lengths at end of each preceding year of life, as calculated from both the diameter (V) and anterior radius (ac) of the scales*

Year	Number of specimens	Average length (K), in millimeters, when captured	Calculated length (K), in millimeters, at end of year[1]											
			I		II		III		IV		V		VI	
			On V	On ac	On V	On ac	On V	On ac	On V	On ac	On V	On ac	On V	On ac
BAY CITY HERRING COLLECTED OCTOBER 29, 1921														
III	50	226	124	111	190	184	-----	-----	-----	-----	-----	-----	-----	-----
IV	127	233	115	102	179	171	216	213	-----	-----	-----	-----	-----	-----
V	61	240	118	104	166	156	200	194	225	223	-----	-----	-----	-----
VI	22	264	117	103	162	151	195	187	224	219	250	247	-----	-----
VII	6	282	118	104	161	149	194	185	222	214	244	240	265	264
BAY CITY HERRING COLLECTED NOVEMBER 1, 1922														
II	4	217	141	128	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
III	148	229	139	128	200	196	-----	-----	-----	-----	-----	-----	-----	-----
IV	245	236	122	109	183	176	217	216	-----	-----	-----	-----	-----	-----
V	95	241	114	99	171	160	205	199	229	227	-----	-----	-----	-----
VI	9	252	117	104	161	150	198	193	224	222	242	241	-----	-----
BAY CITY HERRING COLLECTED NOVEMBER 12, 1923														
II	2	221	137	126	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
III	170	233	142	-----	201	-----	-----	-----	-----	-----	-----	-----	-----	-----
IV	240	243	133	120	192	186	224	223	-----	-----	-----	-----	-----	-----
V	90	251	119	105	179	170	213	209	237	236	-----	-----	-----	-----
VI	15	263	113	99	166	155	203	198	228	225	247	247	-----	-----
VII	2	263	119	106	157	150	184	174	210	204	234	230	248	248

[1] Average of the differences, (K on V)-(K on ac), year I, 13.2; year II, 8.7; year III, 5.3; year IV, 3.6; year V, 2.4; year VI, 0.5.

TABLE 17.—*Comparison of calculated length values, based on diameter (V) and anterior radius (ac) with each other and with actual length values. The actual lengths are based on all available Bay City herring (collected 1921, 1922, and 1923), while calculated lengths are based on the scales of these herring, all age groups and year classes being combined* [1]

End of growth year	I	II	III	IV	V	VI	VII
Actual length (K), in millimeters		[2] 208 (11)	229 (415)	237 (776)	243 (390)	256 (91)	273 (14)
Calculated (K), in millimeters based on (V)	125 (1,116)	184 (1,110)	215 (912)	230 (300)	247 (54)	261 (8)	
Calculated (K), in millimeters based on (ac)	112 (1,116)	177 (1,110)	212 (912)	228 (300)	245 (54)	260 (8)	
Difference between (K) and (K on V)		+24	+14	+7	−4	−5	
Difference between (K) and (K on ac)		+31	+17	+9	−2	−4	
Difference between (K on V) and (K on ac)	+13	+7	+3	+2	+2	+1	

[1] The number of specimens employed is given in parentheses.
[2] As presumably only the large individuals of this age group matured or straggled along with the older mature fish, this average must be considered as being too high.

TABLE. 18.—*Comparison of actual length with calculated length based on diameter (V) and anterior radius (ac) of scales from Bay City herring* [1]

Year class	Number of fish employed	Age of fish	Character of length value (K)	Dimension of scale employed	Length, in millimeters, of fish in year I	II	III	IV	V	VI	VII
1917			Actual						240 (205)	252 (9)	263 (2)
	2	VII	Calculated	V	119	157	184	210	234	248	
	2	VII	do	ac	106	150	174	204	230	248	
	9	VI	do	V	117	161	198	224	242		
	9	VI	do	ac	104	150	193	222	241		
	61	V	do	V	118	166	200	225			
	61	V	do	ac	104	156	194	223			
1918			Actual					232 (291)	241 (95)	263 (15)	
	15	VI	Calculated	V	113	166	203	228	247		
	15	VI	do	ac	99	155	198	225	247		
	95	V	do	V	114	171	205	229			
	95	V	do	ac	99	160	199	227			
	127	IV	do	V	115	179	216				
	127	IV	do	ac	102	171	213				
1919			Actual				224 (97)	236 (245)	251 (90)		
	90	V	Calculated	V	119	179	213	237			
	90	V	do	ac	105	170	209	236			
	245	IV	do	V	122	183	217				
	245	IV	do	ac	109	176	216				
	50	III	do	V	124	190					
	50	III	do	ac	111	184					
1920			Actual			[2] 195 (5)	229 (148)	243 (240)			
	240	IV	Calculated	V	133	192	224				
	240	IV	do	ac	120	186	223				
	148	III	do	V	139	200					
	148	III	do	ac	128	196					
	5	II	do	V	[2] 121						
Average (K on V)-(K on ac) in millimeters					+13.3	+8.2	+4.6	+2.7	+1.7		
Average (K)-(K on V) in millimeters						±4	+7.7	+2.7	−4	+4	
Average (K)-(K on ac) in millimeters						±5	+9.7	+4	−4	+4	

[1] The numbers in parentheses indicate numbers of individuals employed. [2] Herring collected Oct. 27 to Nov. 4, 1921.

Length computations corroborate this conclusion. In Table 16 are given two extensive series of computed lengths—the one derived from the measurements of the diameter (*V*), the other from those of the anterior radius (*ac*) of the scale. The average of the differences between the computations of the two series is given at the bottom of the table for each year. In Table 17 these data are summarized. That is, the computed lengths for corresponding years are combined into one average, irrespective of the age group or the year class to which the fish belonged. In Table 18 the computed lengths are arranged according to the year class to which the fish

measured belong. The average of the differences between the calculated lengths of the two series is shown at or near the bottom in each table for each year of life. These data show that the length computations based on the diameter are always higher than those based on the anterior radius of a scale, and that the difference between the computations of the two series increases consistently with each earlier year of life for which calculations are made, so that the maximum average difference of 13 millimeters is found in year I.

TABLE 19.—*Differences between calculated length values based on different scale dimensions, according to number of years intervening between the age of the fish at death and age for which calculations are made*

Year of life in which taken	Number of specimens	Average length, in millimeters	Year in which captured	(K on V)—(K on ac) 1 year intervening	2 years intervening	3 years intervening	4 years intervening	5 years intervening	6 years intervening
				Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
II	4	217	1922	+13					
	2	221	1923	+11					
III	50	226	1921	+6	+13				
	148	229	1922	+4	+11				
IV	127	233	1921	+3	+8	+13			
	245	236	1922	+1	+7	+13			
	240	243	1923	+1	+6	+13			
V	61	240	1921	+2	+6	+10	+14		
	95	241	1922	+2	+6	+11	+15		
	90	251	1923	+1	+4	+9	+14		
VI	22	264	1921	+3	+5	+8	+11	+14	
	9	252	1922	+1	+2	+5	+11	+13	
	15	263	1923	0	+3	+5	+11	+14	
VII	6	282	1921	+1	+4	+8	+9	+12	+14
	2	263	1923	0	+4	+6	+10	+7	+13
Average				[1] +3.3 (1.7)	[1] +6.1 (5.0)	+9.2	+11.9	+12.0	+13.5

[1] Value in parentheses excludes the differences of years II and III.

TABLE 20.—*Amount of correction necessary to bring calculated length values, based on anterior radii, into agreement with those based on diameters. Correction factors are based on values of Table 19*

For year of life	For herring in year — II	III	IV	V	VI	VII	Average for herring in any year
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
I	+12	+12	+13	+14	+14	+14.0	+13.0
II		+5	+7	+10	+11	+10.0	+9.0
III			+2	+5	+6	+10.0	+5.0
IV				+2	+3	+7.0	+4.0
V					+1	+4.0	+2.0
VI						+.5	+.5

When we arrange the differences between the computations according to the time that intervenes between the age of the fish at death and the age for which the length is computed (Table 19) we see that, except in young fish, the disagreement between the values of the two series is insignificant when only one year intervenes but becomes increasingly significant with each additional intervening year until the maximum difference of 13 to 15 millimeters is reached for the first year of life. It is to be noted in Table 19 that the values of each column steadily decrease from top to bottom. This means that the difference increases more rapidly with each additional intervening year in the young than in the old herring. The difference for corresponding years of life is less in the young than in the old fish, however. This is indicated more clearly in Table 20, in which is shown the amount of correction required to bring the computations of the two series into agreement.

TABLE 21.—*Amount of deviation of computed length values (calculated K) from actual (K) length values according to length of time that intervenes between the age of the fish at death and age for which length is calculated*

Year of life in which taken	Year class	Year captured	Number of specimens involved in calculated K averages	K-calculated K								Number of specimens involved in actual K averages	
				1 year intervening		2 years intervening		1 year intervening		2 years intervening			
				X and non-X scales				On diameter (V) of—				When 1 year intervenes	When 2 years intervene
				On V	On ac	On V	On ac	X	Non-X	X	Non-X		
				Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*		
VII	1917	1923	2	+4.0	+4.0	+6	+10.0					9	205
VI	1917	1922	9	−2.0	−1.0							205	
	1918	1923	15	−6.0	−6.0	+4	+7.0	−7	−5.0	+4.0	+4.0	95	291
V	1918	1922	95	+3.0	+5.0			−3	+6.0			291	
	1919	1923	90	−1.0	0.0	+11	+15.0	−3	+1.0	+10.0	+12.0	245	97
IV	1919	1922	245	+7.0	+8.0			+4	+10.0			97	
	1920	1923	240	+5.0	+6.0	+3	+9.0	+4	+6.0	+2.0	+4.0	148	5
III	1920	1922	148	−5.0	−1.0			−9	−1.0			5	
	1921	1923	170	[1] +16.0								4	
Average deviation				±4.1	±3.9	+6	+10.3	±5	±4.8	+5.3	+6.7		

[1] This deviation is not included in the average. The discrepancy is large on account of the small number of nonrepresentative 2-year fish available for comparison.

The question now arises, Which series contains the most accurate computations? To provide an answer to this question Tables 17, 18, and 21 have been constructed. In Table 18 the computed lengths are compared with the measured lengths for certain years of life, while in Table 21 the differences between these computed and measured lengths are compared according to the number of years that intervene between the age of the fish at death and the age for which the computations are made. Unfortunately no reliable actual values for the early years of life are available. It is during these years that the most significant differences occur. To indicate the trend of the discrepancies, however, the general averages of the measured lengths of all available herring are compared with similar general averages of the computed lengths as shown in Table 17.

An analysis of Table 18 reveals that for the fifth year of life the computations of both series deviate from the measured values to the same extent and are too high, and that for the fourth and third years the calculated values are, on the whole, too low, those based on the anterior radius being slightly lower than those based on the diameter. Further, the discrepancy is greater for the third than for the fourth or fifth year. The calculated values of Table 17 show the same characteristics—they are too high in the fifth and sixth years and too low in earlier years, the discrepancies in the latter years being the greater.

Further, the figures of Table 21 show that when one year intervenes between the age of the fish at death and the age for which computations are made (that is, when the length is computed for the preceding winter) either dimension may be employed, as the calculations of both series vary from the measured values in the same degree, but that the discrepancy increases considerably more in the computations

based on the anterior radius than in those based on the diameter dimension when two years intervene. The discrepancy in the former calculations increased 164 per cent, that in the latter 46 per cent.

Unquestionably, we would find, if actual values were available, that the discrepancies in the computations based on the anterior radius increase rapidly with each additional intervening year. Doctor Järvi (1920) found this to be true in his calculations for *Coregonus albula*. The trend of the available data at least indicates that this is true in the lake herring. The available data likewise suggest that this phenomenon is also present in the computed values based on the diameter dimensions of herring scales. Whether it occurs in similar computations in other species of fish is not known, as diameter dimensions never have been employed before in life-history work so far as I know. It must be apparent at least that the increase in the discrepancy in computations based on diameters will be much less than that in the error in the calculations based on anterior radii.

In the above discussion of the accuracy of length computations it has been assumed that the values of measured lengths represented all the individuals of the age groups considered. Strictly, this may not be true. As I shall show later (p. 334), the lengths given for the 2, 3, and probably 4 year fish are in all likelihood nonrepresentative of these age groups and are too high, inasmuch as they are based on the mature and presumably the bigger individuals of the age groups. If this be true, the calculated and actual lengths for the fifth and older years of life should coincide, but the calculated values of all age groups should be less than the measured for the fourth and earlier years of life. It has been shown that the latter statement generally holds for all computations of length, whether based on diameters or anterior radii.

As it is not known to what extent the measured length values are exaggerated, probably no absolutely safe criterion is available by which to judge the accuracy of the computed length values; but the following conclusions, previously stated, indicate that the calculations based on diameters are more accurate than those based on anterior radii: (1) The K/V ratio is more constant with the individuals of an age group and with the age groups of a year class than the K/ac (p. 323). (2) As both K/V and K/ac ratios decrease with age, we know that very probably (almost certainly) the calculated values, in general, will be too low. However, the computed lengths based on anterior radii will differ more from the true values than those derived from diameter measurements, as the K/ac ratios decrease more rapidly with age than the K/V. (3) Virtually all investigators who studied the accuracy of calculated lengths concluded that those based on the radii measurements of scales are generally too low, especially those length values computed for the earlier years of life. The computed length values based on diameter measurements may, then, in all probability, approach the actual values more closely than those based on anterior radii.

The data presented in this section are believed to show (1) that the diameter of a scale grows in length more nearly proportional with the body than does the anterior radius, (2) that the diameter dimension is less variable than the anterior radius, (3) that the computed lengths based on the diameter dimension are always higher than those based on the anterior radius, and (4) that the computed lengths based on the diameter, though in general still too low, are more accurate than those based on the anterior radius.

FACTORS INVOLVED IN APPARENT DISCREPANCIES OF LENGTH COMPUTATIONS BASED ON THE SCALES OF HERRING

As the conclusion has been reached that computations based on the diameters of the herring scales are more accurate than those based on the anterior radii, the diameters only form the basis of further discussion unless the contrary is stated.

It has been pointed out that average calculated lengths are lower, in general, than corresponding measured lengths. This is seen by comparing the average measured lengths shown in the third column of Table 16 with the calculated lengths of fish of the same age. Thus, 50 3-year fish average 226 millimeters in length, but the calculated lengths of 3-year fish vary from 194 to 216 millimeters (Table 16, column 8). The differences between actual and calculated lengths are greatest, in general, for the early years of life. This is illustrated in Table 17, where it may be seen that these differences for years II to VI, inclusive, are 24, 14, 7, 4, and 5 millimeters, respectively. The computed length values of Table 16 show another peculiarity, which has been found in the uncorrected computed lengths of virtually all species of fish. In the fourth column of Table 16 are shown calculated lengths at the end of the first year of life. The values decrease from top to bottom; that is, the older the fish whose scale is used for the calculation the lower the value obtained. This peculiarity is even more striking in calculated lengths for years II to V, as seen in the columns headed "on V."

Thus, while all computed values apparently are too low, the error for a particular year is greater the older the fish whose scales are used for the calculation. In general, when we compare the computed values of the various age groups of a sample for equivalent years we find, as shown in Table 16, that in each year of life these values tend to vary inversely with the age of the groups from which the scales are taken. This characteristic of length computations based on scales usually is referred to as "Lee's phenomenon of apparent change in growth rate."

Miss Lee (1912) has suggested seven possible explanations of this phenomenon. These involve either the change in the composition of the year classes with age, selective elimination by death, or change in the scale itself. The suggestions are listed below.

1. The samples of fish are not representative of a year group; that is, the youngest year groups are represented only by their biggest individuals, and as we proceed toward the older groups there appear more and more of those that had been the smaller individuals in their earliest years, so that the average sizes of these older groups tend to show a less increment of growth and a leveling in values is attained (some such thing occurs, according to Lea). This Lee termed "the selective effect of size."
2. The nets are selective, retaining only the largest fish of the youngest year group and excluding the largest fish of the oldest year groups.
3. Conditions of growth are improving and the fish actually are growing more rapidly at present.
4. Females and males that have different growth rates are present in varying proportion.
5. The scale, especially the flexible newest part, contracts when new increments are added. Miss Lee noted that the newest increment in the scale is usually wider than the scale increment of the preceding year (the reverse of the natural law of decrease of scale increment with age and slower growth rate of body), which seems to prove that the scale increment of the year contracts after being deposited.
6. A part of the scale is absorbed in the maturation of sex organs during the spawning period, as, for example, in the salmon.
7. Occasionally more than one ring forms per year.

The author concludes that the "phenomenon of apparent change in growth rate" is most likely due to some natural feature in the fish's or the scale's growth or to the contraction of scales.

Miss Lee's second suggestion, that the nets may act selectively in that they retain only the largest fish of the youngest year group and exclude the largest of the oldest year group, does not seem to apply to the lake herring. The pound nets in which the herring are taken certainly do not exclude any fish because of large size. When it is remembered that the greatest dimensions of the openings in the mesh of the pot in which the herring are captured are only 1½ to 1¾ inches (2¼ to 2½ inches stretched mesh), it appears highly improbable that any considerable selection of size occurred in the 3-year group. If we assume an average length of only 200 millimeters (8 inches) for the smaller fish (the captured 3-year fish averaged 229 millimeters in length), their depth would be about 1¾ inches.[13] Thus, the largest mesh of the pot about equals the depth of the smallest 3-year fish; but the mesh that forms the back of the pot is very much smaller (2 inches), and becomes the bottom in lifting. It is during lifting that small fish escape through the bottom, and clearly the smallest 3-year herring could hardly, if at all, get through the small mesh of the bottom while it is being lifted. Their escape might account for the higher calculated and measured average lengths of the 3-year fish, but it would not account for Lee's phenomenon in the calculated lengths of fish of greater age.

The third suggestion of Miss Lee that conditions of growth may be improving and the younger fish actually are growing more rapidly is applicable to some of the Saginaw Bay herring. I have found (p. 367) that the herring of all age groups actually had grown faster during the first three years of life in the year 1919 and subsequently than before 1919; but such increased growth rates can not affect the individuals of the same year class but of different age groups differently in corresponding years of life. And yet that is what must have happened if Miss Lee's third suggestion be true, for the "phenomenon" appeared even when the age groups of the same year class are compared. Thus, in Table 35, in the 1919 year class, the lengths for all growth years increase with the use of younger age groups for calculation. All fish of this year class presumably were living under the same conditions in 1920 and doubtless reached about the same length at 2 years of age, yet the calculated lengths vary inversely with the age groups.

Elsewhere (Tables 32 and 33) it is shown that the male and female herring grow at the same rate. This precludes, for the lake herring, Miss Lee's fourth suggestion that females and males have different growth rates and may be present in the samples in varying proportion.

Miss Lee's sixth suggestion is that a part of the scale is absorbed at the time of maturation of the sex organs. In that case a zone of the scale laid down in the year

[13] This value for depth was obtained for 84 Lake Huron herring 220 millimeters or less in length (average 203 millimeters). Both length and depth measurements were made by Doctor Koelz.

of spawning, of a width proportional to the growth of the fish in length during that year, is reduced in width at the spawning time and, with the resumption of growth after breeding, a spawning mark is left on the scale. However, this suggestion apparently does not hold for the lake herring, as no spawning mark nor any evidence of absorption is shown in the relief structures on the surface of their scales.

Miss Lee's seventh suggestion is that occasionally more than one ring (annulus) forms in a year. If such accessory annuli were not recognized as such, but were treated as normal annuli, the "phenomenon" might appear in the calculations. This suggestion does not apply to the lake herring, however, if my conclusions are well founded that normally only one annulus is produced each year and that this is distinguished readily from the occasional accessory annuli.

There remains Lee's first suggestion that the samples of fish are not representative of the year group, and her fifth that the newer part of the scale contracts with age. Miss Lee is inclined to accept her fifth suggestion that the scale, especially the flexible newest part, may contract whenever additional material is added to its margin. To ascertain whether this is true in the herring scales, I measured, for the year classes 1918, 1919, 1920, and 1921, the scale diameters at the end of each growth year (Table 22). The average diameter increments derived from these measurements are shown in the right half of the table. The increment of the fourth year of the 1918 year class increases as the age of the fish whose scales were measured increases. Likewise, the increment of the fifth year of this year class is less (0.27) in the 5-year herring than in the 6-year fish (0.44). Similarly, in the herring of the year classes 1919, 1920, and 1921 the newly deposited portion of the scale, which presumably had not yet contracted, is nearly always narrower than the corresponding older deposits, which presumably had contracted. The increments of the third growth year are the same (0.71) in the 3 and 6-year fish of the 1919 year class. It is realized that the most recently deposited portion of the scales of these fish may not represent a completed growth year, but as the fish were taken in November it is hardly probable that the newly deposited zones of the scales of the younger fish would increase sufficiently during the winter to exceed those of corresponding years of older fish. From the foregoing it appears that those zones of the scale deposited after the third year grow broader with time; they seem to expand instead of to contract as the fish grows older and additional material is added to the margin of its scale.

TABLE 22.—*Average total length and average increment in length, in millimeters, attained by the diameter of non-X scales at end of each growth year of Bay City herring hatched in 1918, 1919, 1920, and 1921 and captured in 1921, 1922, 1923, and 1924*

Year class	Age of fish	Number of individuals	Total length of scale in year						Increment in year					
			I	II	III	IV	V	VI	I	II	III	IV	V	VI
1918	IV	215	2.65	4.08	4.86	[1] 5.27	------	------	2.65	1.43	0.78	0.41	------	------
	V	87	2.54	3.81	4.58	5.11	5.38	------	2.54	1.27	.77	.53	0.27	------
	VI	7	2.75	3.90	4.65	5.28	5.72	6.02	2.75	1.15	.75	.63	.44	0.30
1919	III	65	2.86	4.31	5.02	------	------	------	2.86	1.45	.71	------	------	------
	IV	211	2.68	4.02	4.78	5.19	------	------	2.68	1.34	.76	.41	------	------
	V	48	2.65	4.01	4.77	5.28	5.58	------	2.65	1.36	.76	.51	.30	------
	VI	18	2.63	3.82	4.53	5.17	5.63	6.07	2.63	1.19	.71	.64	.46	.44
1920	III	136	3.06	4.38	5.03	------	------	------	3.06	1.32	.65	------	------	------
	IV	132	2.89	4.19	4.90	5.31	------	------	2.89	1.30	.71	.41	------	------
	V	74	2.59	3.91	4.66	5.21	5.60	------	2.59	1.32	.75	.55	.39	------
1921	III	92	3.16	4.48	5.19	------	------	------	3.16	1.32	.71	------	------	------
	IV	355	3.02	4.25	4.95	5.38	------	------	3.02	1.23	.70	.43	------	------

[1] The last total length value of each row represents actual diameter measurements; the others represent the lengths of "annular" diameters, tha t is, the parts of the diameter included in the various annuli.

While apparently, then, the outer zones of the scales expand with age, perhaps the inner zones undergo a contraction at the same time. The data of total lengths of Table 22 indicate that apparently they do contract. In the 1918 year class the diameters of the scales of the 5-year fish averaged consistently shorter than the corresponding diameters of the scales of the 4-year fish (compare values 4.86 and 4.58 of the third growth year). The scale diameters of the 6-year herring, however, averaged longer than those of the 4-year fish in the first growth year, the same in the fourth year, but shorter in the second and third growth years. In the 1919 year class the scale diameters of the fourth and fifth age groups, which, except for the fourth growth year, averaged approximately the same, were consistently shorter than those of corresponding years of the third age group. So, also, the scale diameters of the 6-year fish of this year class averaged consistently shorter than those of corresponding growth years (the fifth excepted) of the 3, 4, and 5 year fish. The 1920 and 1921 year classes show even more striking results. In these fish, without any exception, the scale diameter of a certain growth year decreases as older age groups are employed.

It is to be noted that the differences between the total lengths of the scale diameters of any two age groups of a year class diminish after the second or third year of life (compare, for example, the diameters of the 1920 year class). By referring to the increments of Table 22 it may be seen that as a result of this decrease in the differences the order of scale increments is reversed after the second or third growth year. Whereas, the scale increments of the first and second growth years usually decrease as the age of the fish whose scales were measured increases, those of the third year change little with age, and those of later growth years increase as the age of the fish increases (see, for example, the increments of the 1920 year class).

Do the scales of herring, therefore, contract with age? Our data suggest that apparently a concentration with age takes place in the first two innermost zones of scales. The data likewise indicate that the third zone changes little with age while the outer zones expand. Do contraction and expansion then occur synchronously in the scales of lake herring? This does not seem possible in view of what is known concerning the structure of teleost scales in general. "In minute structure each scale consists of an outer layer of bone, which, like the bone of the endoskeleton, may either be homogeneous, except for a feeble lamination, or it may contain bone cells, arranged in successive layers parallel to the surface of the scale. In addition, there is an inner fibrous stratum in which the fibrous bundles in any one plane cross those in planes above or below them." (Bridge, T. W., in Cambridge Natural History, 1910, Vol. VII, p. 189.) The fibrous bundles of any one plane form a thin lamella. During the growth of the scale these lamellæ are deposited on the lower surface of the scale, each new lamella growing larger than and extending beyond the one most recently formed. Lea (1919) found that in the marine herring (Clupea) the breadth of the zones of these lamellæ "exhibits an irregular progression, broader belts suddenly appearing after a series of narrow zones, * * * that the transition from narrow to broader zones takes place just where the surface of the scale shows a winter ring. Thus, the elementary plates are seen to form their own system of annual rings, corresponding to that of the surface layer, but otherwise differing greatly from this, and more resembling that found in the scales of many salmonoids and gadoids, etc., where the winter rings are not so sharply marked, but a gradual transition from summer to winter is seen [p. 90]." As is the case with the circuli, the number of lamellæ deposited each year varies as the growth rate of the scale. Lea found further that the outer or "upper covering layer is of almost equal thickness at the edge and near the center of the scale and evidently does not grow thicker; it is thus easy to understand that the winter rings, for instance, upon the surface of this layer, continue equally distinct many years after formation * * * [p. 89]." "The scale may thus be considered as a greatly flattened cone composed of fibrillary plates * * *. This cone is evidently covered entirely by a nonfibrillary layer, on the upper side of which, however, is found finely marked relief which gives the scale its characteristic appearance [p. 87]."

Miss Lee's fifth suggestion, then, does not seem tenable. We may look for some other and more plausible factor or factors to account for our paradoxical results.

It was obvious in our discussion of the scale-diameter measurements of Table 22 (p. 331) that there we were, in reality, confronted with Lee's "phenomenon of apparent change in growth rate." This was to be expected but only on the assumption that the scale-diameter measurements and the computed length values based on them are correlated more or less positively, that when the "annular" scale diameters are large, the lengths calculated from them will be large, and when small, the lengths calculated from them will be small. It is conceivable that such a direct correlation does not exist, as length computations for a particular year vary as the proportionate length of the scale diameter of that year in the total length of the scale and not as the actual length of that diameter. A length calculated from a large scale diameter may be small, and vice versa. That this is not generally true is evident from the following facts. It has been shown already that the bigger herring of an age group averaged larger at the end of the first year of life than the smaller fish (Table 5). Computations show that the average length of the scale diameters of the first year of life is consistently greater in these large fish than in the small. The same 3-year herring and the same size groups employed on page 316 for scale-diameter measurements were used here. It was found that the length of the scale diameters of the first year of life averaged 2.85 millimeters in the 40 small 3-year herring of 1921 and 2.94 millimeters in the 26 large fish; 3.01 millimeters in the 48 small 3-year fish taken at Bay City in 1922 and 3.10 millimeters in the 88 large herring; and 2.78 millimeters in the 71 small 3-year fish taken at Oscoda in 1922 and 2.87 millimeters in the 72 large individuals. The grand average for the 159 small herring was 2.87 millimeters and for the 186 large fish 2.99 millimeters. As Lee's "phenomenon" appeared in the computed lengths, it must, as the result of this correlation, appear in the measurements of the scale diameters. Likewise, a more or less perfect direct correlation exists between the total increments of scales and those of the body computed from these scales. The paradoxical results shown in the scale increments of Table 22 and discussed on page 330 must, of necessity, then, also occur in the body increments calculated from these scales.

Table 23.—*Average computed increments in length, in millimeters, of various age groups of Bay City herring hatched in the years 1917 to 1921, inclusive, for each growth year*

Year class	Age group	Number of individuals	Average computed increments in length					
			I	II	III	IV	V	VI
1917	V	205	115	49	35	25	16	
	VI	9	117	44	37	26	18	10
1918	IV	291	116	63	35	18		
	V	95	114	57	34	24	12	
	VI	15	113	53	37	25	19	16
1919	III	97	127	65	32			
	IV	245	122	61	34	19		
	V	90	119	60	34	24	14	
	VI	21	116	53	32	27	22	18
1920	III	148	139	61	29			
	IV	240	133	59	32	19		
	V	74	117	60	34	25	18	
1921	III	170	142	59	32			
	IV	356	136	55	32	20		

Table 23 shows this tŏ be true. In this table are shown the computed average increments of length reached in different years of life by various year classes of lake herring. It may be seen that whereas the computed increments of the first and second years of life usually decrease as the age of the fish whose scales were measured increases, those of the third year change little with age while those of the fourth and later years increase with age. (See, for example, year class 1919). Obviously the factor or factors that explain the "phenomenon" in the scale diameters and the apparent contraction and expansion of the scales (Table 22) will also explain these characteristics in the body lengths and increments computed from these scales. We may then discuss either the measurements of the scales or those dimensions of the fish computed from the scales. To avoid repetition, the former course is convenient. As the scale measurements are direct and do not involve the assumption relative to the proportionate growth of body and scale, they are to be preferred to the computed lengths even though they involve fewer specimens.[14] The computed values are resorted to when the number of specimens involved in the averages of the scale measurements is unusually small; as, for example, in the sixth and seventh age groups.

Any factor or factors suggested to account for Lee's "phenomenon" in the "annular" diameter measurements of the scales and for the apparent contraction and expansion of scales with age must determine (1) why the scale increments of the first and second growth years of a year class generally decrease as the age of the fish whose scales are studied increases, (2) why the scale increment of the third growth year increases or remains constant with age, and (3) why the scale increments of the fourth and fifth years increase with age.

With these facts in mind we may now consider Lee's first suggestion that the youngest year groups may be represented in the catch only by their biggest individuals, and that, as we proceed toward the older groups, more and more of those that had been the smaller individuals in their earliest years appear in these older groups. If

[14] Fewer specimens were employed for scale diameter averages because non-X scales only were used. The computed length values of fish were based on non-X and X scales.

this be true the younger age groups contain a larger proportion of fast-growing fish than do the older groups, and the "annular" diameter measurements of their scales give higher values. In my discussion of the data of Table 30, on page 384, I state that most herring attain sexual maturity in the third and fourth years of life, and that in relatively few is the first spawning delayed until the fifth year. It is possible that the herring that spawn in their third year are the bigger individuals of their year class, and that those that do not spawn until their fourth or fifth year are smaller. Some evidence that this is true may be found on page 390, where I show for the third and fourth age groups of the Oscoda herring that the immature individuals of an age group average less in length than the sexually mature. The influx of the smaller individuals into the fourth and fifth age groups would presumably tend to lower the average "annular" diameter measurements of these age groups as well as their average actual measured body lengths. The average lengths of the "annular" scale diameters would then be less for all corresponding years of life in the 4 and 5 year fish than in the 3-year fish, and similarly they would, in general, be less in the 5-year fish than in the 4. It is assumed here that the number of fish that reach sexual maturity in the fourth or fifth year is large enough to alter the average growth rate of their respective age group. Otherwise the corresponding scale diameters should be approximately the same in the three age groups under consideration. However, the 6-year and older fish of a year class composed wholly of the surviving mature 5-year individuals ought to show, for the same years of life, scale-diameter measurements similar to those of the 5-year group. Lee's "phenomenon," if conditioned wholly by the growth-rate composition of the age groups, should not be present in the scale diameter measurements of the fifth and older age groups of the same year class. These age groups should have identical growth-rate compositions.

An examination of the total length values of scales given in Table 22 shows that these data agree fairly well with the above theoretical deductions derived from Lee's first suggestion, in so far as the interrelations of the scale measurements of the third, fourth, and fifth age groups are concerned. In general, the scale diameters of these three age groups decrease in length with age in each year class; but whether Lee's "phenomenon" is absent from the scale-diameter measurements of the fifth and older age groups of a year class is not so evident. No data are given in Table 22 for the 7-year fish, while the sixth age group is represented there by 7 individuals of the 1918 year class and by 18 individuals of the 1919 year class. These age groups are somewhat better represented in the table (35) of computed body lengths. Even here the 7-year fish are too sparsely represented to permit a comparison of their calculated lengths with those of the 5 and 6 year groups of the same year class, while the sixth age group, though better represented, still comprises comparatively few individuals. Notwithstanding these small numbers, Table 35 shows that the computed lengths of the 6-year fish of the 1917 year class nearly coincide with the corresponding lengths of the 5-year fish of that year class in all years, while the calculated lengths of the 6-year group of the 1918 year class agree fairly well with the corresponding lengths of the 5-year fish of that year class; Lee's "phenomenon," if present at all, is certainly not very prominent in the computed lengths of the 6 and 5 year

groups of these two year classes. It is decidedly conspicuous, however, in these age groups in the 1919 year class. In this year class the calculated lengths of the 6-year fish are noticeably lower in most years than the corresponding lengths of the 5-year fish. Our data, then, do not appear to be sufficient to enable us to decide definitely whether Lee's "phenomenon" is present in the scale-diameter measurements or in the calculated lengths of the fifth and older age groups of a year class.

Can the assumption that a selection occurs in the matured age groups, whereby comparatively slow-growing individuals are introduced into the fourth and fifth age groups, explain the apparent contraction and expansion of scales? It is apparent that such a selection could account for the progressive decrease in the scale increments with age in the first two years of life of the herring of age groups III to V, inclusive; but it is not clear how this selection can explain why the presumably slow-growing fish of a year class should, in their third or fourth year of life, become the fast-growing fish of their year class, and why the presumably slowest-growing fish should change into the fastest-growing. In other words, it can not explain the progressive increase in the scale increments of the fourth and later years of life with age.

Another factor—sexual maturation—may be involved here, however. Spawning takes place in the lake herring in November or December. The annual ripening of the sexual products and the attendant change in the habits of the fish may cause an earlier cessation of body and scale growth in mature fish than occurs in immature fish. The growth zone of the year may be narrower in the scales of mature fish than it would have been had the fish remained immature. That sexual maturation retards growth is shown in some fish (for example, the salmon) by a spawning mark. It is also common knowledge that in fishes (at least in those of the northern latitudes) the first prominent break in the curve of growth generally occurs in that year in which a large percentage of individuals reach sexual maturity. This holds, also, for the lake herring, whose curve of growth, as shown in Figure 39, bends sharply in the third year. Sexual maturation and retardation in growth are probably positively correlated in the lake herring.

As the lake herring reach sexual maturity in either the third, fourth, or fifth year of life, it follows that the fourth and older age groups (practically all individuals in the Bay City samples were sexually mature) include individuals that were immature in their third year. These immature fish, which, according to Lee's first suggestion, were the slower growing individuals of their year class, were not retarded in their growth in the third year by sexual maturation. The fast-growing, mature, 3-year fish may have been retarded sufficiently in their third year growth rate to allow the slow-growing, immature individuals of their age group and year class to approach closely their growth rate, to equal it, or to exceed it. These immature individuals, on becoming sexually mature in their fourth or fifth year and joining the mature fourth and (or) older age groups, would then affect the averages of the third-year scale increments of these age groups in such a way that they would be slightly lower than or equal to or exceed the average of the third-year scale increment of the mature 3-year fish of the same year class. A retardation in the growth of the sexually mature 3-year herring could account for the increase in the width of the third year growth zone in the scales of the 4-year fish, but, as I shall show shortly (p. 336), not for any further increase in the width of this zone in older age groups. In fact, the average of the third year scale increments should probably decrease in the 5-year fish. (See below.) The data of Table 22 show that this average usually increases in the 4-year fish and varies little with the older age groups.

As we assumed was the case in the mature 3-year fish, so, we may believe, must the mature 4-year herring have been retarded in their growth rate by sexual maturation. This retardation in the growth of the mature 4-year fish would permit the slower growing immature individuals of the same age and year class to approach closely the growth rate of the mature, to equal it, or to exceed it. These immature 4-year individuals when joining, in the following year, the mature 5-year fish would tend to raise the average scale increment of the fourth year of these fish, so that it would approach more closely that of the captured mature 4-year fish of the same year class, equal it, or exceed it. The larger fourth-year scale increments in all the 5-year groups, when compared with corresponding increments of the 4-year group (Table 22), seem to indicate that retardation in the growth of the 4-year fish is always so great that the immature 4-year fish when in their fifth year are able to increase the fourth year scale increment of the fifth age group considerably above that of the fourth age group of the same year class.

However, as explained elsewhere (p. 334), inasmuch as the sixth age group of a year class is composed wholly of the surviving mature members of the fifth, the scale increments of these two age groups of a year class ought to be the same in corresponding years. The 6-year fish did not seem to be represented adequately in the various year classes to permit a definite statement as to the presence or absence of Lee's "phenomenon" in the sixth age group (p. 334). They gave inconsistent results. It is a question, therefore, whether the sixth age group should be considered in the present discussion. If considered, it is at once apparent that the tendencies that exist in the scale and computed growth (Table 23) increments of the younger age groups continue into the sixth. The scale and body increments of the first two years of life continue their decrease in this age group, while those of the fourth and fifth years continue their increase. The 6-year fish agree in these characteristics—contrary to what was stated on page 334, they are here consistent. If the data of Tables 22 and 23 of the 6-year fish are valid, we are unable, on the basis of the two assumptions considered above, to account for the continued decrease and increase in the growth increments in the sixth age group.

Another apparent discrepancy appears in the increment data of Tables 22 and 23. The progressive decrease in the increments of the first and second years of life with age was explained by assuming that the third age group included the fast-growing individuals of the year class, the fourth the surviving, fast-growing mature 3-year fish and the more slowly growing individuals that reach sexual maturity in the fourth year, and the fifth age group the surviving, mature 4-year fish and the most slowly growing individuals of the year class that reach sexual maturity in the fifth year. Obviously, we should expect the average third year increment (scale and body) of the 5-year fish (also of the 6) to be less than that of the faster growing 4-year group of the same year class; but Tables 22 and 23 show it to be the same, less, or greater.

Is probably another factor involved? The only other plausible factor that I can suggest at present is the "law of compensation in growth" developed by Gilbert

(1914) and others. This law states that those fish that grow most slowly during the earliest years of life grow most rapidly during the later years of life, and vice versa. Later (p. 370) I shall show that this principle actually holds for the lake herring. This law would still leave unexplained why the increments of the first two years of life tend to be least in the sixth age group of a year class, but it would account for the rapid growth of these fish later in life. So, also it may account for the fact that the third-year increment of the 5-year fish of a year class is not less than that of the 4-year fish.

To recapitulate, of Miss Lee's seven suggestions (p. 328) only the first is acceptable in explanation of her "phenomenon" in the scale diameter and computed body-length measurements of the lake herring. That the herring that reach sexual maturity late in life are the smaller individuals of their year class appears highly probable from the data of the Oscoda fish (p. 390). This fact would explain why the scale diameters of the fish of a younger age group of a year class generally exceed in length those of the fish of an older group; but it could not explain the progressive increase with age in the scale and body increments of the later years of life. To account for this, two other factors were considered—sexual maturity and compensation in growth. It was stated that in fish (at least in the northern species) sexual maturation usually is accompanied by a retardation in the growth of body and scale and that a compensation in growth occurs; that is, fish that grow slowly during the earliest years of life grow rapidly during the later years of life, and vice versa. Virtually all the data of Tables 22 and 23 on the increments of scale and body growth can be brought into agreement and quite satisfactorily explained by these three factors. In fact, only the first and third factors are required to explain all the data; but, inasmuch as the second one (sexual maturation) is also actually involved, it can not be ignored. Lee's "phenomenon," then, in so far as the lake herring are concerned, seems to be largely the result of perfectly natural events in the life history of the fish.

TABLE 24.—*Uncorrected and corrected (by Lee's formula) computed lengths of various year classes of Saginaw Bay herring for each year of life. Identical fish were used for both series.*

Year class	Age group	Number of individuals employed	Average uncorrected calculated length, in millimeters for year—						Average corrected calculated length, in millimeters for year—					
			I	II	III	IV	V	VI	I	II	III	IV	V	VI
1918	IV	215	116	178	212	[1] 230	......	......	133	186	215	[1] 230	......	......
	V	87	113	170	204	228	240	......	132	180	210	230	240	......
1919	III	65	128	193	225	......	......	......	143	198	225	......	......	......
	IV	211	121	182	216	235	......	......	138	190	219	235	......	......
	V	48	118	178	212	235	248	......	136	188	217	237	248	......
	VI	18	116	168	199	227	248	267	136	181	208	233	250	267
1920	III	136	139	199	229	......	......	......	153	204	229	......	......	......
	IV	132	131	190	222	241	......	......	147	198	225	241	......	......
	V	74	117	177	211	236	254	......	136	188	217	239	254	......
1921	III	92	141	199	231	......	......	......	154	204	231	......	......	......
	IV	355	136	192	224	243	......	......	152	199	226	243	......	......

[1] The last value of each age group represents actual body measurements.

TABLE 25.—*Comparison for identical individuals of calculated lengths, averaged after having been corrected by Lee's formula in the usual manner (that is, the formula is applied separately to measurements of each individual), with corresponding calculated length averages derived by application of the formula to averages of measurements of scale diameters and body lengths.* (*See text*)

Age group	Number of specimens	Average body length, in millimeters	Average length of scale diameter, in millimeters	Average length, in millimeters, of scale diameter at end of year—				Computed length, in millimeters, based on individual scale diameters at end of year—				Computed length, in millimeters, based on scale diameter averages at end of year—			
				I	II	III	IV	I	II	III	IV	I	II	III	IV
II	11	208	4.62	2.92	------	------	------	145	------	------	------	146	------	------	------
V	9	238	5.31	2.50	3.70	4.48	5.00	133	177	207	226	133	177	207	226

In a more recent publication Miss Lee (1920) considers another factor as a possible explanation of the "phenomenon of apparent change in growth rate." It is well known that scales do not begin their development until the fish has grown to a certain length. The growth history of the early part of the first year of life is not registered on the scales, therefore. This, if ignored, presumably introduces an error into the computations of length, which are based on the assumption that the entire history of the growth of the body of a fish is registered faithfully in its scales. Lee supplied a general formula (see p. 306) patterned after that of Fraser to correct the errors due to tardy appearance of scales. To determine whether such a correction actually eliminates the "phenomenon" from my computed lengths, I applied the formula to a series of calculated lengths computed from the scale-diameter averages of Table 22. That is, I determined the average actual length of the fish of an age group whose scale diameters were measured and from this length and the scale-diameter averages (Table 22) computed the length attained by that age group at the end of each year of life.

That this method of length computation is valid may be seen by comparing the computed lengths of the seventy-four 5-year fish of the 1920 year class, as given in the left half of Table 24, with those given in Table 35. The former computations were derived from the scale-diameter averages of Table 22, the latter in the usual manner—that is, the lengths were calculated for each individual and then averaged. The compared lengths are identical in corresponding years of life. To the average lengths, determined as explained above, Lee's formula was applied. That this method of correcting computed lengths is valid is indicated by the data of Table 25. I applied the formula separately to the measurements of each of the 11 individuals of the second age group (Table 25) and obtained an average corrected calculated length of 145 millimeters for the first year of life. I then ascertained the averages of the scale diameters of these fish for the two years of life and applied the formula to these averages and average actual length of the age group (208 millimeters). The corrected calculated length for the first year of life obtained in this manner was 146 millimeters, or 1 millimeter more than was obtained above. Repeating the above procedure with nine individuals selected at random from the fifth age group, I obtained by the two methods identical calculated length values for corresponding years of life (Table 25). Application of Lee's formula to the averages of the body and scale-length measurements

of an age group appears to give corrected computed lengths, which are at least approximately accurate.

As stated on page 317, scale formation in the lake herring very probably begins at a body length of approximately 35 to 40 millimeters. Assuming 35 millimeters to be correct, the corrective formula, then, is $L_1 = 35 + \frac{v_1}{V}(L-35)$, etc. Both uncorrected and corrected computed lengths are shown in Table 24. Identical fish were employed for both series. The uncorrected computed average lengths are shown in the left half of the table; the corrected computed lengths in the right half. If we compare the corresponding values of each age group of Table 24 we find that three principal changes occur when the computed lengths are corrected by Lee's formula. First, the averages are raised in an amount that decreases gradually from the early to the late years of life. Thus, the averages of the 4-year fish of the 1918 year class (Table 24) when corrected are raised 17, 8, and 3 millimeters in years I to III, respectively. Second, the increments are decreased in all years except the first. Thus, the increments of the 4-year fish of the 1918 year class (derived from Table 24) for years I to IV are, when the computed lengths are uncorrected, 116, 62, 34, and 18 millimeters, respectively, but when the computed lengths are corrected they are 133, 53, 29, and 15 millimeters, respectively. Third, the "phenomenon" is less pronounced so that the lengths of the different age groups of the same year class become more comparable. This is seen in the computed lengths of the 1919 year class (Table 24). The lengths computed for the first year of life for the sixth, fifth, fourth, and third age groups are, when uncorrected, 116, 118, 121, and 128 millimeters, respectively, a difference of 12 millimeters between the extremes, and 136, 136, 138, and 143 millimeters, respectively, when corrected, a difference of 7 millimeters between the extremes. Similarly, for the lengths of the second and third years of life the difference between the extremes is reduced from 25 to 17 millimeters and from 26 to 17 millimeters, respectively.

A study of the computed lengths of Table 24 shows that though Lee's "phenomenon" becomes less pronounced when the lengths are corrected by her formula, the "phenomenon" is still strikingly evident in the corrected calculated lengths.

Table 24 shows further that for the third and later years of life the corrected computed lengths of a year class agree more nearly with the actual measured lengths for corresponding years than do the uncorrected computed lengths. Thus, computations show that in the year class 1919 the average deviation of the calculated lengths from the actual for year III is 16 millimeters for the uncorrected values and 10 millimeters for the corrected (Table 24). Similar results may be obtained for the later years of life. Whether the corrected values for years I and II likewise coincide more nearly with the measured than do the uncorrected can not be definitely determined at the present time owing to the lack of 1 and 2 year fish in my samples. If, however, the 34 Saginaw Bay herring of year II, with an average length of 202 millimeters (Table 14), be taken as a standard, then we may state that for year II the corrected values are the more accurate. Attention may be called again to the fact that the actual measured lengths of the younger age groups may be too high (see p. 334) and that the uncorrected values, therefore, may, in reality, be more accurate than the corrected values.

The corrected values for year I, however, may be too high. It has been found already that the calculated length averages for year I, based on the measurements of scale diameters, averaged 13 millimeters higher than those based on the measurements of anterior radii (Table 16). A correction now by Lee's formula raises these averages from diameters approximately 17 millimeters (computed from Table 24) more—a total average raise, therefore, of 30 millimeters. These corrected values from diameter measurements for year I, however, at times appear to be rather high. (See year classes 1920 and 1921, Table 24.) Measurements of young herring from localities other than Saginaw Bay suggest that the corrected values for year I of Table 24 are rather too high than too low. A herring of year I, taken in September at Alpena, Mich., from Lake Huron, measured 108 millimeters in length; another taken from an inland lake in Michigan in October also measured 108 millimeters in length. Clemens (1922) gives a length of 75 millimeters to Lake Erie herring (*artedi*) of age group I. Six whitefish (*C. clupeaformis*) 7 months old (whitefish grow as fast or faster than herring), which were reared accidentally in the ponds of the bureau's hatchery at Northville, Mich., and which subsisted on the natural food found in the pond, ranged from 97 to 111 millimeters in length.

Lee's formula does not take into consideration the rapid increase in length of the scale as compared with that of the body, especially the rapid increase occurring immediately after the scale appears (see Tables 10 and 13, and figs. 12, 13, and 14) during the first year of life. The effect of this relatively rapid scale growth upon the calculated lengths is exactly opposite that produced by the late appearance of the scale, and the former neutralizes the latter, at least in part. The relation between the two factors—tardy scale formation and the relatively rapid increase in the length of the scale—and their effect on computed lengths may be stated as follows: If we assume for the moment that the body and scale begin their growth in length at the same time and continue that growth at the same relative rates throughout life, the body-scale (K/V) ratio will remain constant throughout life and lengths computed from the scales will be correct. That is, if the body-scale ratio of an older group of a year class equals the true ratio of a younger, the calculated values for the younger group, based on the scales of the older, will be accurate; but as the scales of the herring do not appear until after the body reaches a length of approximately 35 millimeters, and are at first so small as not to be in contact, the actual body-scale ratio at this body length is much higher than it should be; that is, higher than the true theoretical ratio. As the scale immediately after its appearance grows relatively very much more rapidly in length than the body (Table 13) it follows that the actual body-scale ratio is lowered rapidly, approaching, with the growth of the fish, the true theoretical ratio. If the actual and the true theoretical ratios coincide during the first year of life, and body and scale thereafter grow directly proportional to each other (that is, the body-scale ratios remain constant with age), calculated length values will be accurate, and no correction for late scale formation is necessary; but if the scale continues to grow in length relatively more rapidly than the body, a correction is necessary, not for tardy scale formation but for the disproportionate growth of body and scale. We do not know what the body-scale ratio (the true theoretical ratio) of the herring should be, therefore we have no means of determining

definitely whether the known ratios are too low or too high. However, in view of the facts that the actual observed ratios undergo a rapid drop during the first year of life, and that each year thereafter the ratio continues to fall, it seems reasonable to believe that the observed ratios of the older fish are lower than they should be theoretically. Tardy scale formation may be ignored, then, as its effect upon computations of length is counterbalanced by that of disproportionate growth of body and scale. The latter factor, rather than the former, may, at least in part, be responsible for Lee's "phenomenon" in the computations of body length.

It is to be noted that Lee's formula proposes to eliminate the "phenomenon" from calculated length values that involve computations based on mathematical proportions. The larger the number of proportional computations involved (as in old fish) the greater will be the correction for the first computation (that is, for year I; see p. 339). Lee's formula assumes that the "phenomenon" is purely the result of the method of calculation from scales. Obviously, then, late scale formation can not be a factor in the "phenomenon" found in direct measurements of scale diameters, as in them no computations are involved. Even so, there is no relation apparent between the late formation of scales and the progressive decrease in the length of scale diameters with age (Table 22) in fish of the same year class. Tardy scale formation was not considered, therefore, in the discussion of scale-diameter measurements (p. 331).

A correction for the disproportionate increase in length of body and scale is possible. If, for example, the body-scale (K/V) ratio of a higher age group equals 95 per cent that of a lower, the length value computed for the lower age group from the scales of the higher will equal 95 per cent of the true value; that is, the calculated result will be too low in the same proportion as the scales grow relatively too fast and an error of 5 per cent is involved in the computation.

TABLE 26.—*Average of actual measured lengths (K) of all available Bay City herring when arranged in age groups; also, in each age group, the calculated lengths for each earlier year of life, calculations based on measurements of V of X and non X scales* [1]

Year	Average of measured lengths, in millimeters	Calculated length, in millimeters, for year—							
		I	II	III	IV	V	VI	VII	VIII
II	208 (11)	131							
III	231 (577)	139	200						
IV	239 (1,132)	127	186	220					
V	245 (464)	116	170	205	229				
VI	258 (112)	115	163	196	223	243			
VII	273 (14)	116	161	190	219	241	258		
VIII	292 (3)	107	149	176	206	239	259	277	
Grand average total length		127 (2,313)	185 (2,302)	213 (1,725)	228 (593)	243 (129)	258 (17)	277 (3)	
Grand average increments of length		127	58	28	15	15	15	19	15

[1] The number of specimens employed is shown in parentheses.

TABLE 27.—*Comparison, for herring of age groups IV to VI of uncorrected computed lengths of various years with computed lengths corrected from body-scale ratios (K/V) for disproportionate growth of body and scale. The K/V ratios are based on X scales and are taken from Table 10*[1]

Year	K/V	Year	K/V	K/V of older fish / K/V of younger fish	Uncorrected calculated length, in millimeters, for younger fish from scales of older (Table 26)	Corrected calculated length, in millimeters (length in column 6 divided by per cent in column 5)
VI	48.16 (52)	V	48.84 (178)	0.986	243 (112)	246
VI	48.16 (52)	IV	49.11 (323)	.981	223 (112)	227
VI	48.16 (52)	III	49.83 (147)	.966	196 (112)	203
V	48.84 (178)	IV	49.11 (323)	.995	229 (464)	230
V	48.84 (178)	III	49.83 (147)	.980	205 (464)	209
IV	49.11 (323)	III	49.83 (147)	.986	220 (1,132)	223

[1] The number of specimens employed is shown in parentheses.

On this basis Table 27 was constructed. I determined what percentage (column 5) the K/V ratio of each age group was of that of each lower age group, then computed the average length for each lower age group from the scales of the higher (Table 26), and finally corrected the calculated value on the basis that it equaled that percentage of the true value that was obtained for the K/V ratio of the corresponding year (Table 27, column 7). An inspection of Table 27 shows that such a correction for disproportionate scale growth raises the computed lengths of all years, and that the amount of correction for corresponding years of life increases with the age of the fish whose scales were used. Thus, in the 6-year fish the averages are raised 3, 4, and 7 millimeters, respectively, for the fifth, fourth, and third years of life; in the 5-year group they are raised 1 and 4 millimeters, respectively, for the fourth and third years; while in the 4-year fish the average for the third year is increased 3 millimeters. As the K/V ratios of the 1 and 2 year herring undoubtedly are higher than those of the fish of year III, the amount of correction for the first and second years of life must increase accordingly, and, if our general K/V ratios of Table 10 are reliable, they must equal more than 7 millimeters in the 6-year herring, more than 4 millimeters in the 5-year fish, and more than 3 millimeters in the 4-year fish. It is apparent that when a correction for disproportionate scale growth is applied to the computed lengths Lee's "phenomenon" becomes less pronounced. As was the case with late scale formation, so also here no factorial relation exists between the disproportionate growth rate of body and scale and the "phenomenon" in the direct measurements of scale diameters in fish of the same year class.

A review of the preceding discussion shows that the presence of Lee's "phenomenon" in the scale-diameter measurements of the lake herring and in the computations of length based on these measurements may be explained best on the assumption that the late-maturing fish of a year class are the more slowly growing individuals of their year class. This accounts for the progressive decrease with age in the scale and body increments of the first two years of life. The disproportionate growth rate of body and scale may be an additional factor for the "phenomenon" in the computed lengths. The progressive increase with age in the increments of the third or fourth and later years of life is, in part, the result of the principle of a compensation in growth

found to be operative among the herring (see p. 370) and in part the result of the retarding effect on growth of sexual maturation. According to these conclusions, Lee's "phenomenon" is largely a natural one and not an error due to a faulty technique or to fallacious assumptions. It should appear in the calculated length values of the mature lake herring of the younger age groups (5 years and younger) of a year class.

Errors in computations of length may arise from causes other than those discussed. Other possible sources of error are: (1) all the scales of an individual do not begin their development at the same time, (2) after they appear they may have different rates of growth, (3) annuli may vary in the time of their completion, and (4) the length of the head, included in all measurements of the length of the body, may vary with the size and the age of the fish.

Some of these sources of error may be avoided easily, while others are known to have virtually no effect upon the length computations of the herring under consideration. Thus, the errors produced by the variation in the time of the appearance of scales in an individual and by the differences in the growth rates of these scales are eliminated largely by employing for study scales selected from a circumscribed area on the body. The errors caused by the variation in the time of the completion of annuli can not, it seems to me, be appreciably large in the herring, as this variation is presumably no greater than that in the time of the resumption of accelerated growth in the spring, which normally would not be expected to exceed a week among individuals living under identical conditions of growth. With respect to the age variations in head length, it has been concluded already (Table 9) that virtually none occur in the adult herring under consideration.

To recapitulate, it now appears that of the various possible factors that could affect the accuracy of the computations of length based on scales, only two seem to be significant in the lake herring. The first factor, the employment of the anterior radius of a scale for computations of length, discussed on pages 322 to 327, does not affect the scale theory but only its erroneous application. Whereas the theory assumes that the diameter of a scale increases in a direct ratio to the increase in the length of the body, the investigators employ, out of necessity or for convenience, the radius. I found (p. 325) "that the length computations based on the diameter are always higher than those based on the anterior radius of a scale, and that the difference between the computations of the two series increases consistently with each earlier year of life for which calculations are made, so that the maximum average difference of 13 millimeters is found in year I." The second significant factor, the disproportionate increase in length of body and scale, involves the theory itself. I found (p. 323) that neither the diameter nor the anterior radius of a scale increased in length strictly proportionally with that of the body. No general formula can correct the errors caused by the disproportionate increase of body and scale length. To eliminate the errors due to this factor corrections must be made for each age group separately. It is probably for this reason that the general corrective factors proposed by Doctor Järvi (see p. 305) for his *Coregonus albula* did not hold for his fish of all ages. Corrections for the above two factors apparently bring the computed lengths for the herring of the third and fourth years of life more nearly into agreement

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with the actual. Owing to the absence of herring of years I and II in my material, I could not determine definitely whether corrections for these two factors would also give more accurate calculated lengths for the first and second years of life.

From the preceding study it is concluded (1) that the structural characters of the scales of the lake herring (*Leucichthys artedi* Le Sueur) are so clearly recognizable as to permit their use by the scale method, and (2) that the fundamental assumptions underlying the scale method are warranted. The scale method, therefore, may be applied with confidence in a study of the life history of the lake herring. In this life-history study, which comprises the second major part of this paper, all computations of body lengths and increments are based on the diameter measurements of scales. No corrections were made in these calculated values. They are regarded as approximately correct for any age-group under consideration.

TIME OF FORMATION OF AN ANNULUS AND FACTORS INVOLVED IN IT

I have recently (Van Oosten, 1923) presented data that, I believe, definitely establish the causal relationship between the growth of scales and the formation of annuli in the whitefish (*Coregonus clupeaformis*). This was done by a study of scales taken at monthly intervals from whitefish segregated and kept living at the New York Aquarium. The growth changes in the scales were followed from November to July. It was shown that the annulus was completely formed some time in April or March, at the time when rapid scale growth was resumed. The data on pages 313 to 322 of this paper indicate that scale and body growth are closely correlated. Any factor, therefore, that can retard the growth rate of the body may have primary influence in the formation of annuli on scales. To hold a factor responsible, it must be shown that this particular factor was altered previous to or synchronously with the change in growth rate, and that no resumption of rapid scale or body growth occurs until the change in the factor is reversed or its effectiveness is lost. It is possible for more than one factor to be active at the same time and for the factors to vary with the years or even with the seasons of the same year.

With this criterion in mind, I found that in the adult whitefish of the New York Aquarium temperature and sexual maturity apparently assumed primary significance in the formation of annuli. My conclusions were recapitulated on page 407, as follows:

> It has thus far been shown that the scales of the aquarium whitefish ceased growing some time in August or September and resumed growth in April or March(?); that sexual maturity was reached some time between September and March or February(?); that the lowest temperatures of the aquarium water occurred in January to March, inclusive; and that the amount of food required by the fish was less for these months of the year. It was suggested that food could only have had secondary significance in the formation of annuli, since the reduction of food was caused by some other factor, which affected the appetite of the fish. It was further suggested that since reduction and increase in food consumption occurred synchronously with the decrease and increase in temperature, respectively, and since the scales resumed their growth at the time of a rise in temperature in April, when sexual maturity could have had no influence on growth, temperature must be considered a primary factor in the formation of annuli. Lastly, since the sex products began their development at approximately the time at which a retardation or cessation of scale growth occurred in late summer, when the environmental factors of food and temperature were known to have been constant, it appears reasonable to assert that sexual maturity is also a primary factor in the formation of annuli in scales. If sexual maturity is not such a factor, then it must be conceded that the retardation or cessation of scale or body growth, and consequently the formation of annuli, is caused by some unknown physiological factor or factors of annual recurrence.

Although food played no significant rôle in the formation of annuli in these mature fish, it does not follow that food can not be such a factor. Undoubtedly it is the normal factor in some species of wild fishes, and in starvation it becomes the principal factor in all species. It is also conceivable that sexual maturation, when accompanied by an abundance of food and a propensity for feeding, leaves no effect on the scale sculpture.

Many experimental and other kinds of data have been accumulated relative to the factors that govern the growth of animals and plants. Even the references that involve fishes only are too numerous to review here. A brief but good review on this subject may be found in Weymouth's paper (1923). In the last paragraph of his review the author writes: "In the end it must be admitted that at present no exact evaluation of the factors involved in seasonal growth is possible [p. 35]."

The time of the formation of the annuli in the wild coregonids has not been determined; but inasmuch as the formation of an annulus is causally related to the retardation of growth, it is safe to assume that in nature, too, the annulus of these species forms during the winter period.

The exact season in other species of wild fishes of the northern latitudes has been ascertained carefully by several investigators. All found that it was the period of growth retardation or cessation during the winter. Such was the conclusion of Hoffbauer (1898, etc.) and Walter (1901) for the carp, of Thomson (1904) for several species of Gadidæ, of Johnston (1905) for the Atlantic salmon, of Gilbert (1913) and Fraser (1917) for the Pacific salmon, of Lea (1911) for the Atlantic herring, of Thompson (1917) for the Pacific herring, and of Reibisch (1911) for the winter band on the otoliths of the halibut. Miss Clark (1925), however, found that as a result of the long protracted spawning season, growth of the mature atherine fish of California (*Leuresthes tenuis*) "ceases during the months of May, June, and July and is resumed again in the fall. This cessation of growth during the summer months results in the formation of a breeding annulus on the scales. Growth continues during the winter and a winter annulus is formed only in rare cases [p. 39]."

Part II.—LIFE HISTORY OF LEUCICHTHYS ARTEDI LE SUEUR, THE BLUEBACK OR LAKE HERRING

HISTORICAL: A SUMMARY OF OUR KNOWLEDGE OF THE LIFE HISTORY OF LAKE HERRING

DESCRIPTION OF ADULTS

According to Jordan and Evermann (1911), two species of herring are common in Lake Huron—*Leucichthys harengus* (Saginaw Bay herring, Georgian Bay herring) found in Saginaw Bay, in Georgian Bay, and in the shallow waters of Lake Huron proper, and *Leucichthys sisco huronius* (Lake Huron herring, blueback) found commonly in Lake Huron proper and occasionally in Georgian Bay. They recognize a third herring, *Leucichthys manitoulinus* (Manitoulin tullibee), which occurs only in the North Channel of Lake Huron. In addition to these three species of herring, two others occur occasionally in Lake Huron, according to Jordan and Evermann—*Leucichthys artedi* (lake herring, Erie herring, common lake herring, grayback) and

Leucichthys eriensis (jumbo herring, Erie great herring), both, according to these authors, typical Lake Erie herring.

The most recent study on the taxonomy of the species of Leucichthys from Lake Huron, that of Dr. Walter Koelz (1929), based on a large amount of material collected or examined at all the more important ports of Lake Huron and Georgian Bay, recognizes but one species of herring in Lake Huron proper and its bays. This species Doctor Koelz designates *Leucichthys artedi* Le Sueur (the blueback or lake herring; fig. 15.)

I am indebted to Doctor Koelz for most of the following description of *L. artedi* and for much of the material in the section on natural history, which follows.

In Lake Huron, herring greater than 12 inches in total length are relatively few in number. The largest specimen I have taken weighed 2 pounds and 3 ounces and measured 395 millimeters (15.6 inches) in standard length. The body of the lake herring is elongate, elliptical, fusiform, and only slightly compressed. In side view the outline is almost perfectly elliptical. The greatest depth is commonly 22 to 25 per cent of the length of the body. The head is nearly conical in form, relatively small and narrow, and usually equals 21 to 23 per cent of the body length (4.3 to 4.6 times in length). The premaxillaries are very short, scarcely longer than wide, and are oblique in position. The snout is short and often equal to the eye in length. The maxillary is short—usually 33 to 35 per cent of the head. The mandible is usually equal to the upper jaw or a little shorter. The eye is rather large—usually 23 to 25 per cent of the head's length. The gill rakers usually number 16–18 + 29–32 = 45–50. The number of scales in the lateral line varies from (68) 72 to 88 (97) (my own counts; see Table 7). The number of rays in the dorsal fin is usually 10 or 11, in the anal and ventral fins usually 11 or 12, and in the pectoral fins usually 15 or 16. The pectorals usually equal 45 to 50 per cent of the pectoral-ventral distance. The ventrals usually equal 55 to 62 per cent of the distance from their origin to the anal. The flesh is somewhat dry and firm. In alcohol the entire dorsal surface is of a deep smoky hue, which extends to the lateral line and which in life is a deep blue green. The top of the head, the premaxillaries, and the tip of the mandible are somewhat darker than the maxillaries and cheeks. The distal half of the pectorals, caudal, and dorsal and sometimes the anal and ventrals are more or less black. The entire caudal fin is smoky, the shortest rays being the darkest. In general, the lake herring may be distinguished from the other species of Leucichthys in Lake Huron by its numerous gill rakers, short maxillaries, short pectoral fins, firm flesh, and elliptical body contour.

NATURAL HISTORY OF ADULTS

The lake herring may be taken at virtually every port on Lake Huron. On account of the dryness of its flesh it does not command a good price, so that many Lake Huron fishermen make no attempt to set nets for it. Saginaw Bay ranks first in the herring industry, while Alpena ranks second. On the Canadian shore the herring fishery has been abandoned almost entirely. Even on the American shore the herring are not sought where other more valuable species are available. They are sold fresh, smoked, or salted. Herring is taken in either pound or gill nets (in trap nets rarely) in the fall and spring of the year. Though unprotected by law and propagated artificially only when it is not possible to fill the hatcheries with eggs of other

BULL. U. S. B. F., 1928. (Doc. 1053.)

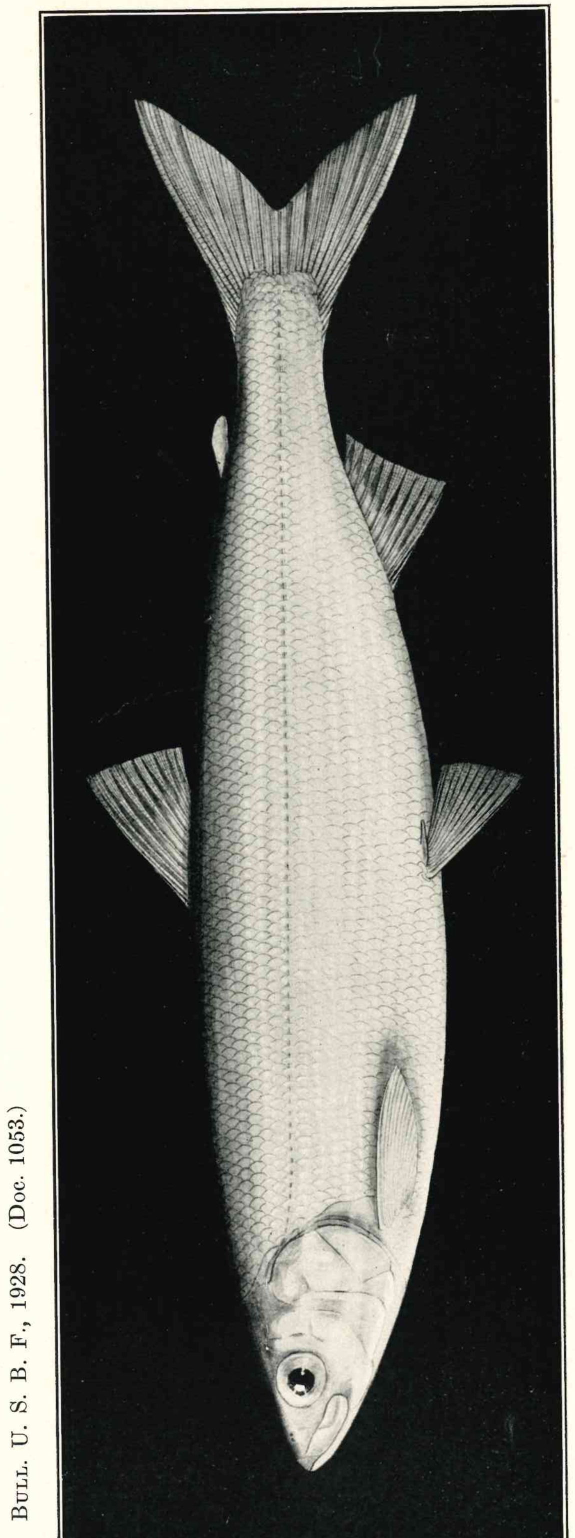

FIG. 15.—*Leucichthys artedi* LeSueur. Lake herring

more desirable species, the herring seems to maintain its numbers in Lake Huron. (See Table 28.)

TABLE 28.—*Statistics of the catch and value of herring taken in Lake Huron in various years during the period 1891 to 1925, published by the State of Michigan*

Year	Pounds	Value	Average price per pound	Year	Pounds	Value	Average price per pound
1891	3, 459, 500	$36, 203	$0. 010	1920	3, 387, 057	115, 199	. 034
1892	2, 575, 200	(?)		1921	2, 164, 233	66, 760	. 031
1893	4, 050, 000	(?)		1922	4, 395, 902	103, 804	. 024
1896	6, 464, 836	28, 556	. 004	1923	3, 038, 570	73, 389	. 024
1897	4, 890, 650	29, 452	. 006	1924	2, 878, 636	62, 616	. 022
				1925	5, 148, 121	112, 452	. 022
Average, 5 years	4, 288, 037	31, 404	. 007	Average, 6 years	3, 502, 087	89, 037	. 026

In the early fall (about October) the herring schools move inshore to spawn, and in late spring, according to Doctor Koelz, they return to deeper water. Doctor Koelz states that in some localities there appear to be two migratory movements—the fish come in and go out both in the fall and spring instead of remaining inshore all winter. The factors that govern these movements are not definitely known. Temperature changes in the water and food undoubtedly play important rôles, if not the most important ones. After June all adult herring have moved out of the shallow water. They probably swim near the surface in June and July and later repair to greater depths. The maximum depth from which the species is known to have been taken is 35 fathoms (Koelz). Only very few have ever been taken in water deeper than 20 fathoms (Koelz).

The lake herring takes its food occasionally from the bottom and more frequently from the free water and subsists on small mollusks, crayfishes, insect larvæ, fish eggs, and especially on the minute plankton forms, principally the Crustacea (Clemens and Bigelow, 1922; Coker, 1922). It spawns chiefly in November in shallow water (3 to 8 fathoms), preferably upon a sandy or gravelly bottom. Saginaw Bay, therefore, provides ideal breeding grounds for herring, and this accounts for the tremendous numbers that gather there in the fall. According to the fishermen at Bay City, before the waters of the Saginaw River were polluted large numbers of herring ascended it to spawn.

LIFE HISTORY OF ADULTS (AGE AND GROWTH)

Little has been published thus far on the growth of the lake herring. A preliminary paper by Clemens (1922) presents one table and two graphs, one illustrating the rates of growth of four species of Leucichthys in Lake Erie—namely, *artedi*, *prognathus*, *eriensis*, and *sisco huronius*—the other illustrating the relation of weight to age of three Lake Erie species—*artedi*, *prognathus*, and *eriensis*. The number of fish of each species examined was as follows: *L. eriensis*, 140; *L. artedi*, 55; *L. sisco huronius*, 55; *L. prognathus*, 150. The maximum age and the maximum average length attained by each of these species are as follows: *L. eriensis*, age 12, length 42 centimeters; *L. sisco huronius*, age 9, length 41 centimeters; *L. artedi*, age 10, length 29 centimeters; *L. prognathus*, age 8, length 27.5 centimeters.

According to Doctor Koelz, to whom Doctor Clemens submitted part of his collection for identification, the above species are all referable to his (Koelz's) *L. artedi* and can not be separated by the characters employed by Jordan and Evermann (1911) or Clemens when abundant material is used. Doctor Clemens states (p. 5) that he found it difficult to separate the young *L. eriensis* from *L. artedi*, and that his specimens of *L. prognathus* are of doubtful determination.

Assuming that the identifications of the above species be correct, then, according to current practice, Doctor Clemens employed too few specimens for his length and weight averages. It is clear that 55 specimens distributed among 7 or more age groups can not furnish very accurate averages for all age groups. Likewise, no attempt was made to obtain homogeneous material for the growth determinations, as the individuals of a species were taken at different ports on Lake Erie.

In his curves illustrating the growth rates an anomaly apparently appears which Doctor Clemens finds it difficult to explain. He finds that his *L. sisco huronius* is a faster growing fish than *L. eriensis*, the jumbo herring of Lake Erie. He refuses to accept this result and states that it is probably due to his difficulty in estimating the age of the former species. "In the majority of scales [of *L. sisco huronius*] some of the winter bands were difficult to distinguish and there was evidence that in some cases at least one winter band was not recorded." What this evidence was he does not state. It appears more probable, however, that Doctor Clemens's difficulty was due to a failure to discriminate between the true and the false annulus. In his drawings of the cisco scales his annuli are represented as broad bands of closely approximated circuli. Presumably these broad bands continue around the scale, though only that part that lies in the anterior field is drawn. As may be seen from my photographs in this paper, such broad annuli are not typical of the coregonid scales. The coregonid annulus is characterized rather by the divergence of the circuli in the lateral fields, the presence of a narrow, clear band, devoid of any sculpture, in the posterior field, and the presence of a narrow, sometimes thickened band of incomplete, broken, anastomosed and usually approximated circuli in the anterior field. A true annulus can be traced with varying distinctness entirely around the scale through all its areas. The author's second annulus in his jumbo scale may not be a year mark at all. It hardly appears reasonable to believe that the fastest growing cisco in the Great Lakes should grow as slowly in its second year as the drawing indicates. For these reasons I am unable to accept Doctor Clemens's results on the age and growth of the herring.

JUVENILE LAKE HERRING

Very little is known about the young herring and very few have ever been reported as taken. Hankinson (1914) found the juveniles (identified by Koelz as very probably young herring) very abundant along the shores of Lake Superior at Whitefish Point in water less than 3 feet deep. Fishermen report that millions swarm around the docks and piers at Bay City and Alpena in the fall, but samples of these so-called herring proved to be the minnow *Notropis atherinoides*. Doctor Koelz's Lake Huron collection contained one specimen in its first year. It measured 180 millimeters in length and was taken by a trout net in 15 fathoms off Alpena. (See fig. 11.)

ABUNDANCE OF LAKE HERRING

I have been unable to find many dependable data on the relative abundance of herring in Lake Huron during past years. In the statistics of the United States Bureau of Fisheries (Radcliffe, 1920, Sette, 1925) the herring are lumped together with all the other species of Leucichthys (chubs and bloaters) under the name of ciscoes. The annual reports of the Game and Fisheries Department of Ontario, Canada, furnish statistics on the production of herring in the Canadian waters of the Great Lakes; but whether these so-called herring include the chubs and bloaters is not clear. No statistics are given for the latter species (unless they are included with the tullibees), though it is known that they are taken by Canadian fishermen. In most of the biennial reports of the Michigan Fish Commission, the predecessor of the present Department of Conservation of Michigan, the herring statistics of all the Great Lakes are lumped together. The tenth, eleventh, and thirteenth reports give herring statistics for the west shore of Lake Huron from Hammond Bay to the mouth of the Detroit River (district No. 4). In the biennial reports of the Department of Conservation of the State of Michigan the herring productions are considered separately for the Michigan waters of Lake Huron proper and for Saginaw Bay.

The published statistics of the lake herring of Lake Huron (including Saginaw Bay) are shown in Table 28,together with the average price per pound received by the fishermen. The table shows that the average catch for the years 1891 to 1897 was 785,950 pounds more than that for the years 1920 to 1925, although the annual catches of the two periods are strikingly similar, while the average price per pound increased from 0.7 cent in the former period to 2.6 cents in the latter. The available statistics can not, perhaps, be employed as exact criteria by which to determine whether the herring are undergoing depletion in Lake Huron; but the fact that the annual catches of herring are no larger now than they were in the years 1891 to 1897, in spite of the great improvements in and of the increase in the number of fishing apparatuses and in spite of the increase in the value of this species, may suggest that the herring are less numerous now than they were 30 years ago.

There is, perhaps, no one thing that needs greater attention on the Great Lakes to-day than the careful collection of fishery statistics. These statistics should be collected every year, and where possible each species should be considered by itself. Some general plan for the taking of statistics should be evolved and adopted by both Canada and the United States. By some such means the statistics of the various lakes and of various parts of one lake would become much more comparable than they now are.

INTERPRETATION OF THE STRUCTURAL FEATURES OF THE SCALES OF THE LAKE HERRING

MATERIAL

The following life history of the lake herring, based upon a study of the scales, involves only the Saginaw Bay fish taken by me or sent to me by Mr. Kavanaugh, of Bay City, Mich., in the fall of 1921, 1922, 1923, and 1924. These Saginaw Bay herring are compared later with the herring collected by Doctor Koelz in 1917 and 1919 from various localities on Lake Huron and by me in 1922 at Oscoda, Mich. Doctor Koelz's collections are usually small, taken for taxonomic purposes, and my conclusions based on them must be accepted with such reserve as the relatively small numbers impose.

ABUNDANCE OF AGE GROUPS AND YEAR CLASSES IN THE SAMPLES[1]

AGE GROUPS

As stated on page 268, the Saginaw Bay herring samples of 1921, 1922, and 1923 were taken in pound nets set at Tobico about 3 miles west of the mouth of the Saginaw River, while those of 1924 were taken in pound nets set at Tobico, Nayanquing, Au Gres, and Gravelly Point, the last three bars being, respectively, about 9, 25, and 32 miles north of the mouth of the Saginaw River. (See fig. 1.) Each collection was taken on or near the spawning grounds and is composed principally of fish that would have spawned shortly, perhaps in a week or so.

In each of the years 1922 and 1923 herring were collected on a single date and in a single locality (one large sample), while in 1921 one large sample was taken on October 29 and several smaller samples were collected on the other days of the period October 26 to November 4; in 1924 herring were collected on various dates throughout the height of the spawning run until ice conditions made fishing impossible. The Tobico, Nayanquing, and Gravelly Point collections of 1924 each comprise two or more small samples. The small sample of Au Gres herring was taken on a single date. I shall later (p. 385) give reasons for concluding that the character of the various samples taken at the same locality does not change consistently as the season advances, so that the Tobico collection of 1924 is entirely comparable with the samples taken at the same point in earlier years. I shall also (p. 387) give reasons for my belief that the herring of Tobico and Nayanquing belong to the same population. The herring taken at Gravelly Point and at Au Gres may belong to the Tobico and Nayanquing races, but the data do not show this indisputably. The Tobico and Nayanquing material, therefore, is treated as a homogeneous collection and as such is strictly comparable with the material taken in 1921 to 1923, while the samples from Gravelly Point and Au Gres are considered separately. The Au Gres collection, however, which comprises relatively few individuals, may not be representative for all age groups. Data of these fish, therefore, are considered in a more or less incidental way. In a strictly comparative study of the samples of different years the Tobico and Nayanquing material alone of the 1924 samples is considered.

[1] A year class refers to fish hatched in the same year; an age group to fish of the same age. Thus, the year class 1914 includes all individuals hatched in 1914, irrespective of their age when captured; age group IV includes fish in their fourth year of life. Fish of the same year class captured in different years belong to different age groups.

TABLE 29.—*Frequency distribution of Saginaw Bay herring according to length and age group*

[Dates refer to year of capture and roman figures to year of life]

Length, in millimeters	1921							1922					1923					
	II	III	IV	V	VI	VII	VIII	II	III	IV	V	VI	II	III	IV	V	VI	VII
160																		
175-180	1																	
181-185																		
186-190																		
191-195	1													1				
196-200	1	2																
201-205	2	3	2						4	1								
206-210		7	3					1	0	0				1				
211-215		7	6	3				1	6	4			1	4	2			
216-220		18	19	6	2				13	6				8	0	1		
221-225		21	50	13	2			2	28	18	3	1		19	2			
226-230		13	76	23	4				33	33	9		1	29	11			
231-235		12	54	35	8				29	52	17	2		39	30	2		
236-240		5	38	43	3	1			26	63	19			42	59	9		
241-245		4	12	33	14	1			6	39	22			17	56	16	3	
246-250		3	15	17	4	2			1	16	8	1		6	44	19	1	
251-255		2	3	10	4	1			1	6	10			1	24	19	0	
256-260			3	5	8				1	3	3	2		3	8	11	3	
261-265			1	4	3		1			2	1	1			2	8	1	2
266-270			2	2	0	1	1				1				1	2	3	
271-275			3	4	2	1				1	1					2	0	
276-280			0	2	3	1						1					1	
281-285			1	1	2					1	1	1					3	
286-290			1	1	0													
291-295			1	1	2	1												
296-300					3										1			
301-305																1		
306-310			1	1														
311-315						2												
316-320				1	1													
321-325																		
326-330																		
331-335					1	1												
336-340					1													
341-345							1											
365																		
Total number of individuals	5	97	291	205	67	12	3	4	148	245	95	9	2	170	240	90	15	2
Per cent of total number	0.7	14.3	42.8	30.1	9.9	1.8	0.4	0.8	29.5	48.9	19.0	1.8	0.4	32.8	46.2	17.3	2.9	0.4
Average length, in millimeters	195	224	232	241	254	275	292	217	229	236	241	252	221	233	243	251	263	263

Length, in millimeters	1924[1]					1924[2]							1924[3]				
	II	III	IV	V	VI	II	III	IV	V	VI	VII	VIII	III	IV	V	VI	VII
160							1										
175-180						1											
181-185						2											
186-190							1										
191-195							1										
196-200						1	7	2									
201-205							8	1									
206-210	1						6	1		1			1				
211-215		3	1				18	2					2				
216-220		5	4				19	9					8				
221-225		13	9				25	11					8				
226-230		25	31	2			29	26					4	8			
231-235		42	60	1			27	35	2				8	10			
236-240		24	56	0			20	40	2				8	11			
241-245		21	63	12	1		21	34	8				8	6	3		
246-250		16	64	16	2		10	27	10	1			3	6	1		
251-255		9	30	19	5		4	20	13	2	1		2	11	1		
256-260		1	13	10	1		0	10	3	5	1		1	3			
261-265		1	7	4	3		2	8	9	0							
266-270		1	4	4	2		1	6	2	1				1	1		
271-275		1	5	3				3	1	2						1	
276-280			5	0			1	3	3								
281-285			1	2				2	4					1	1		
286-290			1	1				4	5								
291-295			1					1	3	1	1						1
296-300			1		2			2	0								

[1] Tobico and Nayanquing samples combined. [2] Gravelly Point herring. [3] Au Gres herring.

TABLE 29.—*Frequency distribution of Saginaw Bay herring according to length and age group*—Con.

Length, in millimeters	1924[1] II	1924[1] III	1924[1] IV	1924[1] V	1924[1] VI	1924[2] II	1924[2] III	1924[2] IV	1924[2] V	1924[2] VI	1924[2] VII	1924[2] VIII	1924[3] III	1924[3] IV	1924[3] V	1924[3] VI	1924[3] VII
301-305					1			1	2								
306-310					1					1		1					
311-315									1		1						
316-320																	
321-325																	
326-330																	
331-335																	
336-340																	
341-345																	
365									1			1					
Total number of individuals	1	162	356	74	18	4	201	248	69	14	4	2	53	57	7	1	1
Per cent of total number	0.2	26.5	58.3	12.1	2.9	0.7	37.1	45.8	12.7	2.6	0.7	0.4	44.5	47.9	5.9	0.8	0.8
Average length, in millimeters	210	236	243	254	267	185	227	243	264	262	280	336	233	243	255	275	295

Length, in millimeters	1924[4] II	1924[4] III	1924[4] IV	1924[4] V	1924[4] VI	1924[4] VII	1924[4] VIII	Length frequency of herring taken in— 1921	1922	1923	1924[1]	1924[2]	1924[3]	1924[4]
160		1										1		1
175-180	1							1				1		1
181-185	2											2		2
186-190		1										1		1
191-195		1						1		1		1		1
196-200	1	7	2					3				10		10
201-205		8	1					7	5			9		9
206-210	1	7	1		1			10	1	1	1	8	1	10
211-215		23	3					16	11	7	4	20	2	26
216-220		32	13					45	19	9	9	28	8	45
221-225		46	20					86	52	21	22	36	8	66
226-230		58	65	2				116	75	41	58	55	12	125
231-235		77	105	3				109	100	71	103	64	18	185
236-240		52	107	2				90	108	110	80	62	19	161
241-245		50	103	23	1			64	67	92	97	63	17	177
246-250		29	97	27	3			41	26	70	98	48	10	156
251-255		15	61	33	7	1		20	17	44	63	40	14	117
256-260		2	26	13	6	1		16	9	25	25	19	4	48
261-265		3	15	13	3			9	4	13	15	19	0	34
266-270		2	11	7	3			6	1	6	11	10	2	23
271-275		1	8	4	3			10	2	2	9	6	1	16
276-280		1	8	3				6	1	1	5	7		12
281-285			4	7				4	3	3	3	6	2	11
286-290			5	6				2			2	9		11
291-295			2	3	1	2		5			1	6	1	8
296-300			3	0	2			3		1	3	2		5
301-305			1	2	1					1	1	3		4
306-310				0	2		1	2			1	2		3
311-315				1		1		2				2		2
316-320								2						
321-325														
326-330														
331-335								2						
336-340								1						
341-345								1						
365				1			1					2		2
Total number of individuals	5	416	661	150	33	5	2	680	501	519	611	542	119	1,272
Per cent of total number	0.4	32.7	52.0	11.8	2.6	0.4	0.2							
Average length, in millimeters	190	231	243	258	265	283	336	236	235	241	244	240	240	242

[1] Tobico and Nayanquing samples combined.
[2] Gravelly Point herring
[3] Au Gres herring
[4] 1, 2, and 3 combined.

In Table 29 the fish captured in each of the years 1921, 1922, 1923, and 1924 have been divided into age groups with those of each age group arranged according to length. The average length of each age group, the total number of individuals in each, and the percentage of that total in the whole number is shown for each year at the bottom of the table. At the right is shown for each year the number of fish of each size. The data on the total number of individuals of each age group in each

year, shown near the bottom of Table 29, are rearranged in the lower part of Table 30 to facilitate a comparative study of the significant figures. The tables show that no individuals in their first year of life and only a few in their second year are taken in these commercial catches. The percentage of 2-year herring present in the samples varied from 0.2 per cent in 1924 to 0.8 per cent in 1922. Likewise, the old fish are poorly represented. The 8-year fish were taken only in 1921 and 1924, in each year representing 0.4 per cent of the sample. No 7-year fish were taken in 1922 or in the Tobico and Nayanquing samples in 1924, while in 1921, 1923, and in the Gravelly Point and Au Gres samples in 1924 they constituted 1.8, 0.4, 0.7, and 0.8 per cent, respectively, of the total catch. The 6-year herring were slightly more abundant, constituting from 1.8 per cent (0.8 per

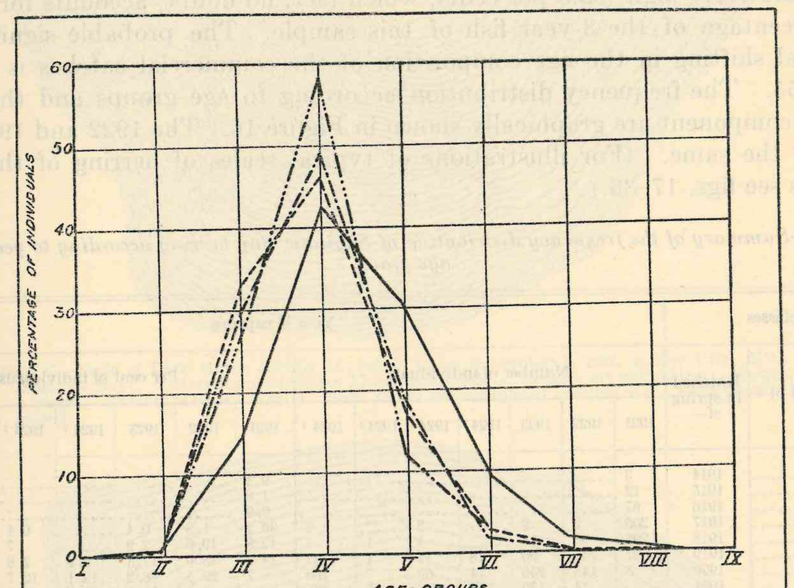

FIG. 16.—Frequency polygons showing for each sample of herring taken in 1921, 1922, 1923, and 1924 the percentage of individuals occurring in each age group. The curves are based on the percentages shown in the lower right half of Table 30. ———, 1921; — · —, 1922; — — —, 1923; — · · · —, 1924 (Tobico and Nayanquing samples combined)

cent in the Au Gres sample of 1924) to 9.9 per cent of the catch. The values for these older age groups are consistently greater in the 1921 sample, because strictly it is not representative, inasmuch as all the exceptionally large fish (a dozen or so) seen in the fish house were taken. The figures for the other samples are accurate, however. The paucity of old individuals in the samples strongly suggests a condition of overfishing or rather of heavy fishing among the herring. A positive statement to that effect can not be made at present with absolute certainty, inasmuch as nothing is known about the normal age distribution of the herring schools of the past.

In 1921 the 4 and 5 year fish formed the bulk of the sample—72.9 per cent of the total. In the three succeeding years the 3 and 4 year fish predominated, representing 78.4 per cent of the total in 1922 and 79 per cent in 1923; in 1924 they formed 84.8 per cent of the Tobico and Nayanpuing material, 82.9 per cent of the

Gravelly Point fish, and 92.4 per cent of the Au Gres sample, or, in general, 84.7 per cent of all the fish taken by me in this year. In each year the fourth age group was the largest, its individuals comprising 42.8 to 58.3 per cent of the total catch. It is to be noted that the percentage of 3-year fish increased each year during the period 1921 to 1923 (14.3 to 29.5 to 32.8 per cent); then, in general, remained stationary (32.7 per cent, 1924 combined) in 1924, though it dropped to 26.5 per cent in the Tobico and Nayanquing material. This general increase in the number of 3-year herring occurred at the expense of the 5-year fish mainly, which each year became progressively less abundant (30.1 to 19.0 to 17.3 to 11.8 per cent (1924 combined); Tobico and Nayanquing, 12.1 per cent). The percentage of 4-year herring remained virtually the same in all samples, except those of Tobico and Nayanquing, in which it is comparatively high (58.3 per cent), which fact, no doubt, accounts for the drop in the percentage of the 3-year fish of this sample. The probable significance of the gradual shifting in the age composition of the commercial catches is discussed on page 355. The frequency distribution according to age groups and the shifting in the age component are graphically shown in Figure 16. The 1922 and 1923 curves are nearly the same. (For illustrations of typical scales of herring of the various age groups see figs. 17–36.)

TABLE 30.—*Summary of the frequency distribution of Saginaw Bay herring according to year class and age group*

Year classes		Year of capture													
		Number of individuals							Per cent of individuals						
Spawned in fall of—	Hatched in spring of—	1921	1922	1923	1924 [1]	1924 [2]	1924 [3]	1924 [4]	1921	1922	1923	1924 [1]	1924 [2]	1924 [3]	1924 [4]
1913	1914	3	----	----					0.4	----	----				
1914	1915	12	----	----	----	----	----	----	1.8	----	----	----	----	----	----
1915	1916	67	----	----	----	----	----	----	9.9	----	----	----	----	----	----
1916	1917	205	9	2	----	2	----	2	30.1	1.8	0.4	----	0.4	----	0.2
1917	1918	291	95	15	----	4	1	5	42.8	19.0	2.9	----	.7	0.8	.4
1918	1919	97	245	90	18	14	1	33	14.3	48.9	17.3	2.9	2.6	.8	2.6
1919	1920	5	148	240	74	69	7	150	.7	29.5	46.2	12.1	12.7	5.9	11.8
1920	1921	----	4	170	356	248	57	661	----	.8	32.8	58.3	45.8	47.9	52.0
1921	1922	----	----	2	162	201	53	416	----	----	.4	26.5	37.1	44.5	32.7
1922	1923		----	----	1	4	0	5		----	----	.2	.7	.0	.4
Total		680	501	519	611	542	119	1,272	100.0	100.0	100.0	100.0	100.0	99.9	100.1
AGE GROUPS															
II		5	4	2	1	4	0	5	.7	.8	.4	.2	.7	.0	.4
III		97	148	170	162	201	53	416	14.3	29.5	32.8	26.5	37.1	44.5	32.7
IV		291	245	240	356	248	57	661	42.8	48.9	46.2	58.3	45.8	47.9	52.0
V		205	95	90	74	69	7	150	30.1	19.0	17.3	12.1	12.7	5.9	11.8
VI		67	9	15	18	14	1	33	9.9	1.8	2.9	2.9	2.6	.8	2.6
VII		12	----	2	----	4	1	5	1.8	----	.4	----	.7	.8	.4
VIII		3	----	----	----	2	----	2	.4	----	----	----	.4	----	.2
Total		680	501	519	611	542	119	1,272	100.0	100.0	100.0	100.0	100.0	99.9	100.1

[1] Tobico and Nayanquing samples combined.
[2] Gravelly Point herring.
[3] Au Gres herring.
[4] 1, 2, and 3 combined.

YEAR CLASSES

The upper part of Table 30 shows the total number of individuals in each year class of each sample taken in 1921, 1922, 1923, and 1924; the percentage of this total in the whole number is shown for each sample. The year classes are shown in chronological order, beginning with the oldest fish (8-year fish) hatched from eggs laid in

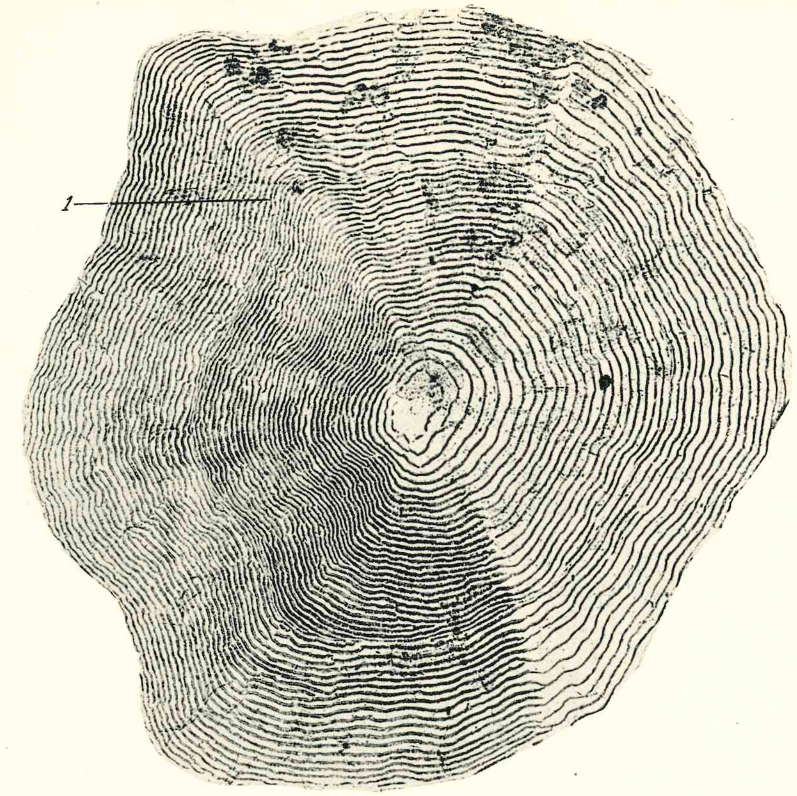

FIG. 17.—Scale of Lake Huron herring (*L. artedi*) taken November 1, 1922, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 58597. Length, 213 millimeters. Weight, 4 ounces. Immature male. Age II. Scale shows one completed annulus and a large marginal growth

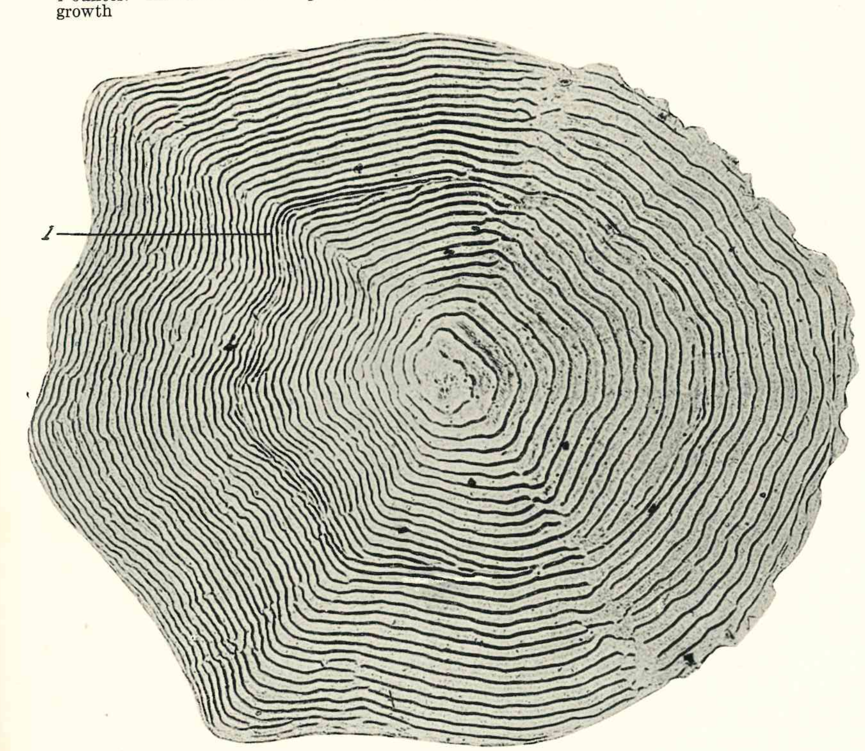

FIG. 18.—Scale of Lake Huron herring (*L. artedi*) taken December 3, 1919, at Wiarton, Ontario (Georgian Bay). University of Michigan Museum No. 52958. Length, 175 millimeters. Immature. Age II. Scale shows one completed annulus and a large marginal growth

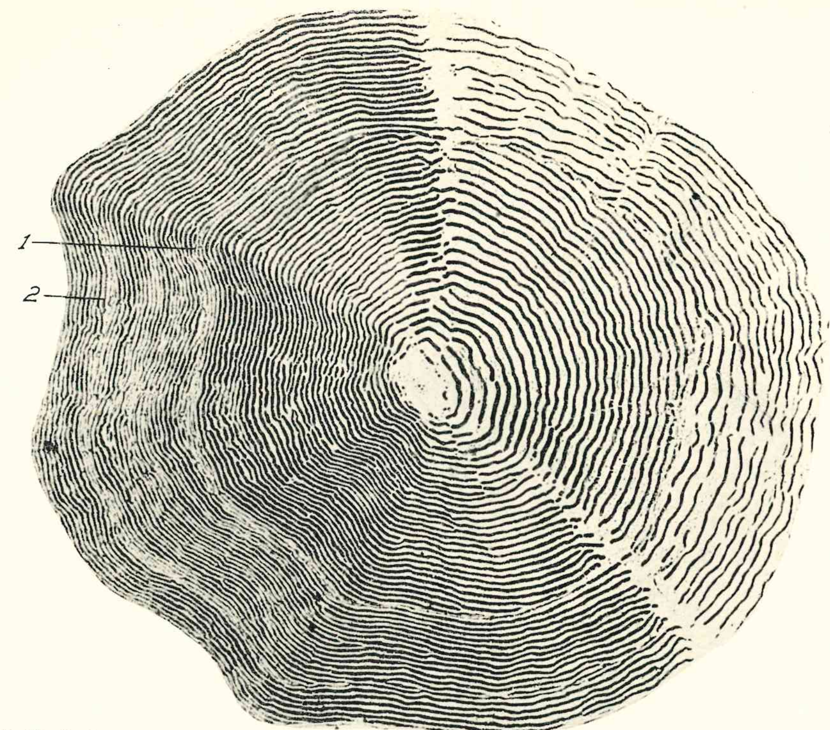

FIG. 19.—Scale of Lake Huron herring (*L. artedi*) taken October 27, 1921, at Bay City, Mich. (Saginaw Bay.) University of Michigan Museum No. 54313. Length, 210 millimeters. Male. Age III. Scale shows two completed annuli and a marginal growth

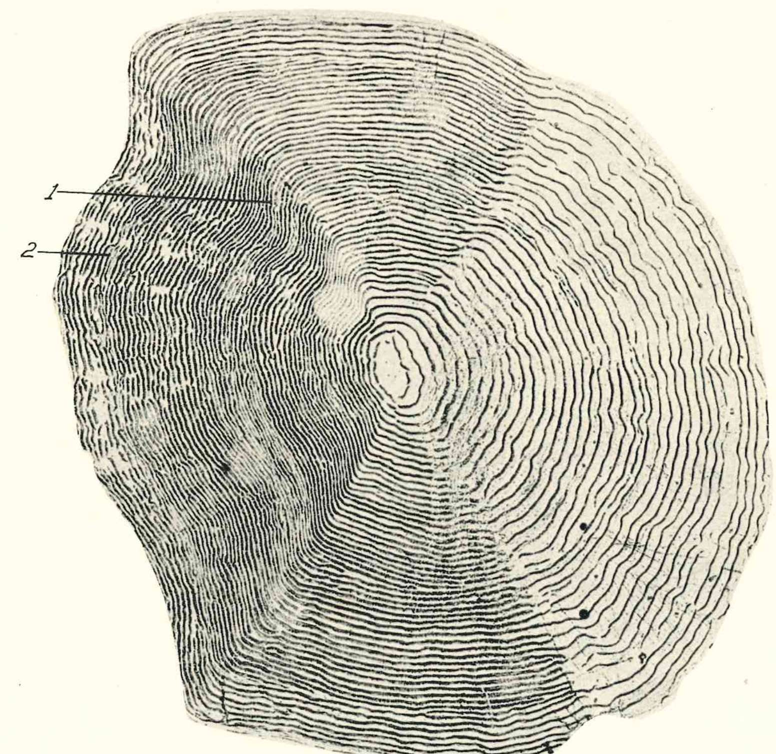

FIG. 20.—Scale of Lake Huron herring (*L. artedi*) taken October 29, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54703. Length, 245 millimeters. Mature male. Age III. Scale shows two completed annuli and a marginal growth

FIG. 21.—Scale of Lake Huron herring (*L. artedi*) taken September 10, 1917, at Alpena, Mich. University of Michigan Museum No. 52195. Length, 175 millimeters. Age III. Scale shows two completed annuli and a marginal growth

FIG. 22.—Scale of Lake Huron herring (*L. artedi*) taken July 17, 1917, at St. Ignace, Mich. Length, 212 millimeters. Male. Age III. Scale shows two completed annuli and a marginal growth

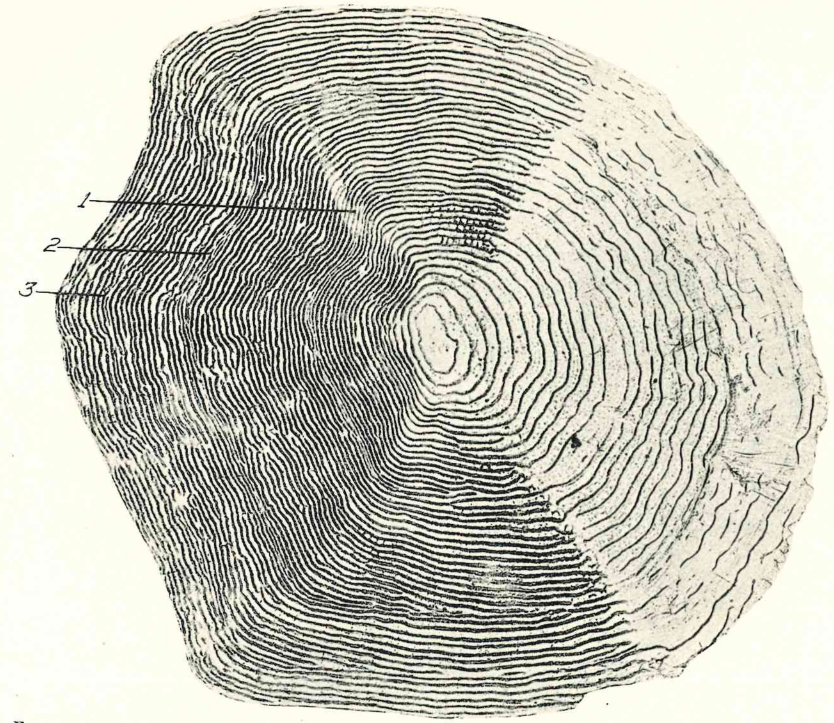

Fig. 23.—Scale of Lake Huron herring (*L. artedi*) taken October 29, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54847. Length, 237 millimeters. Mature male. Age IV. Scale shows three completed annuli and a marginal growth

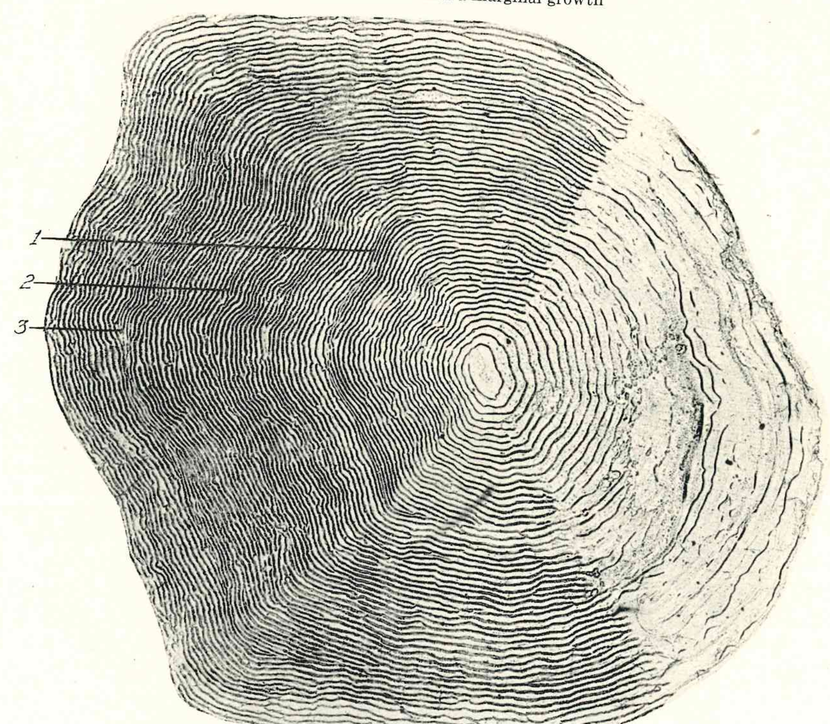

Fig. 24.—Scale of Lake Huron herring (*L. artedi*) taken October 29, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54692. Length, 293 millimeters. Mature male. Age IV. Scale shows three completed annuli and a large marginal growth

Bull. U. S. B. F., 1928. (Doc. 1053.)

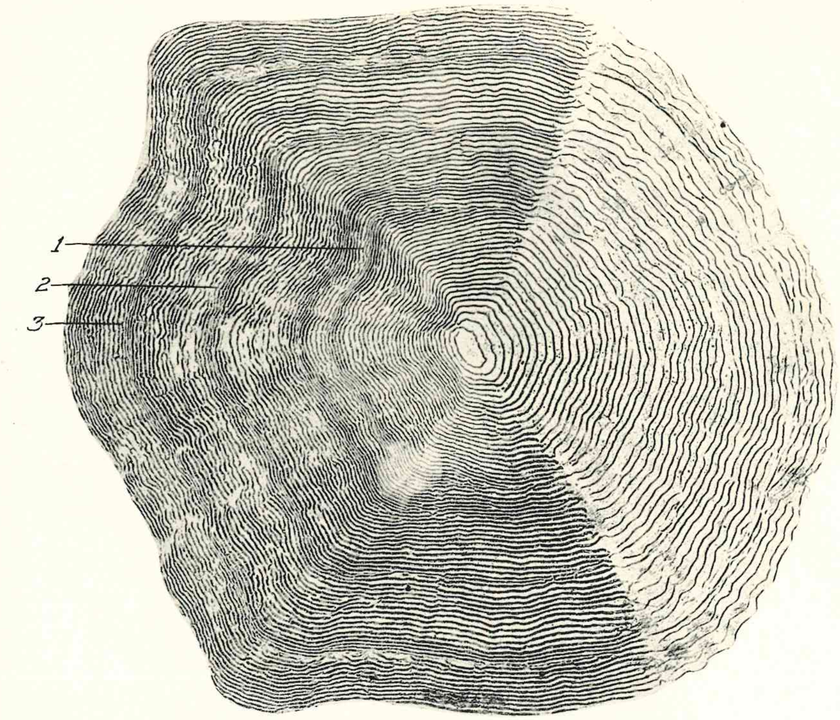

Fig. 25.—Scale of Lake Huron herring (*L. artedi*) taken October 29, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54661. Length, 308 millimeters. Mature female. Age IV. Scale shows three completed annuli and a marginal growth

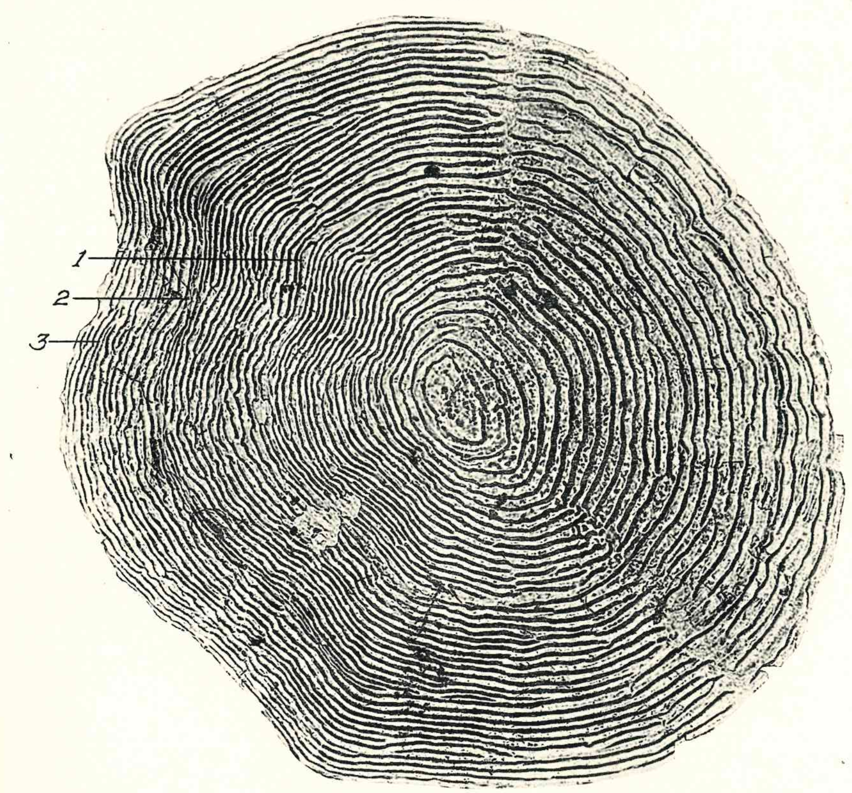

Fig. 26.—Scale of Lake Huron herring (*L. artedi*) taken September 8, 1917, at Alpena, Mich. University of Michigan Museum No. 52208. Length, 176 millimeters. Age IV. Scale shows three completed annuli and a small marginal growth

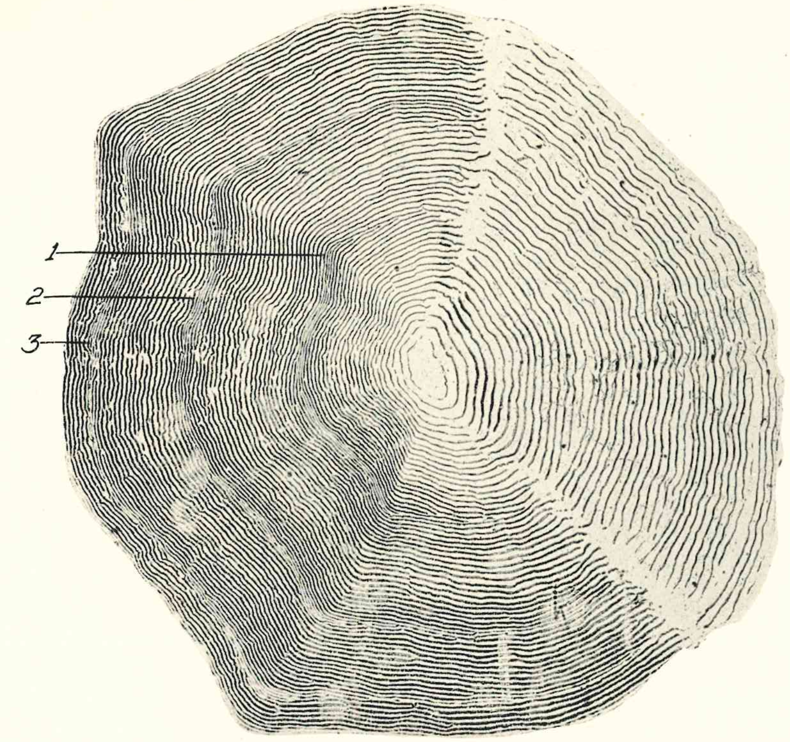

Fig. 27.—Scale of Lake Huron herring (*L. artedi*) taken July 17, 1917, at St. Ignace, Mich. Length, 220 millimeters. Male. Age IV. Scale shows three completed annuli and a marginal growth

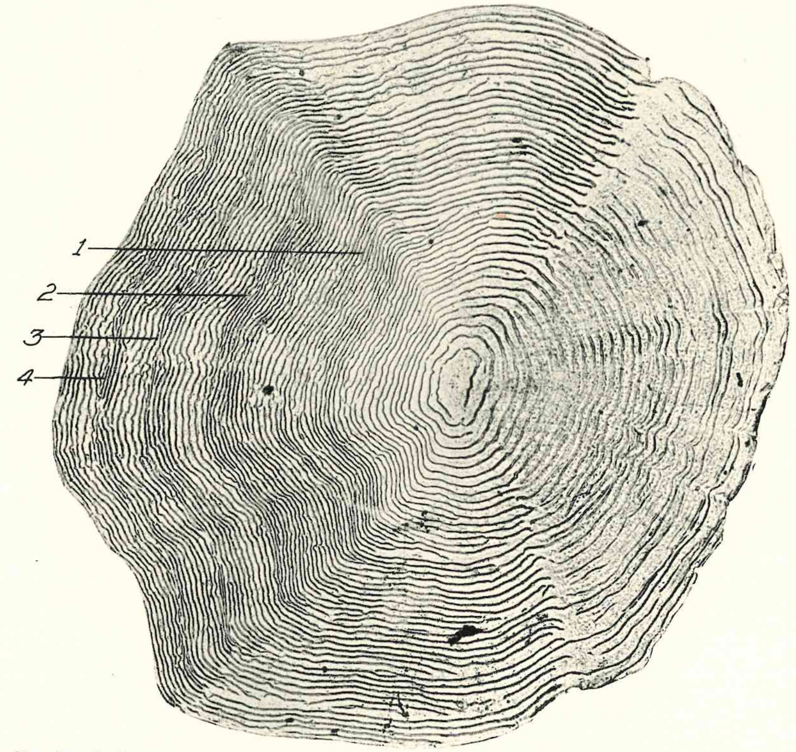

Fig. 28.—Scale of Lake Huron herring (*L. artedi*) taken October 2, 1919, at Tobermory, Ontario. Length, 209 millimeters. Age V. Scale shows four completed annuli and a marginal growth

Bull. U. S. B. F., 1928. (Doc. 1053.)

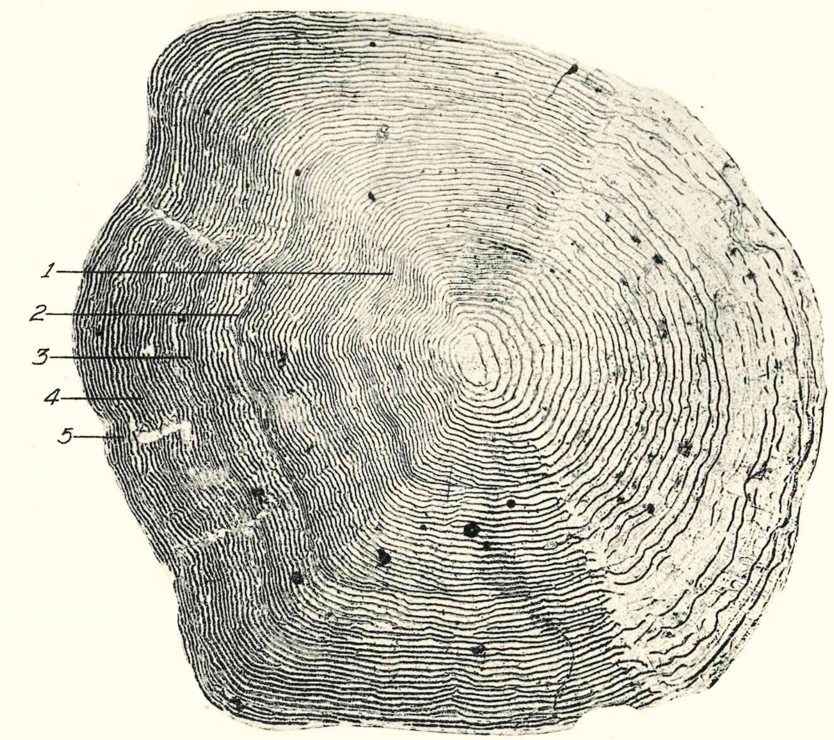

Fig. 29.—Scale of Lake Huron herring (*L. artedi*) taken November 1, 1922, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 58693. Length, 281 millimeters. Weight, 10 ounces. Mature female. Age VI. Scale shows five completed annuli and a marginal growth

Fig. 30.—Scale of Lake Huron herring (*L. artedi*) taken October 29, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54662. Length, 295 millimeters. Mature female. Age VI. Scale shows five completed annuli and a marginal growth

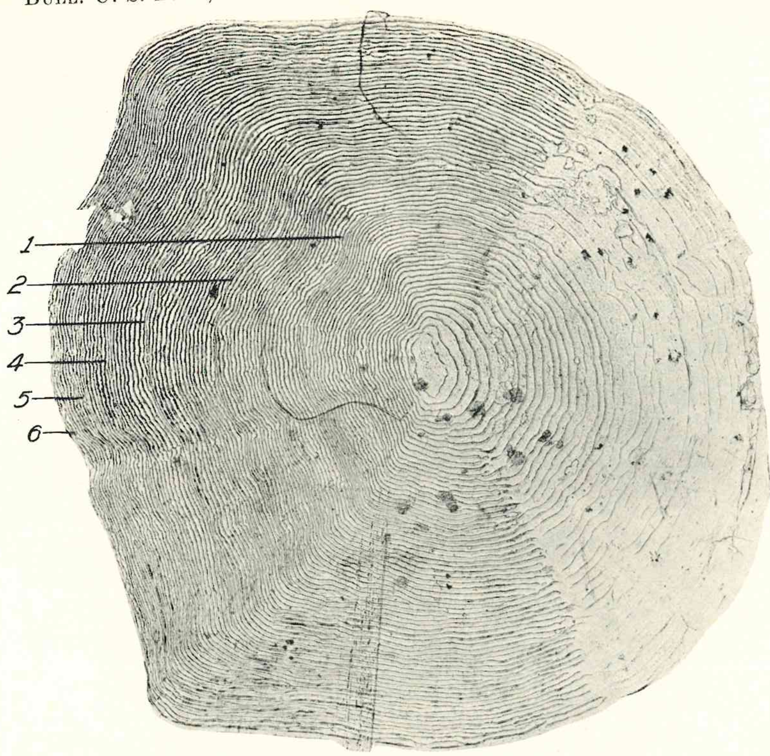

Fig. 31.—Scale of Lake Huron herring (*L. artedi*) taken October 27, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54478. Length, 272 millimeters. Mature male. Age VII. Scale shows six completed annuli and a marginal growth

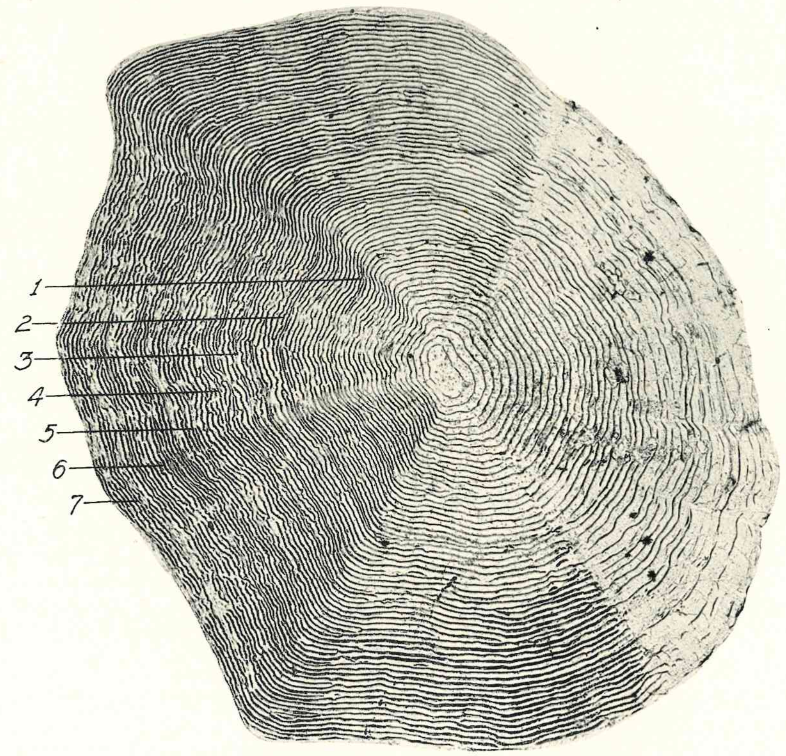

Fig. 32.—Scale of Lake Huron herring (*L. artedi*) taken October 27, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54470. Length, 263 millimeters. Male. Age VIII. Scale shows seven completed annuli and a marginal growth

Fig. 33.—Scale of Lake Huron herring (*L. artedi*) taken October 12, 1919, at Killarney, Ontario (Georgian Bay). University of Michigan No. 52377. Length, 310 millimeters. Age VIII. Scale shows seven completed annuli and a marginal growth

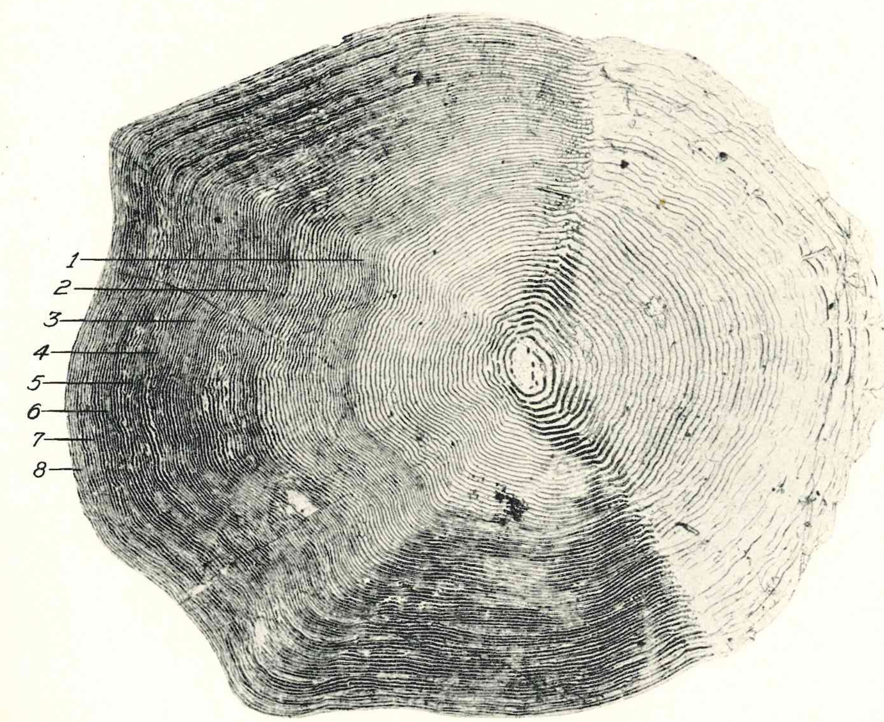

Fig. 34.—Scale of Lake Huron herring (*L. artedi*) taken October 12, 1919, at Killarney, Ontario (Georgian Bay). University of Michigan Museum No. 52369. Length, 302 millimeters. Male. Age IX. Scale shows eight completed annuli and a marginal growth

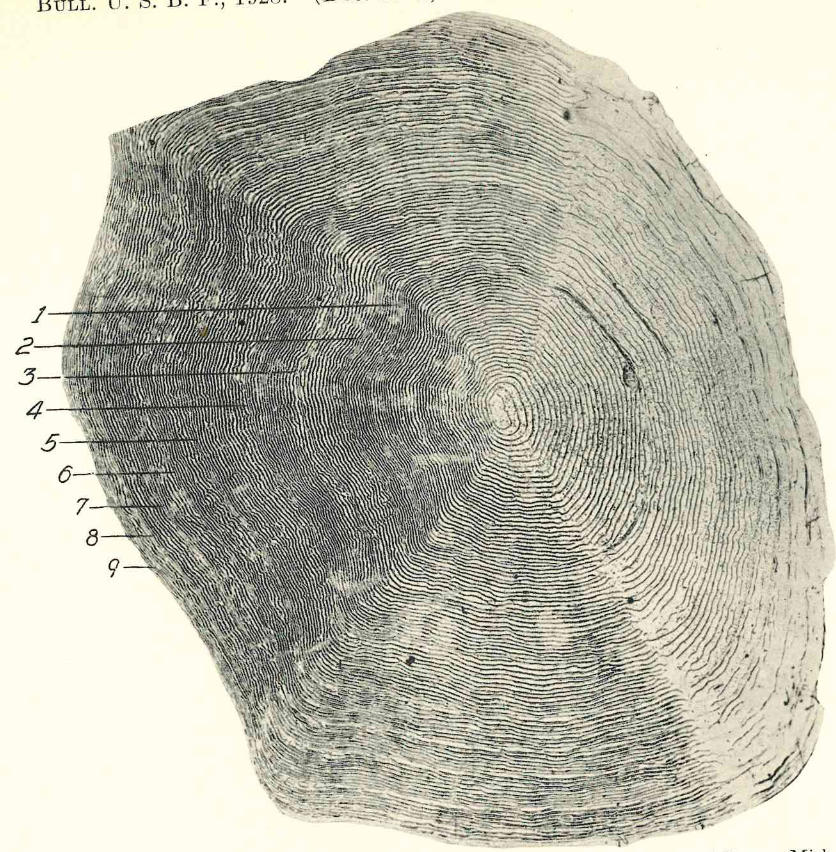

FIG. 35.—Scale of Lake Huron herring (*L. artedi*) taken October 22, 1917, at East Tawas, Mich. University of Michigan Museum No. 52272. Length, 377 millimeters. Weight, 2 pounds. Age X. Scale shows nine completed annuli and a small marginal growth

FIG. 36.—Scale of Lake Ontario herring (*L. artedi*) taken June 18, 1921, at Brighton, Ontario. Length, 412 millimeters. Age XI. Scale shows 10 completed annuli and a marginal growth

the fall of 1913. Hjort (1914) found that in the marine herring (*Clupea harengus*) of the North Sea one year class predominated heavily in the commercial catches for many successive years. Järvi (1920) found a similar phenomenon among "Die kleine Maräne" (*Coregonus albula*) of the Keitelesee, an inland lake of Finland. This dominance of one year class in the commercial catches for two or more consecutive years was explained by both Hjort and Järvi as due to the unusually favorable conditions for hatching in that year in which the dominating year class was hatched. No such phenomenon appears in the lake-herring samples. The 1917/1918 year class formed the bulk of the 1921 sample, the 1918/1919 year class that of the 1922 sample, the 1919/1920 year class that of the 1923, and the 1920/1921 year class that of the 1924 samples. Each year class drops off rapidly in the years following the year of its dominance, which, as shown in the lower part of Table 30, was the fourth.

The data of Table 30 show that 87.2 to 97.4 per cent of the commercial catches are composed of 3, 4, and 5 year fish, and that no one year class predominates for a longer period than a year.

The data of Tables 29 and 30 suggest that commercial fishing for herring is very intense. The first symptom of this heavy fishing is the paucity of old individuals. Herring are known to reach an age of 11 years (p. 358, fig. 36), and if permitted to live they would probably attain a greater age. Yet, in Saginaw Bay extremely few individuals reach their sixth year of life (Table 30), the second year after the majority of them first join the commercial schools. Table 30 shows that the majority of herring do not even reach their fifth year of life. The percentages of this table indicate that on the average the 5-year herring are, roughly, not quite one-third as numerous as the 4-year fish, in spite of the fact, as I shall show later (p. 384), that some of the former are recruited from the immature stock—that is, from fish that are still immature in their fourth year and that join the sexually mature commercial schools in their fifth year of life. In terms of fishing intensity, the above facts suggest that relatively few 4-year herring escape the nets to comprise, a year later, the 5-year group. As stated on page 353, we are not absolutely certain that the high mortality among the older age groups is due to commercial fishing. It is possible, though not probable, that the life span of the herring terminates in the fourth or fifth year of life. It is difficult to believe, however, that in this species old age and sexual maturity are reached in the same year.

That fishing intensity is the important factor is suggested further by the shifting in the age composition of the samples (p. 354). In 1921 the 5-year fish were more numerous than the 3, but since this year the former became progressively less, the latter progressively more abundant. The percentages of the 5-year fish of Table 30 seem to tell us that since 1921 fishing intensity each year grew more severe, permitting fewer and fewer 4-year fish to complete their fifth year of life. So intense does commercial fishing appear to be that a year class is practically wiped out during its year of dominance—the fourth (Table 30). Briefly stated, the history of the majority of adult individuals of a year class seems to be as follows: They are spawned in the fall, hatched in the spring, grow as immature fish for two or three years, attain sexual maturity in the third or fourth year, and are captured by the fishermen before or during their fifth year of life. Each year class predominates for one year only; it is rapidly depleted.

AVERAGE AND EXTREME LENGTH AND WEIGHT OF HERRING

FISH OF DIFFERENT SCHOOLS

The average standard length of the 266 herring taken on October 29, 1921, from 1 pound net is 237 millimeters (9.3 inches), of the 414 herring taken on different days between October 26 and November 4, 1921, 236 millimeters (9.3 inches), or of all the 1921 fish 236 millimeters. The average size of the 501 fish taken November 1, 1922, is 235

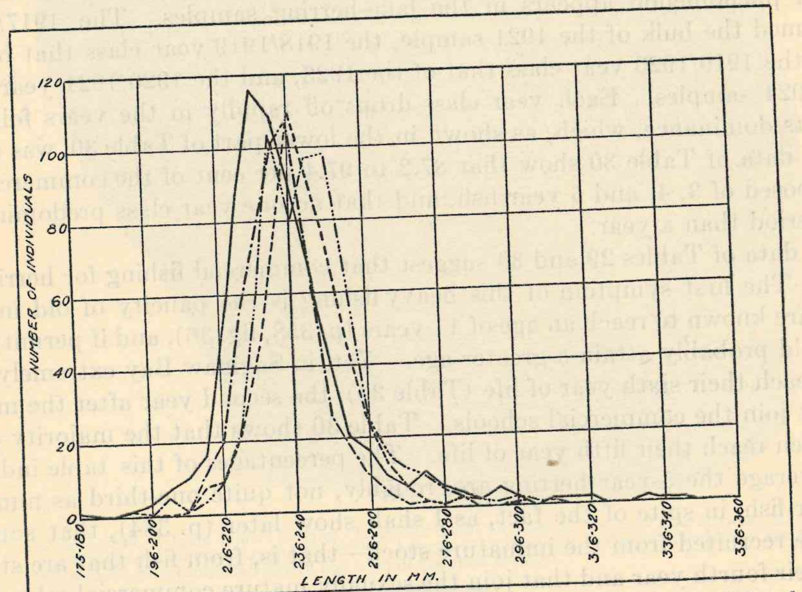

FIG. 37.—Frequency polygons showing for each sample of herring taken in 1921, 1922, 1923, and 1924 the number of individuals in each size group at 5-millimeter intervals. The data are shown in Table 29. — — —, 1921; — · —, 1922; ———, 1923; — · · · —, 1924 (Tobico and Nayanquing samples combined)

millimeters (9.3 inches); of the 519 herring taken November 12, 1923, 241 millimeters (9.5 inches); and of the 611 herring taken in 1924 at Tobico and Nayanquing, 244 millimeters (9.6 inches). The 542 Gravelly Point fish and the 119 Au Gres specimens taken in 1924 averaged the same in length—240 millimeters (9.4 inches). All the 1924 herring together, 1,272 in number, measured 242 millimeters (9.5 inches) in length (bottom of Table 29). The length frequencies of Table 29 and the frequency curves of Figure 37 show that the mode for these herring shifted from 226–230 millimeters in 1921 to 236–240 millimeters in 1922 and 1923 to 231–235 millimeters in 1924. The smallest specimen taken in these samples measured 160 millimeters (6.3 inches) in length, the largest 365 millimeters (14.3 inches) (Table 31).

TABLE 31.—*Actual average, minimum, and maximum length and weight for each age group of a year class attained by the Saginaw Bay herring*

Year and month of capture	Year class	Age group	Length, in millimeters				Weight, in ounces			
			Number of individuals	Minimum	Average	Maximum	Number of individuals	Minimum	Average	Maximum
1921, October to November	1919/1920	II	5	178	195	202	3	2.0	2.8	3.5
1922, November	1920/1921	II	4	210	217	224	4	3.0	4.06	5.0
1923, November	1921/1922	II	2	213	221	229				
1924, November [1]	1922/1923	II	1	210	210	210				
Do. [2]	1922/1923	II	4	177	185	196				
Do. [3]	1922/1923	II	5	177	190	210				
1921, October to November	1918/1919	III	97	198	224	255	19	3.0	4.11	6.0
1922, November	1919/1920	III	148	201	229	257	148	2.5	4.71	7.0
1923, November	1920/1921	III	170	192	233	260				
1924, November [1]	1921/1922	III	162	211	236	271	112	3.5	5.61	11.0
1924, November to December [2]	1921/1922	III	201	160	227	276				
1924, November [4]	1921/1922	III	53	210	233	260				
1924, November to December [3]	1921/1922	III	416	160	231	276				
1921, October to November	1917/1918	IV	291	204	232	308	42	3.0	5.08	7.0
1922, November	1918/1919	IV	245	204	236	283	243	3.0	5.22	13.0
1923, November	1919/1920	IV	240	213	243	300				
1924, November [1]	1920/1921	IV	356	215	243	296	236	4.5	6.11	12.0
1924, November to December [2]	1920/1921	IV	248	200	243	303				
1924, November [4]	1920/1921	IV	57	226	243	285				
1924, November to December [3]	1920/1921	IV	661	200	243	303				
1921, October to November	1916/1917	V	205	214	241	319	37	4.5	6.36	16.5
1922, November	1917/1918	V	95	224	241	284	92	4.0	5.65	11.0
1923, November	1918/1919	V	90	231	251	302				
1924, November [1]	1919/1920	V	74	226	254	290	41	5.5	7.17	12.5
1924, November to December [2]	1919/1920	V	69	233	264	305				
1924, November [4]	1919/1920	V	7	242	255	281				
1924, November to December [3]	1919/1920	V	150	226	258	305				
1921, October to November	1915/1916	VI	67	217	254	337	11	5.0	7.73	10.0
1922, November	1916/1917	VI	9	224	252	281	9	4.75	6.64	9.5
1923, November	1917/1918	VI	15	242	263	283				
1924, November [1]	1918/1919	VI	18	242	267	306	9	6.0	9.00	13.0
1924, November to December [2]	1918/1919	VI	14	{208 248}	262	308				
1924, November [4]	1918/1919	VI	1	275	275	275				
1924, November to December [3]	1918/1919	VI	33	{208 242}	265	308				
1921, October to November	1914/1915	VII	12	239	275	331				
1923, November	1916/1917	VII	2	263	263	263				
1924, November [2]	1917/1918	VII	4	255	280	314				
Do. [4]	1917/1918	VII	1	295	295	295				
Do. [3]	1917/1918	VII	5	255	283	314				
1921, October to November	1913/1914	VIII	3	263	292	343				
1924, November to December [2]	1916/1917	VIII	2	306	336	365				

[1] Tobico and Nayanquing samples combined.
[2] Gravelly Point herring.
[3] 1, 2, and 4 combined.
[4] Au Gres herring.

As shown in Table 31, the smallest 2-year herring measured 177 millimeters in length; the lightest 2-year fish weighed 2 ounces. The largest 2-year herring measured 229 millimeters in length; the heaviest weighed 5 ounces. The smallest sexually mature male measured 160 millimeters in length; the smallest sexually mature female 190 millimeters. The youngest sexually mature male and female were in their second year. The largest sexually mature male was in its eighth year and measured 365 millimeters in length. The largest sexually mature female measured 335 millimeters in length and was in its sixth year (Table 32). The largest sexually immature or nonspawning male was 238 millimeters long; the oldest was in its fifth year. The largest sexually immature or nonspawning female was 257 millimeters long; the oldest was in its fifth year. The heaviest male weighed 16.5 ounces, the heaviest female 13.0 ounces. The oldest male and female were in their eighth year of life. The oldest herring I have ever seen was a female in its eleventh year, taken in 1917 from a pound net at Blind River in Georgian Bay. The largest herring I have ever seen was a female 395 millimeters (15.6 inches) long, weighing 2 pounds and 3 ounces. It was taken in 1924 from Saginaw Bay. The largest herring of which I have a record was captured at Brighton, Ontario (Lake Ontario), in 1921; it measured 412 millimeters in length and was in its eleventh year (see fig. 36).

TABLE 32.—*Actual average, minimum, and maximum length and weight attained by Saginaw Bay herring taken in 1921, 1922, and 1923, for each sex of each age group of a year class*

Year and month of capture	Year class	Age group	Sex	Length, in millimeters				Weight, in ounces			
				Number of individuals	Minimum	Average	Maximum	Number of individuals	Minimum	Average	Maximum
1921, October to November	1918/1919	III	Male	48	198	224	255	13	3.0	4.38	6.0
Do	1918/1919	III	Female	49	199	224	249	6	3.0	3.50	4.0
1922, November	1919/1920	III	Male	78	201	228	247	78	2.5	4.53	6.0
Do	1919/1920	III	Female	70	201	230	257	70	3.25	4.90	7.0
1923, November	1920/1921	III	Male	118	192	233	260	----	----	----	----
Do	1920/1921	III	Female	52	213	233	259	----	----	----	----
1921, October to November	1917/1918	IV	Male	163	205	232	293	29	4.0	5.01	7.0
Do	1917/1918	IV	Female	128	204	233	308	13	3.0	5.23	7.0
1922, November	1918/1919	IV	Male	149	218	237	273	149	3.25	5.23	8.25
Do	1918/1919	IV	Female	95	204	234	283	93	3.0	5.22	13.0
1923, November	1919/1920	IV	Male	155	213	243	300	----	----	----	----
Do	1919/1920	IV	Female	84	226	243	257	----	----	----	----
1921, October to November	1916/1917	V	Male	118	215	241	319	26	4.50	6.52	16.50
Do	1916/1917	V	Female	87	214	240	308	11	5.0	6.00	9.0
1922, November	1917/1918	V	Male	47	224	241	267	47	4.50	5.54	8.0
Do	1917/1918	V	Female	48	224	241	284	45	4.0	5.78	11.0
1923, November	1918/1919	V	Male	59	233	251	274	----	----	----	----
Do	1918/1919	V	Female	30	231	251	302	----	----	----	----
1921, October to November	1915/1916	VI	Male	43	217	252	337	7	5.0	7.57	10.0
Do	1915/1916	VI	Female	24	223	259	335	4	7.0	8.00	9.0
1922, November	1916/1917	VI	Male	5	224	245	277	5	5.75	6.25	10.0
Do	1916/1917	VI	Female	4	246	260	281	4	4.75	7.13	9.50
1923, November	1917/1918	VI	Male	8	242	264	283	----	----	----	----
Do	1917/1918	VI	Female	7	249	261	276	----	----	----	----
1921, October to November	1914/1915	VII	Male	8	239	275	331	----	----	----	----
Do	1914/1915	VII	Female	4	245	277	315	----	----	----	----

AGE GROUPS

In Table 31 are shown for the fish captured in 1921, 1922, 1923, and 1924 the actual average, minimum, and maximum lengths and weights of each age group (male and female) of a year class. The average length of the 2-year herring increased from 195 millimeters in 1921 to 217 millimeters in 1922 and to 221 millimeters in 1923; in 1924 the general average dropped to 190 millimeters. The average length of the 3-year herring increased from 224 millimeters in 1921 to 229 millimeters in 1922 to 233 millimeters in 1923 and to 236 millimeters in 1924.[2] The 4-year fish likewise show an increase in average length. It increases from 232 millimeters in 1921 to 236 millimeters in 1922 and to 243 millimeters in 1923 and 1924. The fish of the remaining age groups also show the same tendency to grow bigger each year. The 5-year herring averaged 241 millimeters in length in 1921 and 1922, 251 millimeters in 1923, and 254 millimeters in 1924; the 6-year fish averaged 254 millimeters in length in 1921, 252 millimeters in 1922, 263 millimeters in 1923, and 267

[2] As stated on p. 350, in a strictly comparative study it is preferable to employ only the Tobico and Nayanquing samples for 1924.

millimeters in 1924. In each age group except the fifth and sixth the 1922 individuals averaged larger than the 1921. Without exception the 1923 fish averaged larger than the 1922, and with the exception of the fourth age group the 1924 herring averaged larger than the 1923.

The average weights of Table 31 tell a similar story. In general, the fish of corresponding age groups become progressively heavier each year. In each age group except the fifth and sixth the fish taken in 1922 averaged more in weight than those taken in 1921, while in each age group without exception the 1924 fish weighed more than the 1922. The herring taken in 1923 were not weighed.

If the average length of the herring population varies as the spawning season advances, as is the case in some age groups of the sockeye salmon runs (Gilbert, 1922, pp. 34 and 64), and if the samples of different years are taken at different periods of the run, then the above averages of length and weight would not be comparable for different years. However, they are believed to be comparable in this case, because each sample collected in 1921–1923 was taken at about the same period; that is, about two weeks after the main spawning run of herring began, and because, as I shall show later (p. 385), the average length of the herring population does not seem to vary much during the height of the spawning season. It will be shown in another place (p. 364) that the same conclusion (the herring are growing bigger) may be drawn from other data not subject to these possible errors.

Apparently, then, these data show that the herring of Saginaw Bay were reaching a bigger size in 1922, 1923, and 1924 than in 1921 and in general were becoming progressively larger at corresponding ages each successive year. The curves of Figure 37, based on the length frequencies of Table 29, point to the same conclusion, as with each year the curve moves farther toward the right. This change in the rate of growth of the herring may be the third symptom of intense fishing. (For the other two symptoms see p. 355.) Briefly stated, this may mean that as the number of herring in the lake is being reduced competition for food among the survivors becomes less severe and consequently they grow faster. The subject is discussed further in the section on growth rate.

MALES AND FEMALES

Table 32, in which are given the actual, average, minimum, and maximum length and weight for each sex of an age group, shows that males and females attain approximately the same length and have the same growth rate in corresponding years of life; that is, no consistent differences in growth rate occur between the sexes. This is brought out more clearly in Table 33 and Figure 38. Table 33 shows, for fish taken in 1921 and 1922, the average total length attained at the end of each year of life by the males and females of each age group. All averages but the last one of each row are computed from the measurements of scales. In Figure 38 the average lengths of the 1921 fish only are plotted. The progressive divergence of the two curves of growth in the fourth and later years of the 6-year fish presumably is due to the small number of females in that age group. In weight the females average a little higher (see Table 32) than the males, due to the greater weight of their partially developed sex organs, although the difference is not as great as was expected. In a further discussion of growth rates the males and females will be considered together.

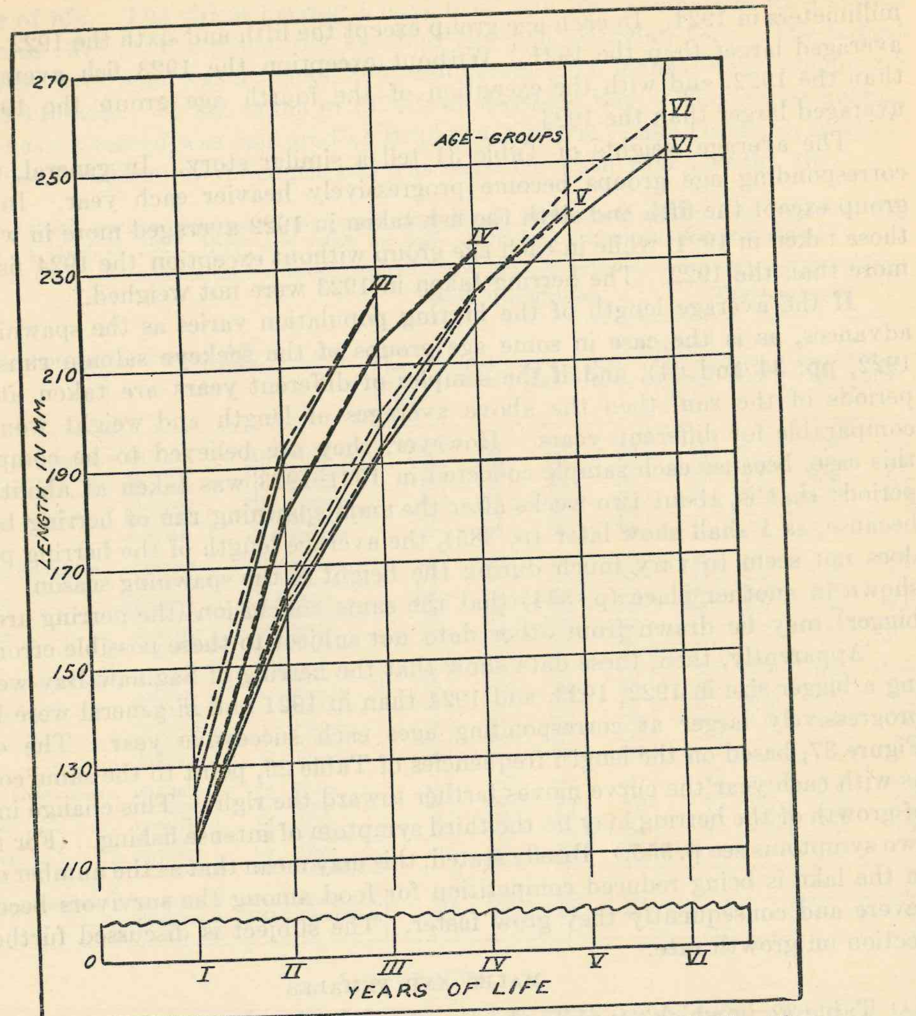

FIG. 38.—Average total length (for Saginaw Bay herring taken in 1921) attained by the male and female of an age group at the end of each year of life. The data are shown in Table 33. — — — — —, male; — — — — —, female

TABLE 33.—*Comparative growth rate of the two sexes of herring belonging to the same age group and year class*

Captured	Age	Number of individuals	Sex	Calculated length, in millimeters, at end of year—					
				I	II	III	IV	V	VI
1921	III	48	Male	124	191	[1] 224			
	III	49	Female	129	193	[1] 224			
	IV	163	Male	116	179	214	[1] 232		
	IV	128	Female	116	180	214	[1] 233		
	V	118	Male	115	164	197	224	[1] 241	
	V	87	Female	115	165	200	224	[1] 240	
	VI	43	Male	114	160	192	218	238	[1] 252
	VI	24	Female	117	162	193	223	245	[1] 259
1922	III	78	Male	140	199	[1] 228			
	III	70	Female	139	200	[1] 230			
	IV	149	Male	123	183	218	[1] 237		
	IV	95	Female	120	181	216	[1] 234		
	V	47	Male	115	169	204	229	[1] 241	
	V	48	Female	114	173	206	228	[1] 241	

[1] Actual length when captured in November.

RATE OF GROWTH

METHOD OF DETERMINATION

By Petersen's method of age determination the individuals of a large collection are grouped according to their size and the size-frequency distribution is plotted on graphs. Each prominent mode or hump in the resultant curve is then assumed to represent an age group, the first mode representing the youngest age group. An examination of the length-frequency curves of Figure 37 shows that they are virtually unimodal, so that this method can not be employed for the herring of my samples, although, if material were available, it might be found applicable to the fish of the two youngest age groups (1 and 2). In the study of growth rates, therefore, I have restricted myself to the methods based on scales. We may assort the individuals of the collections of different years according to their year classes, as determined by reckoning back from the year of capture, according to the number of annuli on the scales. We may then separate the various age groups of each year class by using the annuli as an indication of age. Having assorted the fish, two procedures are possible. First, we may compare the actual length measurements of these various age groups. Second, we may compute, from the scale diameters (or other dimension) of all the specimens, the lengths at the end of each year of life and thus determine for each year class its rate of growth throughout life. The second method affords a much larger series of data. By combining both actual and computed lengths of fish of the same ages of all the year classes a general norm of growth characteristic of the species may be obtained. The actual measurements, both lengths and weights, of all the age groups of all my comparable samples are summarized in Table 34. The grand averages are given near the bottom of the table. Similarly, the estimated lengths for each year of life of all age groups, computed from the measurements of scales, are summarized in Table 26. The length values of fish of the same age groups of both of these tables are combined in Table 43.

TABLE 34.—*Rate of growth of all year classes of Saginaw Bay herring, in terms of length and weight, as determined by direct measurement and weighing* [1]

Year class	Average length, in millimeters, of males and females in year—						
	II	III	IV	V	VI	VII	VIII
1913/1914							292 (3)
1914/1915						275 (12)	
1915/1916					254 (67)		
1916/1917				241 (205)	252 (9)	263 (2)	[2] 336 (2)
1917/1918			232 (291)	241 (95)	263 (15)	[2] 280 (4)	
1918/1919		224 (97)	236 (245)	251 (90)	267 (18)		
1919/1920	195 (5)	229 (148)	243 (240)	[3] 254 (74)			
1920/1921	217 (4)	233 (170)	[3] 243 (356)				
1921/1922	221 (2)	[3] 236 (162)					
1922/1923	[5] 190 (5)						
Grand average	202 (16)	231 (577)	239 (1,132)	245 (464)	257 (109)	275 (18)	309 (5)
Grand average increments		29	8	6	12	18	34

[1] Number upon which an average is based is shown in parentheses.
[2] Gravelly Point herring.
[3] Tobico and Nayanquing herring.
[5] 2, 3, and Au Gres herring combined.

TABLE 34.—*Rate of growth of all year classes of Saginaw Bay herring, in terms of length and weight, as determined by direct measurement and weighing*—Continued

Year class	Average weight, in ounces, of—									
	Males in year—					Females in year—				
	II	III	IV	V	VI	II	III	IV	V	VI
1913/1914										
1914/1915										
1915/1916					7.57 (7)					8.00 (4)
1916/1917				6.52 (26)	6.25 (5)				6.00 (11)	7.13 (4)
1917/1918			5.01 (29)	5.54 (47)				5.23 (13)	5.78 (45)	
1918/1919		4.38 (13)	5.23 (149)				3.50 (6)	5.22 (93)		
1919/1920	[4] 2.8 (3)	4.53 (78)				[4] 2.8 (3)	4.90 (70)			
1920/1921	[4] 4.06 (4)					[4] 4.06 (4)				
1921/1922										
1922/1923										
Grand average	[4] 3.53 (7)	4.51 (91)	5.19 (178)	5.89 (73)	7.02 (12)	[4] 3.53 (7)	4.79 (76)	5.22 (106)	5.82 (56)	7.56 (8)
Grand average increments		.98	.68	.70	1.13		1.26	.43	.60	1.74
Grand average weight, in ounces, of males and females	3.53 (7)	5.03 (279)	5.61 (521)	6.18 (170)	7.78 (29)					
Grand average increment in weight of males and females		1.50	.58	.57	1.60					

[4] Male and female.

UNCORRECTED AND CORRECTED COMPUTED LENGTHS

then you are not warranted in calculating lengths for these ages

The computed lengths in these tables have not been corrected for disproportionate growth of body and scale. A correction for the error from this source would be valuable if it could be made for fish of all ages so as to permit comparisons. However, it is impossible to make this correction for the first two years of life because, owing to the lack of fish of these years in my samples, body-scale ratios could not be computed for them. The general conclusions derived from a comparative study of the uncorrected computed lengths would not be altered by a study of the corrected lengths (see Table 24). The relative rates of growth of the various year classes would be unaffected by the correction. It can not be argued, therefore, that my findings relative to the growth of the herring may be vitiated by the probable inaccuracy of my computed data.

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GROWTH OF AGE GROUPS AND YEAR CLASSES

Total lengths.—An examination of the vertical columns of figures of Table 34, representing measured lengths, shows that the values for each age group generally are greater in successive years, which indicates that the Saginaw Bay herring of the same age were gradually increasing their rate of growth. This is especially clear for the 3 and 4 year fish.

TABLE 35.—*Uncorrected calculated total length attained by various year classes of Saginaw Bay herring at end of each year of life. Each year of life is given in terms of calendar years* [1]

Year class	Age group	Average calculated length, in millimeters, attained at end of year—											Number of individuals
		1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924	
1914	VIII	107	149	176	206	239	259	277	292				3
1915	VII		116	161	191	221	242	260	275				12
1916	VI			115	161	192	220	241	255				67
1917	VII				119	157	184	210	234	248	263		2
	VI				117	161	198	224	242	252			9
	V				115	164	199	224	240				205
1918	VI					113	166	203	228	247	263		15
	V					114	171	205	229	241			95
	IV					116	179	214	232				291
1919	VI						116	168	199	227	248	267	18
	V						119	179	213	237	251		90
	IV						122	183	217	236			245
	III						127	192	224				97
1920	V							117	177	211	236	254	74
	IV							133	192	224	243		240
	III							139	200	229			148
	II							121	195				5
1921	IV								136	191	223	243	356
	III								142	201	233		170
	II								141	217			4
1922	III									143	202	236	162
	II									137	221		2

[1] The last value of each horizontal row is the actual average length when captured in November.

TABLE 36.—*Calculated total length attained by various year classes of Saginaw Bay herring at end of each year of life. The data are those of Table 35 rearranged according to age groups* [1]

Year class	Age group	Average computed length, in millimeters, attained at end of year—											Number of individuals
		1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924	
1914	VIII	107	149	176	206	239	259	277	292				3
1915	VII		116	161	191	221	242	260	275				12
1917	VII				119	157	184	210	234	248	263		2
1916	VI			115	161	192	220	241	255				67
1917	VI				117	161	198	224	242	252			9
1918	VI					113	166	203	228	247	263		15
1919	VI						116	168	199	227	248	267	18
1917	V				115	164	199	224	240				205
1918	V					114	171	205	229	241			95
1919	V						119	179	213	237	251		90
1920	V							117	177	211	236	254	74
1918	IV					116	179	214	232				291
1919	IV						122	183	217	236			245
1920	IV							133	192	224	243		240
1921	IV								136	191	223	243	356
1919	III						127	192	224				97
1920	III							139	200	229			148
1921	III								142	201	233		170
1922	III									143	202	236	162
1920	II							121	195				5
1921	II								141	217			4
1922	II									137	221		2

[1] The last value of each horizontal row is the actual average length when captured in November.

TABLE 37.—*Computed lengths reached at end of different years of life by various age groups of Saginaw Bay herring. The data are those of Table 36 rearranged so as to group the lengths of each year of life together* [1]

Age group	Year of life	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924
		Average computed length of year classes, in millimeters, at end of year—										
VIII	I	107 (3)										
VII	I		116 (12)		119 (2)							
VI	I			115 (67)	117 (9)	113 (15)	116 (18)					
V	I				115 (205)	114 (95)	119 (90)	117 (74)				
IV	I					116 (291)	122 (245)	133 (240)	136 (356)			
III	I						127 (97)	139 (148)	142 (170)	143 (162)		
II	I							121 (5)	141 (4)	137 (2)		
VIII	II		149 (3)									
VII	II			161 (12)		157 (2)						
VI	II				161 (67)	161 (9)	166 (15)	168 (18)				
V	II					164 (205)	171 (95)	179 (90)	177 (74)			
IV	II						179 (291)	183 (245)	192 (240)	191 (356)		
III	II							192 (97)	200 (148)	201 (170)	202 (162)	
II	II								[2]195 (5)	[2]217 (4)	[2]221 (2)	
VIII	III			176 (3)								
VII	III				191 (12)		184 (2)					
VI	III					192 (67)	198 (9)	203 (15)	199 (18)			
V	III						199 (205)	205 (95)	213 (90)	211 (74)		
IV	III							214 (291)	217 (245)	224 (240)	223 (356)	
III	III								[2]224 (97)	[2]229 (148)	[2]233 (170)	[2]236 (162)
VIII	IV				206 (3)							
VII	IV					221 (12)		210 (2)				
VI	IV						220 (67)	224 (9)	228 (15)	227 (18)		
V	IV							224 (205)	229 (95)	237 (90)	236 (74)	
IV	IV								[2]232 (291)	[2]236 (245)	[2]243 (240)	[2]243 (356)
VIII	V					239 (3)						
VII	V						242 (12)		234 (2)			
VI	V							241 (67)	242 (9)	247 (15)	248 (18)	
V	V								[2]240 (205)	[2]241 (95)	[2]251 (90)	[2]254 (74)
VIII	VI						259 (3)					
VII	VI							260 (12)		248 (2)		
VI	VI								[2]255 (67)	[2]252 (9)	[2]263 (15)	[2]267 (18)
VIII	VII							277 (3)				
VII	VII								[2]275 (12)		[2]263 (2)	
VIII	VIII								[2]292 (3)			

[1] The number of specimens employed is shown in parentheses.
[2] Actual length when captured in November.

Tables 35 to 37 have been compiled to find whether the more extensive data derived from calculated lengths afford evidence of a change in growth rate. In Table 35 the year classes are arranged chronologically, so that the various age groups of each year class are brought together. The fish of the various age groups of the 1918 year class are seen to have been 113, 114, and 116 millimeters long at the end of their first year (1918), while those of the 1919 year class were 116, 119, 122, and 127 millimeters long at the same age; that is, in 1919. This apparent increase in length in 1919 continues for the first-year fish of 1920, 1921, and 1922, the figures being 117, 133, 139, and 121 for 1920, 136, 142, and 141 for 1921, and 143 and 137 for 1922. Similar increases in length in fish of the same age in successive years appear in fish in their second, third, fourth, and fifth years. Mere inspection of the figures as they stand in Table 35 seems, then, to strengthen, from calculated lengths, the view suggested by the measured lengths of Table 34 that the growth rate of the herring increased after 1918; but Table 35 seems also to show evidence of Lee's phenomenon—that lengths calculated for a given year from scales of young fish are always greater than lengths calculated for the same year from older fish. Thus, the 1919 year class of Table 35 shows age

groups III, IV, V, and VI with calculated lengths of 127, 122, 119, and 116 millimeters, respectively; that is, the calculated length at the end of year I is less the older the fish from which the calculation is made. A similar relation appears in the calculated lengths of fish of different age groups in the 1918, 1920, and 1921 year classes but not in the other year classes. Obviously, if the scales used for the length calculations for the year 1919 and following years were from younger fish than those used for length calculations for the year 1918 and preceding years, they would give higher values. In that case, although the growth rate in 1919 might, in reality, be the same as that of 1918, it would appear to be greater. In order to compare calculated lengths attained at a given age in any two years, it is therefore necessary that the scales used be taken from fish of the same age. By such a procedure whatever error is involved in Lee's "phenomenon of apparent change in growth rate" is the same for all year classes in fish of the same age.

In Table 36 the data of Table 35 are regrouped. The year classes are no longer in chronological order, but the age groups of different year classes are brought together. The 8 and 7 year herring of the year classes 1914 and 1917 are too few to give dependable averages. An examination of Table 36 shows that the 7-year fish of the 1915 year class and the 6-year fish of the 1916 year class reached about the same length in corresponding years throughout life. The 6-year herring of the 1917 year class reached the same length as those of the 1916 year class at the end of each of the first two years of life but exceeded them in length at the end of their third year (1919). This excess in length then gradually grew less, until the actual length of the 1917 fish at death was slightly less than that of the 1916 fish. The 6-year individuals of the 1918 year class were slightly smaller than those of the 1917 or 1916 year class at the end of the first year of life but were larger at the end of the second year (1919) and continued to be larger in the remaining corresponding years of life. The 6-year fish of the 1919 year class attained the same average length as those of the 1916 and 1917 year classes at the end of the first year of life but exceeded them in length at the end of the second year (1920) and at the end of the later corresponding years. The 1918 and 1919 6-year fish, however, seemed to have had similar rates of growth. The 5-year fish of the 1918 year class were approximately the same in length as those of the 1917 year class at the end of the first year of life, then exceeded them in length in the second year (1919), and continued to exceed them in corresponding years, though in diminishing amounts, throughout life. The 5-year-old fish of the 1919 and 1920 year classes, which had similar rates of growth, however, reached greater lengths than those of the two preceding year classes in corresponding years throughout life. In the fourth (year class 1921 excepted), third, and second age groups each younger year class of each age group successively attained greater lengths than its predecessor for corresponding years throughout life.

Summarizing this detailed analysis, we find that the 1915 and 1916 year classes grew at corresponding rates throughout life. Although the fish used for calculating the lengths of these two year classes were respectively 7 and 6 years old, the difference in age is so little that there is no evidence of apparent change in growth rate. We find that the 6-year fish of the 1917 year class grew at the same rate as the two previously mentioned year classes during the first two years of life (1917 and 1918), then reached a greater length in the third year in 1919 and in the corresponding later years of life. The 1918 year class (age groups V and VI) reached about the same length in the first year of life as the three preceding year classes but exceeded them in length in corresponding later years. The 1919 year class (age groups IV, V, VI), however, in general reached greater average lengths at corresponding ages than its predecessors in all years of life. The same tendency to attain greater lengths than its predecessor at corresponding ages is found among the remaining year classes considered. Two exceptions are noted—the rates of growth are approximately the same in the 5-year fish of the 1919 and 1920 year classes and in the 4-year herring of the 1920 and 1921 year classes. It is to be noted, then, that an acceleration in growth occurred in 1919 in the third year of life in the fish of the 1917 year class, in the second year in the fish of the 1918 year class, and in the first year in the fish of the 1919 year class, but apparently not in the fourth year in the 6-year individuals of the 1916 year class; and that the herring of all age groups attained greater lengths in the early years of life after 1919 than before this year. As comparisons are made between fish of the same age groups, the increases in length are believed to be actual and not Lee's "apparent change in growth rate." It appears, then, that the year 1919 introduced a period favorable for the growth of herring.

These facts probably are brought out more clearly in Table 37, in which the data of Table 36 are rearranged so as to group together the lengths of each year of life. Age groups VIII and VII of the year classes 1914 and 1917, respectively, are not considered in the following discussion, as they contain too few individuals to give dependable averages. Table 37 shows that the computed total lengths of the first year of life (115, 117, 113, 116 millimeters) fluctuate with the year classes in the sixth age group. In the fifth age group they remain constant in 1917 and 1918 (115 and 114 millimeters), but increase to 119 and 117 millimeters in 1919 and 1920, respectively. In the fourth age group the length attained in 1918 is about the same as in the older age groups but is greater in 1919 and again in 1920 and 1921. In the second and third age groups there is a progressive increase in length attained at the same age with the successive calendar years. In general, the average lengths of the first year are relatively small and are very nearly the same for all age groups and year classes in the calendar years 1915 to 1918, inclusive, but with one exception[3] are relatively large in 1919 and increase in each successive year thereafter.

The total length of the second year of life remains constant in 1917 and 1918 but increases in 1919 and 1920 in the sixth age group. It increases progressively for two successive years in the fifth, fourth, and second age groups and then remains the same. In the third age group the total length of the second year increases in 1921, then remains virtually constant for two successive years. The average lengths of the second year are approximately the same for all age groups and year classes in the years 1916 to 1918, inclusive, and are smaller than those of the years following 1918.

The total lengths of the third year of life show a progressive increase in each successive year, except in the last one of each series, when they either remain constant or decrease slightly, in all age groups considered. As was the case in the lengths of the first and second years of life, those of the third year are about the same for the age groups in the years preceding 1919 and are smaller than those of the years following 1918. The average lengths of the fourth year of life also show a progressive

[3] See footnote 4, p. 368.

increase in each successive year, except in the last one of each series, in all age groups considered. In this year, however, the increase in length begins in 1920 instead of in 1919, as was the case with the preceding years of life. Most of the lengths of the fifth year are the same. An increase is shown for this year in the sixth age group in 1922 and 1923 and in the fifth age group in 1923 and 1924, fish that hatched in 1918 and 1919 and in 1919 and 1920, respectively. In the sixth year of life the lengths fluctuate more or less with the year classes, although the 6-year fish hatched in 1918 and 1919, especially the latter, average larger in 1923 and 1924, respectively, than those hatched before 1918.

A study of total calculated and actual lengths, then, shows (1) that the herring of Saginaw Bay attained approximately the same length in corresponding years of life during the period 1915 to 1918, inclusive; (2) that all fish, with two exceptions (see age groups VI and V, year of life I, of year classes 1919 and 1920, Table 37), three years of age and younger were larger in 1919 and thereafter than were fish of equal age before 1919; (3) that all fish, with exception noted in (2) above, 3 years of age and younger, showed acceleration in growth in 1919 while older fish apparently did not show acceleration in this year; (4) that all fish 3 years of age and younger reached progressively greater lengths each successive year after 1918 (except in the last one of each series, when the average length remained constant, decreased, or increased slightly), while the 4-year fish did likewise after 1919; and (5) that fish older than 4 years hatched after 1917 attained greater average lengths at the same age than those hatched before or in 1917, the fifth age group of year class 1918 excepted.

From a study of both measured and calculated lengths it is concluded that the year 1919 initiated a period of increased growth rate in all Saginaw Bay herring 3 years of age or younger.

TABLE 38.—*Uncorrected calculated length increment attained by various year classes of Saginaw Bay herring during the calendar growth years 1914 to 1924, inclusive. The increments are derived from Table 35* [1]

Year class	Age group	Average calculated length increment, in millimeters, attained during the year—											Number of fish
		1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924	
1914	VIII	107	42	27	30	33	20	18	15				3
1915	VII		116	45	30	30	21	18	15				12
1916	VI			115	46	31	28	21	14				67
1917	VII				119	38	27	26	24	14	15		2
	VI				117	44	37	26	18	10			9
	V				115	49	35	25	16				205
1918	VI					113	53	37	25	19	16		15
	V					114	57	34	24	12			95
	IV					116	63	35	18				291
1919	VI						116	52	31	28	21	19	18
	V						119	60	34	24	14		90
	IV						122	61	34	19			245
	III						127	65	32				97
1920	V							117	60	34	25	18	74
	IV							133	59	32	19		240
	III							139	61	29			148
	II							121	74				5
1921	IV								136	55	32	20	356
	III								142	59	32		170
	II								141	76			4
1922	III									143	59	34	162
	II									137	84		2

[1] The last value of each horizontal row shows the increment reached by November, when fish were captured.

Increments.—The computed annual average increments of growth of the Saginaw Bay herring are shown in Table 38. The increments are derived from the lengths of Table 35 and are arranged according to the year classes, each year of life being represented by a calendar year shown at the head of each vertical column. As in the case of the total lengths of Table 35, the increments of Table 38 are rearranged in Table 39 according to the age groups and in such a way that the increments of each year of life are grouped together. The increments of the first year are the same as the total lengths of that year and have been considered already. If we use the procedure employed for the study of total lengths and follow the increments of the various years of life of each age group through successive calendar years, we come to conclusions similar to those arrived at in the study of total lengths. (1) The herring grew at approximately the same rate in corresponding years of life during the years 1915 to 1918, inclusive. (2) The herring grew more rapidly in their first, second, and third years in 1919 and thereafter than before 1919. The scanty data indicate that the increments of the fourth year of life are somewhat less in 1919 and thereafter than before 1919. (3) The acceleration in growth occurred suddenly in 1919 in herring in their first, second, and third years, but apparently not in herring of greater age. (4) The increments of the first year became suddenly larger in 1919 and with one exception[4] increased progressively thereafter. Those of the other years of life fluctuated with the year classes during the period 1919 and thereafter, remained constant, or decreased during those years.

Table 39.—*Computed average length increments reached in different years of life by various age groups of Saginaw Bay herring. The data are those of Table 38 rearranged so as to group the increments of the same year of life together* [a]

Age group	Year of life	Average computed increments of length, in millimeters, attained during the year—										
		1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924
VIII	I	107 (3)										
VII	I		116 (12)		119 (2)							
VI	I			115 (67)	117 (9)	113 (15)	116 (18)					
V	I				115 (205)	114 (95)	119 (90)	117 (74)				
IV	I					116 (291)	122 (245)	133 (240)	136 (356)			
III	I						127 (97)	139 (148)	142 (170)	143 (162)		
II	I							121 (5)	141 (4)	137 (2)		
VIII	II		42 (3)									
VII	II			45 (12)		38 (2)						
VI	II				46 (67)	44 (9)	53 (15)	52 (18)				
V	II					49 (205)	57 (95)	60 (90)	60 (74)			
IV	II						63 (291)	61 (245)	59 (240)	55 (356)		
III	II							65 (97)	61 (148)	59 (170)	59 (162)	
II	II								[b] 74 (5)	[b] 76 (4)	[b] 84 (2)	
VIII	III			27 (3)								
VII	III				30 (12)		27 (2)					
VI	III					31 (67)	37 (9)	37 (15)	31 (18)			
V	III						35 (205)	34 (95)	34 (90)	34 (74)		
IV	III							35 (291)	34 (245)	32 (240)	32 (356)	
III	III								[b] 32 (97)	[b] 29 (148)	[b] 32 (170)	[b] 34 (162)
VIII	IV				30 (3)							
VII	IV					30 (12)		26 (2)				
VI	IV						28 (67)	26 (9)	25 (15)	28 (18)		
V	IV							25 (205)	24 (95)	24 (90)	25 (74)	
IV	IV								[b] 18 (291)	[b] 19 (245)	[b] 19 (240)	[b] 20 (356)
VIII	V					33 (3)						
VII	V						21 (12)		24 (2)			
VI	V							21 (67)	18 (9)	19 (15)	21 (18)	
V	V								[b] 16 (205)	[b] 12 (95)	[b] 14 (90)	[b] 18 (74)
VIII	VI						20 (3)					
VII	VI							18 (12)		14 (2)		
VI	VI								[b] 14 (67)	[b] 10 (9)	[b] 16 (15)	[b] 19 (18)
VIII	VII							18 (3)				
VII	VII								[b] 15 (12)		[b] 15 (2)	
VIII	VIII								[b] 15 (3)			

[a] The number of specimens employed is shown in parentheses.
[b] Increment up to November when captured.

[4] The small average first-year length (116 millimeters) of the 6-year herring of the 1919 year class appears to be consistent with the corresponding lengths of the younger fish of this year class, allowing a decrease due to Lee's "phenomenon"; but this small average length (117 millimeters) of the 5-year fish of the 1920 year class does not seem to be thus consistent. It is not apparent why the 5-year fish grew so much more slowly during the first year of life than the younger age groups of the same year class, while in the later years of life the former grew at the same rate as the latter. This seems to be the only outstanding inconsistency in the computed values and it may or may not be significant. It militates against the general conclusion that the growth rates of the 1-year herring increased in 1919 and again in 1920.

The increasingly greater mean lengths of the 2, 3, and 4 year fish after the year 1918, noted above and shown in Table 37, are thus due largely, if not entirely, to the accelerated growth of the first year of life. To illustrate this, we may compare, for example, the growth rates of the 3-year herring of the year classes 1919 to 1922, inclusive. At death the fish of each year class averaged 224, 229, 233, and 236 millimeters, respectively, in length (Table 34). From Table 39 it may be seen that they grew 127, 139, 142, and 143 millimeters, respectively, in their first year of life; 65, 61, 59, and 59 millimeters, respectively, in their second year; and 32, 29, 32, and 34 millimeters, respectively, in their third year. It is evident that the large size of the 3-year fish of the 1921 or 1922 year class was not due to an increase in the growth rates of the second and third years of life but wholly to the increase in the growth rate of the first year. Similarly, the greater average length of the 3-year fish of the 1920 year class was due entirely to the acceleration in growth of the first year of life. Similar results may be obtained from a study of the increments of the second and fourth age groups. In the age groups considered, the relative size of the mature fish was correlated with the size reached by them at the end of the first year of life. The growth history of the 1-year fish was then of great significance to the herring fisheries of 1921 to 1924, inclusive. The growth rate of the first year determined largely the size, and indirectly the weight, of most of the individuals of the commercial catches of these years, for, as has been shown (Table 30), the bulk of these catches consisted of fish of years III and IV. If the growth rate of the first year generally controls the size and weight of the 3 and 4 year herring, then, from the point of view of the fisheries, the growth history of the herring of year I is especially significant; for, not only do the herring complete nearly 50 per cent of their growth in length in the first year of life, as I shall show later, but the rate of growth of this year would determine the size and weight of most of the individuals taken in the commercial nets.

SUGGESTED EXPLANATION OF RAPID GROWTH OF YOUNG HERRING IN 1919 IN SAGINAW BAY

If we assume that improved conditions are responsible for the increased growth rate ushered in by the year 1919, how may we account for the fact that only those Bay City herring were affected that were 3 years of age and younger? I believe this is explained if we assume that the young herring hatched in Saginaw Bay remain there during at least the first year and the early part of the second and of the later years of life. The 2-year and even the 3-year herring may remain in the bay throughout the year, though, as I shall show later (p. 394), this is not probable. It is known that many 3-year herring join the spawning schools in the fall (p. 384) and depart with them in the following winter or early spring to the summer feeding grounds in Lake Huron proper. (See p. 394.) I shall later give reasons for my belief that growth conditions were improved in Saginaw Bay during 1919 but not elsewhere in the lake. If the above statements are true, all age groups were subjected during the growth season to the improved conditions of Saginaw Bay in 1919 and later years, the fourth and older age groups for a short period in the fall and spring, the second and third age groups during either the entire growing season or a part thereof, and the first age group during the entire season. The measurable effect of any environmental change that alters growth rate should be more noticeable in the years of rapid growth than in those of relatively slow growth. The 1-year herring, with their large growth increment, would, in general, show more clearly changes in the conditions of growth than the 2-year fish; the latter would show alterations of growth rate more clearly than the 3-year-old. In each older age group, as the growth increment decreased, changes in it would be detected less easily and more likely to be obscured by other factors affecting growth increments. Again, if the 1-year herring were subjected to the improved conditions of Saginaw Bay throughout the entire growing season, while the older fish were subjected to them during only part of the season, the growth of the former naturally would be influenced more by these improved conditions than that of the latter. As, then, the growth increment of the herring is greatest in its first year of life and diminishes progressively in later years, any factor that tended to alter growth rate should show larger measurable effects and therefore be detected more readily in the first year than in later years. As first-year fish are believed to spend a larger part of the growing season in Saginaw Bay than do older fish, growth-controlling alterations in the conditions in the bay should affect them more than they would older fish. They showed growth acceleration in 1919 and later years, over that obtaining in 1918 and years immediately preceding. In the section of this paper dealing with factors of growth in Saginaw Bay the probable causes of this acceleration are discussed.

LAW OF GROWTH COMPENSATION

Gilbert (1914) concludes from a study of the computed growth increments of some 4-year sockeye salmon (*Oncorhynchus nerka*) that a compensation in growth occurred in the third and fourth years of life. That is, salmon that were large at the end of the second year grew, on the average, more slowly in succeeding years than the salmon that were small at the end of the second year, so that eventually all individuals reached a uniform size at maturity. Delsman (1914) noted that in the marine herring of Holland the big yearlings grew more slowly in the second year than the small yearlings. Fraser (1916) observed that the handicapped or slowly growing Pacific spring salmon of the "stream type" gradually catch up (or nearly do so) to the size of the fast-growing individuals of the "sea type." In the herling sea trout, however, Mottram (1916a) found that the fast-growing young fish continued to grow rapidly throughout life, while the slowly growing fish continued to grow relatively slowly throughout life. Dahl (1918) states that this is also true for the trout of Norway, although the disparity between the slow and rapid growers decreases somewhat with increasing age. Molander (1918) divided his marine herring of the ninth age group into three groups, according to the size of the central field (first year's growth) on the scales. He then discovered that scales with large central fields remained the largest throughout the nine years of life, but that the difference in size between the scales with a large central field and those with a small central field is less in the ninth than in the first year of life. Molander referred to this as undulating growth, though it is really the same phenomenon designated by Gilbert as compensating growth. According to Hubbs (1921), a "law of growth compensation" is also evident in *Labidesthes sicculus* and probably in *Amphigonopterus aurora* (Hubbs 1921a). This law was found operative also in the Atlantic salmon by Menzies and Macfarlane (1926, 1926a) and in the sea trout by Nall (1926). Does this law hold for the lake herring? Perhaps the slow growth of years 1915 to 1918 of the herring in Saginaw Bay was compensated by a rapid growth in the later years of life in Lake Huron proper.

TABLE 40.—*Computed average length increments reached in different years of life by various age groups of Saginaw Bay herring. The data are taken from Table 38 and are rearranged according to age groups*

Age group	Year class	Average computed length increment, in millimeters, in year—						Number of specimens
		I	II	III	IV	V	VI	
VI	1916	115	46	31	28	21	14	67
	1917	117	44	37	26	18	10	9
	1918	113	53	37	25	19	16	15
	1919	116	52	31	28	21	19	18
V	1917	115	49	35.	25	16		205
	1918	114	57	34	24	12		95
	1919	119	60	34	24	14		90
	1920	117	60	34	25	18		74
IV	1918	116	63	35	18			291
	1919	122	61	34	19			245
	1920	133	59	32	19			240
	1921	136	55	32	20			356
III	1919	127	65	32				97
	1920	139	61	29				148
	1921	142	59	32				170
	1922	143	59	34				162

If we rearrange the increments of length of Table 38 in such a way that those of the same age groups are brought together as shown in Table 40 they may be compared more rapidly. An examination of this table shows that the 6-year herring hatched in 1916—that is, during a period of slow growth—grew slightly faster in the fourth and fifth years of life (28 and 21 millimeters) than did those of the same age hatched in 1917 and 1918 in the corresponding years (26 and 18 millimeters and 25 and 19 millimeters) and at the same rate in the third, fourth, and fifth years as the 6-year herring hatched in 1919. It shows, also, that the slow-growing fish of the fifth age group grew no faster in the third, fourth, and fifth years than the fast-growing fish of that age group. The fourth and third age groups, however, seem to show a decided compensating growth. In the former age group the order of the succession of the amount of growth of the first year for the four year classes is exactly reversed in the second and third years, while that of the latter age group is reversed in the second year. A further indication of compensation is seen in Table 36, which shows that the difference between the final total lengths of the adults of an age group was, in general, less than that between the computed lengths of the earlier years of these fish. This appears by comparing the 4-year fish of 1918, 1919, 1920, and 1921; but the differences between earlier years seldom were compensated entirely at death. The big juveniles were, on the average, also the big adults, and the slow-growing young fish seldom reached the length of the fast-growing ones in corresponding adult years. Thus, at first sight it seems that the evidence for the law of growth compensation is conflicting for the lake herring.

Table 41.—*Computed average total length and average increment of length for each year of life for each of three size groups of the 4-year herring taken at Bay City, Mich., in 1923. The size groups are based on lengths at the end of the first year of life*

Size group, millimeters	Number of specimens	Average computed length, in millimeters in year—				Average computed increment of length in year—			
		I	II	III	IV	I	II	III	IV
Under 126	73	113	179	219	240	113	66	40	21
126 to 140	85	134	194	225	243	134	60	31	18
Over 140	82	148	201	228	245	148	53	27	17

Note.—The last total length value of each horizontal row is derived from direct measurements of fish.

In spite of the apparently conflicting evidence of the last paragraph, that compensation in growth occurs in the herring seems clear from Table 41. The computed lengths of the first year of the 4-year herring taken in 1923 were divided into three size groups, each group including approximately the same number of fish. The average length of the fish of each size group was then determined for each year of life. From these total lengths the average annual increments were derived. It may be seen from this table that the big yearlings were, on the average, the big fish in all succeeding years, but that the differences between the lengths of the three size groups diminished each year, so that the fish became more uniform in size each successive year of age. Or, as seen from the increments, the smallest yearlings were the fastest growing fish and the largest yearlings the slowest.

We may reverse the procedure employed in Table 41 and divide the actual lengths at death (instead of the computed lengths of the first year) into size groups. We may then average the computed length and increment values of each size group for each year of life, as shown in Table 42. We find on examining these computed values (1) that the large fish of an age group were the large fish in each preceding

year of life, and (2) that, as shown by the increments, the large fish of an age group apparently grew more rapidly in each year of life than the small fish of that age group. The second statement apparently contradicts that based on Table 41, that "the smallest yearlings were the fastest growing fish and the largest yearlings the slowest;" but the seeming contradiction is due to the method of grouping the data of Table 42. In Table 41 the fish were grouped according to the length of the yearlings, irrespective of whether these yearlings grew slowly or fast in later years. The table shows that small yearlings were rapid growers and large yearlings slow growers. In Table 42 the fish were grouped according to the length at death, irrespective of whether they were small or large as yearlings. Because both size groups of an age group of Table 42 consisted of small and large yearlings, the difference between the computed lengths of the first year is consistently less than that between the actual lengths of the fish at death. The table, therefore, warrants only the first statement derived from it and not the contradictory second statement.

Table 42.—*Computed average length and average increment of length for each year of life for each size group of various age groups of Saginaw Bay herring taken in 1922 and 1923*

Year of capture	Age group	Size group, body length, in millimeters, at death	Average length, in millimeters, at end of year—					Average computed increment of length in year—				Number of specimens
			I	II	III	IV	V	I	II	III	IV	
1922	III	Under 230	137	196	222			137	59	26		75
		Over 230	142	203	236			142	61	33		73
	IV	Under 237	121	179	211	229		121	58	32	18	130
		Over 237	123	186	224	243		123	63	38	19	115
	V	Under 240	110				233					45
		Over 240	118				249					50
1923	III	Under 234	139	195	225			139	56	30		79
		Over 234	144	207	241			144	63	34		91
	IV	Under 243	130	188	219	236		130	58	31	17	121
		Over 243	135	195	230	250		135	60	35	20	119
	V	Under 251	113				243					47
		Over 251	126				259					43

Note.—The last total length value of each horizontal row is derived from direct measurements of fish.

It appears, then, that the "law of growth compensation" holds for the lake herring. We found that, on the average, the big yearlings were the big fish in all succeeding years of life, but that the differences between the small and large yearlings diminished each year of age—that is, the small yearlings were rapid growers, the large yearlings slow growers. We also found that the "growth compensation" did not overcome entirely, in their later years, the effect of unfavorable growth conditions to which the Saginaw Bay herring were subjected in 1915–1918.

NORMS OF GROWTH

Lengths.—As suggested at the beginning of this section, in order to obtain the norm of growth in a long-lived species, which is not influenced by seasonal cycles of growth or annual fluctuations in it, we must combine the rates of growth for corresponding ages of all year classes. Such an incomplete general norm, based on direct measurements of fish, is shown near the bottom of Table 34. A complete one, based on the measurements of scales, is shown at the bottom of Table 26. A third, based on both uncorrected computed averages and actual averages, is shown in the grand averages of Table 43. The grand averages of Tables 26, 34, and 43, both total lengths and increments of length, are plotted in Figure 39. Those of Table 43 really represent the average growth rate for the whole period covered by the years 1915 (1914) to 1924, inclusive. The curve plotted from the grand averages of Table 43 shows graphically the average growth of the lake herring during the last 10 years.

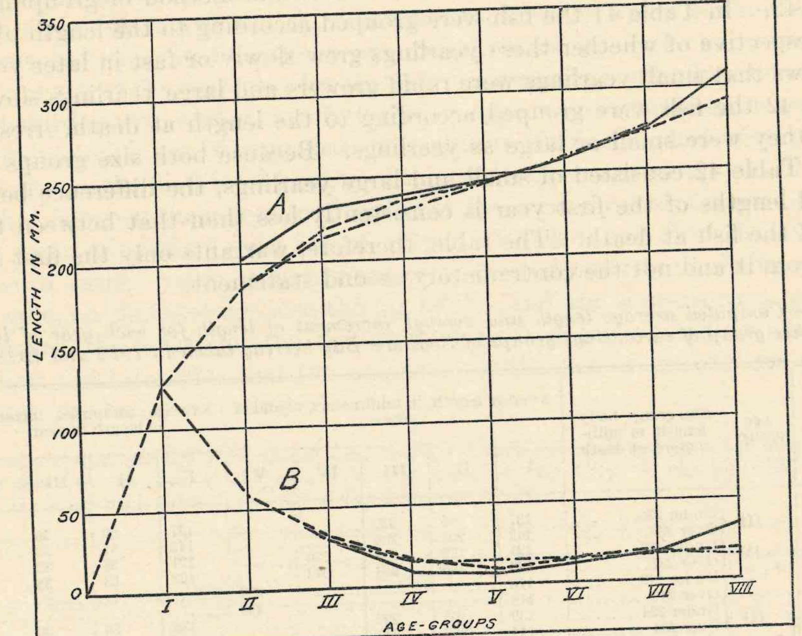

FIG. 39.—Total length and increment in length attained by Saginaw Bay herring at the end of each year of life. A, curves based on grand averages of total lengths: — — —, curve plotted from the grand averages obtained by combining the actual lengths of all fish belonging to the same age group. (See Table 34.) — · —, curve plotted from the grand averages obtained by combining the computed lengths of corresponding years of life of all the available herring of all age groups. (See Table 26.) ————, curve plotted from the grand averages obtained by combining for corresponding years of life the actual and computed lengths of all available herring of all age groups. (See Table 43.) B, curves based on grand averages of annual increments: — — —, curve plotted from grand averages based on actual measurements of fish. (See Table 34.) — · —, curve plotted from grand averages based on computed values. (See Table 26.) ————, curve plotted from grand averages based on actual and computed values. (See Table 43.)

TABLE 43.—*Total average length attained by each year class of Saginaw Bay herring at end of each year of life when uncorrected computed averages are combined with actual averages for corresponding years of life. (Tables 26 and 34 combined.)* [1]

Year class (year of hatching)	Number of individuals	Average length, in millimeters, at end of year—							
		I	II	III	IV	V	VI	VII	VIII
1914	3	107	149	176	206	239	259	277	[2] 292
1915	12	116	161	191	221	242	260	[2] 275	------
1916	67	115	161	192	220	241	[2] 255	------	------
1917	216	115	164	198	224	[3] 240	[3] 251 (11)	[2] 263 (2)	------
1918	401	115	177	211	[3] 231	[3] 242(110)	[2] 263 (15)	------	------
1919	450	122	183	[3] 217	[3] 236 (353)	[3] 250(108)	[2] 267 (18)	------	------
1920	467	132	[3] 192	[3] 224 (462)	[3] 241 (314)	[3] 254 (74)	------	------	------
1921	530	138	[3] 195	[3] 226 (526)	[2] 243 (356)	------	------	------	------
1922	164	143	[3] 203	[2] 236 (162)	------	------	------	------	------
1923	5	113	[2] 190	------	------	------	------	------	------
Grand average lengths	------	127 (2, 315)	185 (2, 315)	218 (2, 299)	235 (1, 722)	244 (590)	258 (126)	274 (17)	292 (3)
Grand average annual increments	------	127	58	33	17	9	14	16	18

[1] Number of specimens employed is given in parentheses.
[2] Based on direct measurement of fish.
[3] Actual and calculated values combined; all unmarked averages are calculated from scales.

The grand averages of Table 43 show that the herring grows very rapidly during the first two years of life. The first sharp break in the curve of total growth (figs. 39 and 40) occurs in the third year—the year during which sexual maturity is first attained by many individuals. If the length at the end of the seventh year is taken as 100 per cent, then at the end of the first year 46.4 per cent, at the end of the second year 67.5 per cent, at the end of the third year 79.6 per cent, at the end of the fourth year 85.8 per cent, at the end of the fifth year 89.1 per cent, and at the end of the sixth year 94.2 per cent of the total growth in length is completed (fig. 40). Otherwise stated, the increment in length of the second year equals 45.7 per cent, of the third year 26 per cent, of the fourth year 13.3 per cent, of the fifth year 7.1 per cent, of the sixth year 11 per cent, of the seventh year 12.6 per cent, and of the eighth

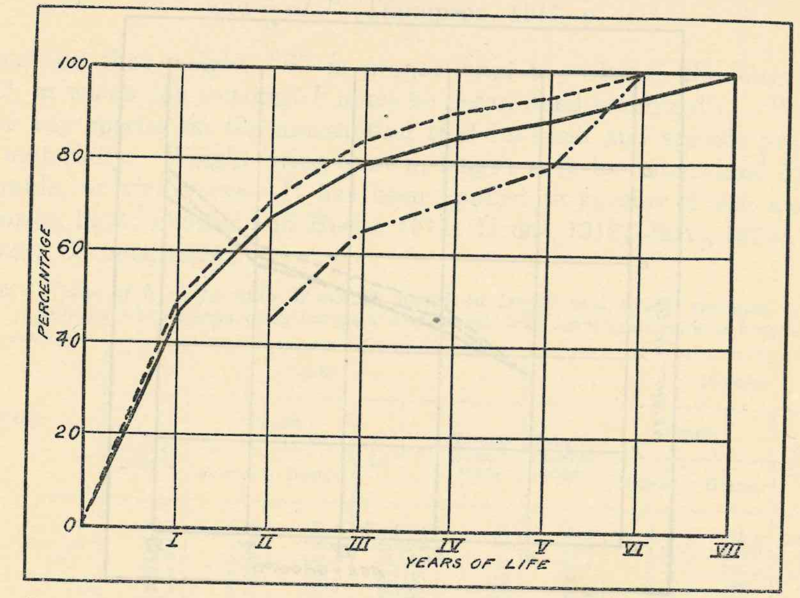

FIG. 40.—Percentage of total growth in length and weight completed at the end of each year of life. The percentages of length are shown on pages 375 to 376 and are derived from the grand averages of Table 43. The percentages of weight are shown on page 376 and are derived from the grand averages of Table 34. — — —, curve based on the average length reached at the end of the seventh year. ————, curve based on the average length reached at the end of the sixth year. — · —, curve based on the average weight attained at the end of the sixth year

year 14.2 per cent that of the first year. After the third year the average yearly increments remain fairly constant, varying from 14 (9) to 18 millimeters in amounts (Table 43).

Weights.—Table 34 furnishes growth data of the herring in terms of weight. The general average weight for each sex is given near the bottom of each column. Curves based on these values are shown in Figure 41. If the total weight at the end of the sixth year is taken as 100 per cent, then at the end of the second year 50.3 per cent, at the end of the third year 64.2 per cent, at the end of the fourth year 73.9 per cent, and at the end of the fifth year 83.9 per cent of the average total weight is attained by the males, while in the females the corresponding values are 46.7, 63.4, 69, and 77 per cent. When the weights of the males and females are combined the percentages at the end of each year are as follows: Year II, 45.4 per cent; year III, 64.7 per cent; year IV, 72.1 per cent; and year V, 79.4 per cent. (Corresponding figures for length, based on year VI are: year I, 49.2 per cent; year II, 71.7 per cent; year III, 84.5 per cent; year IV, 91.1 per cent; and year V, 94.6 per cent; see fig. 40.)

In comparison with length, the rate of the proportional total weight increase is small during the first years of life, for while more than three-fourths of the total length reached by the species is attained at the end of the third year more than five years are required for a similar amount of weight increase. The curves of Figure 40, based on the above percentages, show that after the second year weight increases more rapidly than length. The sudden final acceleration in weight may be due to the small number of individuals in the sixth year. Of course this rapid increase in

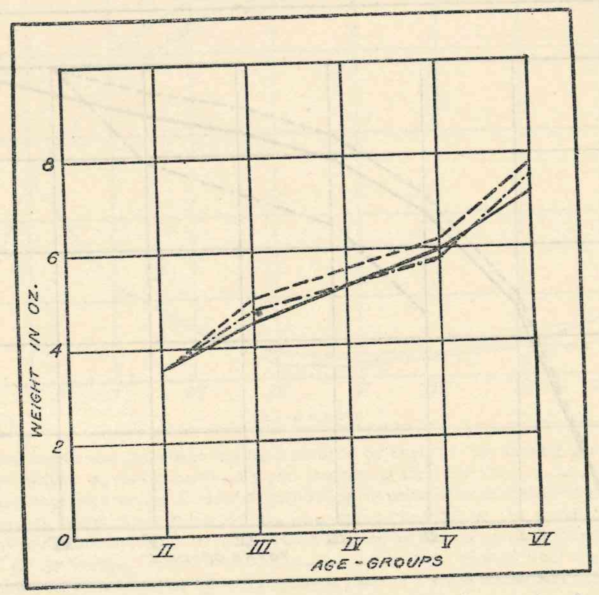

FIG. 41.—Average weight, in ounces, reached by male (— — —) and female (— · —) Saginaw Bay herring in different years of life. The curve based on males and females (————) involves larger numbers of specimens. Curves are plotted from the grand average weights of Table 34

weight is but an expression of the fact that at first these fish grow chiefly along the horizontal axis and are therefore comparatively slender, while later growth occurs principally along the other axes and the body acquires more depth and thickness.

From the point of view of the commercial fisheries it is not profitable to allow the herring, at their present rate of growth, to become much older than 3 or 4 years. The increase in their average weight is about 19.3 per cent in the third but only 7.4 per cent in the fourth and 7.3 per cent in the fifth year; or, stated otherwise, the herring gain on the average 1.50 ounces in the third but only 0.58 and 0.57 ounce in the fourth and fifth years, respectively (Table 34); that is, the increase in weight in the fourth and fifth years together is less than that of the third year alone. If the nets are regulated for the 4-year fish (235 millimeters, or 9.3 inches, long measured snout to base of caudal and 5.61 ounces

in weight), then many herring can spawn twice and a greater number can spawn at least once, thus insuring the perpetuation of the species, provided the number of spawners is not reduced below the number required for the maintenance of the species.

RELATIONSHIP BETWEEN LENGTH AND WEIGHT

"In similar solid figures the surface increases as the square, and the volume as the cube, of the linear dimensions. * * *. And, taking L to represent any linear dimension, we may write the general equations in the form

$$S \alpha L^2,\ V \alpha L^3,$$
$$\text{or } S = k.L^2, \text{ and } V = k^1.L^3;$$
$$\text{and } \frac{V}{S} \alpha L." \text{ (Thompson, 1917, p. 16.)}$$

Assuming that weight (W) is proportional to volume, the formula becomes $W = k.L^3$, in which the constant k must be determined empirically. The formula is valid for any species on the assumption that its form and specific gravity do not change materially. Weight being known, length may be determined by the use of this formula, or vice versa. It has been applied to species of fish and Mollusca. (See Crozier, 1914; Crozier and Hecht, 1914; Hecht, 1916; Järvi, 1920; Weymouth, 1918, 1923; Corbett, 1922.)

TABLE 44.—*Value of k in formula $W = k.L^3$, based on length and weight averages of different age groups, shown separately for male and female lake herring of various lengths*

Age group	Males					Females				
	Length, in centimeters	Weight		$\frac{W}{L^3}$ or k	Number of specimens	Length, in centimeters	Weight		$\frac{W}{L^3}$ or k	Number of specimens
		Ounces	Grams				Ounces	Grams		
II and III	22.2	4.29	121.6	0.011114	14	20.4	3.31	93.8	0.011049	8
III	22.8	4.53	128.4	.010833	78	23.0	4.90	138.9	.011416	70
IV	23.3	5.01	142.0	.011226	29	23.4	5.22	148.0	.011551	93
IV	23.7	5.23	148.3	.011140	149	23.5	5.23	148.3	.011427	13
V	24.1	5.54	157.1	.011223	47	24.1	5.78	163.9	.011709	45
V	25.0	6.52	184.8	.011827	26	24.5	6.00	170.1	.011567	11
VI	25.6	7.02	199.0	.011861	12	26.1	7.56	214.3	.012053	8
Average				.011317					.011538	

TABLE 45.—*Value of k in formula $W = k.L^3$ for lake herring of various lengths and without reference to sex, age, or year classes*

Limits of size group, in centimeters	Average length, in centimeters	Average weight		Number of specimens	Value of $k = (W/L^3)$
		Ounces	Grams		
19.4-21.0	20.4	3.19	90.4	17	0.01064
21.1-22.0	21.7	3.82	108.3	40	.01059
22.1-22.5	22.3	4.51	127.9	61	.01153
22.6-23.0	22.8	4.70	133.2	81	.01123
23.1-23.3	23.2	4.91	139.2	65	.01114
23.4-23.5	23.4	5.05	143.2	46	.01117
23.6-23.8	23.7	5.20	147.4	80	.01107
23.9-24.0	23.9	5.27	149.4	49	.01094
24.1-24.5	24.3	5.65	160.2	74	.01116
24.6-25.0	24.8	6.07	172.1	35	.01128
25.1-25.5	25.3	6.53	185.1	19	.01142
25.6-26.9	26.1	7.23	205.0	25	.01153
27.0+	28.1	9.96	282.4	17	.01272
Average					.01126

Table 44 shows the value of k for male and female lake herring taken in the fall just before spawning. The lengths and weights are the averages for various age groups, as shown in Table 32. The k averages for males (0.01132) and females (0.01154) differ only in the fourth decimal place. In Table 45 age and sex are disregarded, and the values for k are based on size only. The herring were arbitrarily divided into size groups with definite limits, which were selected so that a sufficient number of specimens would be included in the group. Thus, the average, 20.4 centimeters, represents the 17 smallest herring collected; that is, herring 21.0 centimeters

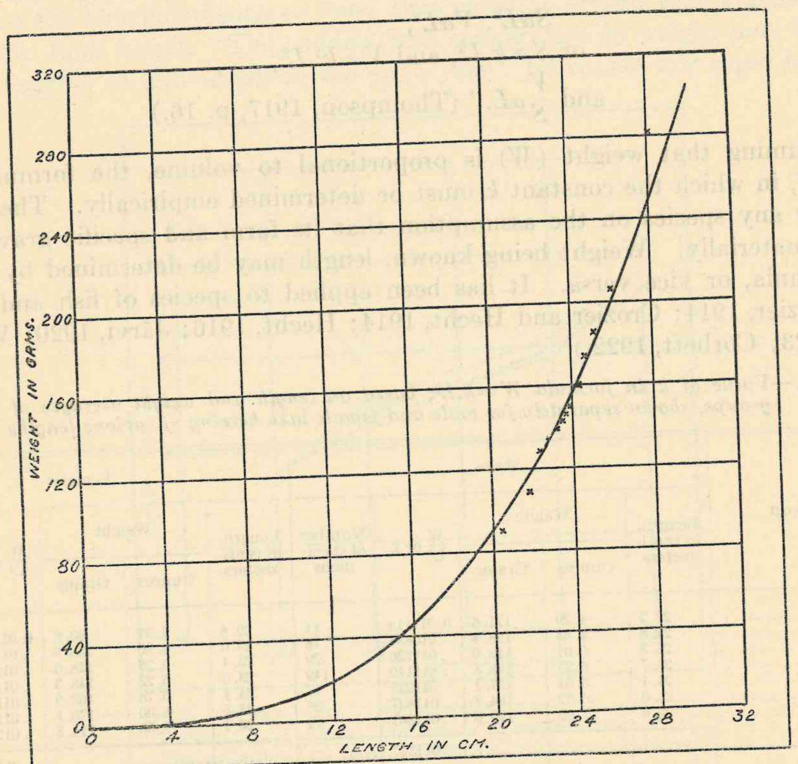

FIG. 46.—Length-weight relationship of Saginaw Bay herring taken in the fall just before spawning. The curve is plotted from theoretical weights computed by means of the length-weight formula $W=k.L^3$, in which $k=0.01126$. The crosses represent actual weights (see Table 46).

or less in length. It may be seen from Table 45 that the value of k changes comparatively little with size, and that the average found for the species is 0.01126.

Substituting this average for the k in the above formula, I computed the theoretical weight of herring of various sizes and compared the calculated values with the actual where possible. These various values are given in Table 46 and plotted in Figure 42. If we exclude the largest size group we find that the average difference between the actual and calculated values amounts to only 2.82 grams. For all fish this difference is 5.10 grams. The crosses in Figure 42 represent actual measurements, the curve the theoretical or calculated values. The agreement between the two

values is very close. It appears, then, that in the lake herring taken just before spawning in the fall of the year the length-weight relationship can be expressed satisfactorily by the formula $W=k.L^3$, in which k has a value of 0.01126.

TABLE 46.—*Comparison of the theoretical weights, computed from the length-weight formula, with actual weights of lake herring*

Length in centimeters	Theoretical weight in grams	Actual weight in grams	Difference, in grams, actual and calculated	Length in centimeters	Theoretical weight in grams	Actual weight in grams	Difference, in grams, actual and calculated
0.8	0.006			22.8	133.458	133.2	−0.26
1.0	.011			23.2	140.606	139.2	−1.41
2.0	.090			23.4	144.273	143.2	−1.07
4.0	.721			23.7	149.894	147.4	−2.49
6.0	2.432			23.9	153.721	149.4	−4.32
8.0	5.765			24.0	155.658		
10.0	11.260			24.3	161.569	160.2	−1.37
12.0	19.457			24.8	171.749	172.1	+.35
14.0	30.897			25.3	182.348	185.1	+2.75
16.0	46.121			26.0	197.906		
18.0	65.668			26.1	200.198	205.0	+4.80
20.0	90.080			28.0	247.180		
20.4	95.594	90.4	−5.19	28.1	249.837	282.4	+32.56
21.7	115.058	108.3	−6.76	30.0	304.020		
22.0	119.897						
22.3	124.869	127.9	+3.03	Average difference			5.10
				Average difference, excluding last figure			2.82

The above k value applies only to the lake herring taken in the fall of the year just before spawning. There is, as D'Arcy Thompson (1914, p. 100) points out, a "regular periodic variation with the course of the seasons" in the value of k, for with unchanging length the weight of the fish falls off after the spawning and winter period. It follows that a study of the fluctuations in the k value through the year furnishes us with a sensitive indicator as to the condition of the fish and as to the season of spawning (its beginning and end) "without ever seeing a fish spawn and without ever dissecting one to see the state of its reproductive system."

RELATIVE ABUNDANCE OF MALES AND FEMALES

Järvi found that of 5,765 individuals of the species *Coregonus albula* L. collected during eight years, 73 per cent were males and 27 per cent females. According to Järvi, Surbeck (1913) obtained similar results for certain Swiss species of the genera Coregonus and Salmo. The latter found that in a large number of *Salmo salvelinus* 72.2 per cent were males and 27.8 per cent were females; but Hefford (1909) found that in the plaice (*Pleuronectes platessa*) both sexes were equally well represented in any large collection. Järvi correlates the relative abundance of the two sexes in his material with Mendel's Law. "All heterozygotes and half of the homozygotes are males, while only the other half of the homozygotes are females. Consequently, the relative abundance of males to females is expressed by the ratio 3:1, or 75 per cent males to 25 per cent females [p. 204]." Gilbert (1922) found that in the sockeye salmon the relative number of males and females may vary with the river basins, the calendar years, the age groups, and with the dates during the course of a season's run. In general, the males showed a decided tendency to precede the females in the spawning migration and to predominate in the annual run. He found that "the relative numbers of males and females in the different year groups is a comparatively constant feature in each river basin" and "thus rises to the dignity of a racial character [p. 17]."

TABLE 47.—*Relative abundance of males and females in samples of lake herring taken at Bay City, Mich., in 1921, 1922, 1923, and 1924*

Year and month of capture	Individuals in age group											
	II			III			IV			V		
	Male and female	Male	Female	Male and female	Male	Female	Male and female	Male	Female	Male and female	Male	Female
1921, October to November	4	2	2	97	48	49	291	163	128	205	118	87
1922, November	4	2	2	148	78	70	244	149	95	95	47	48
1923, November	2	0	2	170	118	52	239	155	84	89	59	30
1924, November to December	1	1	0	403	134	269	660	256	404	150	48	102
Total	11	5	6	818	378	440	1,434	723	711	539	272	267
	Number	*Per cent*	*Per cent*	*Number*	*Per cent*	*Per cent*	*Number*	*Per cent*	*Per cent*	*Number*	*Per cent*	*Per cent*
1921, October to November	4	50.0	50.0	97	49.5	50.5	291	56.0	44.0	205	57.6	42.4
1922, November	4	50.0	50.0	148	52.7	47.3	244	61.1	38.9	95	49.5	50.5
1923, November	2	.0	100.0	170	69.4	30.6	239	64.9	35.1	89	66.3	33.7
1924, November to December	1	100.0	.0	403	33.3	66.7	660	38.8	61.2	150	32.0	68.0
Grand average	11	45.5	54.5	818	46.2	53.8	1,434	50.4	49.6	539	50.5	49.5

Year and month of capture	Individuals in age group											
	VI			VII			VIII			All years II–VIII		
	Male and female	Male	Female	Male and female	Male	Female	Male and female	Male	Female	Male and female	Male	Female
1921, October to November	67	43	24	12	8	4	3	3	0	679	385	294
1922, November	9	5	4	--	--	--	--	--	--	500	281	219
1923, November	15	8	7	2	1	1	--	--	--	517	341	176
1924, November to December	33	12	21	5	2	3	2	1	1	1,254	454	800
Total	124	68	56	19	11	8	5	4	1	2,950	1,461	1,489
	Number	*Per cent*	*Per cent*	*Number*	*Per cent*	*Per cent*	*Number*	*Per cent*	*Per cent*	*Number*	*Per cent*	*Per cent*
1921, October to November	67	64.2	35.8	12	66.7	33.3	3	100.0	0.0	679	56.7	43.3
1922, November	9	55.6	44.4	--	--	--	--	--	--	500	56.2	43.8
1923, November	15	53.3	46.7	2	50.0	50.0	--	--	--	517	66.0	34.0
1924, November to December	33	36.4	63.6	5	40.0	60.0	2	50.0	50.0	1,254	36.2	63.8
Grand average	124	54.8	45.2	19	57.9	42.1	5	80.0	20.0	2,950	49.5	50.5

The upper half of Table 47 shows the number of males and females in each age group of each collection, while the lower half shows the percentage of these numbers in the total number. At the bottom are shown the percentage of males and females in each age group. At the right of the table the number and percentage of males and females in each collection are given, while at the bottom of these figures the percentage of males and females in the entire collection are shown. Table 47 shows that of 2,950 lake herring 49.5 per cent were males and 50.5 per cent females. It is quite evident that the ratio 3 : 1 does not apply to *Leucichthys artedi*. The males predominated in the individual collections of 1921 to 1923, forming from 56.2 to

66 per cent of the sample. In the 1924 sample, however, a sharp and complete reversal in this relative abundance of males occurs. In it 36.2 per cent were males and 63.8 per cent females. This striking change is probably due to the fact that the samples of 1924 were taken later in the season (November 21 to December 4) than those of the years 1921 to 1923 (October 26 to November 12). It is possible that the relative abundance varies, as in the salmon, during the course of the spawning season, the males preceding the females to the breeding grounds. In that case samples taken late in the season would perhaps consist more largely of females.

TABLE 48.—*Percentage of males and females present at various dates during the course of the spawning season, shown for each individual sample of Saginaw Bay herring taken in the years 1921 to 1924*

Date of capture	Locality in Saginaw Bay														
	Tobico			Nayanquing			Gravelly Point			Au Gres			Various unknown localities		
	Total number	Per cent males	Per cent females	Total number	Per cent males	Per cent females	Total number	Per cent males	Per cent females	Total number	Per cent males	Per cent females	Total number	Per cent males	Per cent females
Oct. 26, 27, 1921													296	54.4	45.6
Oct. 29, 1921	266	53.8	46.2												
Nov. 1, 1922	500	56.2	43.8												
Nov. 3, 4, 1921													109	68.8	31.2
Nov. 12, 1923	517	66.0	34.0												
Nov. 21, 1924										117	51.3	48.7			
Nov. 23, 1924	109	34.9	65.1												
Nov. 24, 1924				143	49.7	50.3									
Nov. 25, 1924	156	27.6	72.4												
Nov. 27, 28, 1924	94	24.5	75.5	109	55.0	45.0									
Nov. 30, 1924							354	28.2	71.8						
Dec. 4, 1924							172	34.3	65.7						

In this connection the data of Table 48 are of some interest. Table 48 shows the relative abundance of males and females in each of the individual samples taken in the years 1921 to 1924 on various dates between October 26 and December 4 during the course of the spawning season. It is realized that the percentages of the different years may be only roughly comparable, as the spawning run of different years may not commence or end on the same dates nor continue at the same rate throughout the season and that the percentages may also vary with the localities in the bay. In the Tobico samples (Table 48) the males show a progressive increase in number early in the season but a progressive decrease late in the season. In the Nayanquing and Gravelly Point samples, however, the males show an increase in number as the late season advances. In this respect the data of the 1924 samples conflict. However, the data of Table 48 do seem to show rather consistently that the relative abundance of males and females varies during the course of the spawning run and that the males are more numerous than the females early in the season but less numerous late in the season. (The Oscoda sample, page 388, Table 55, taken early in the season, November 1, 1922, seems to contradict the latter conclusion. In this sample the females were conspicuously preponderant. This was due in part, however, to the large number of immature fish, 70.8 per cent of which were females.)

The percentages of Table 47 show that the relative abundance of males and females also varies with the age groups. The grand averages at the bottom of the table suggest that, in general, the males become relatively more numerous than the females with each higher age group (45.5 to 46.2 to 50.4 to 50.5 to 54.8 to 57.9 per cent). This increasing relative abundance of the males with increasing age indicates that the females of a year class are captured earlier in life than the males. This appears to be substantiated by the data of Table 49, in which the percentages are arranged according to the year class to which the herring belong.[5] From this table it may be seen that when the averages are based on more than 15 specimens, the percentage, with one exception (5 of 1918), of the males increases while that of the females decreases with age. The percentages of the 6 and 7 year fish of 1917 and of the 6-year fish of 1918 are based on too few specimens to be reliable. This early reduction in number of the females of a year class can not be due to the selective effect of the pound nets, as the pots of these nets have such a small mesh (2¼ to 2½ inches, stretched mesh) that all adult herring that get into these pots are retained by them. The only other explanation seems to be that a bigger percentage of the females than of the males of a year class reach sexual maturation for the first time in the third year; that is, the females mature earlier in life than the males, and that consequently more males than females mature for the first time in the fourth and probably fifth years. If this is true, the percentage of the relative abundance of the males of a year class should show a big increase in the fourth age group and should then either remain approximately constant or perhaps show a slight increase in the older age groups. The facts seem to evidence the truth of this theoretical conclusion. The percentage of the males (Table 49) increased 11.6 and 12.2 per cent in the fourth age group but decreased 6.5 per cent in the 1918 year class and increased 5.2 per cent in the 1919 year class in the fifth age group.

TABLE 49.—*Relative abundance of males and females in different age groups of various year classes of Bay City herring* [1]

Year class	Percentage of individuals in year—									
	III		IV		V		VI		VII	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1917					57.6 (205)	42.4	55.6 (9)	44.4	50.0 (2)	50.0
1918			56.0 (291)	44.0	49.5 (95)	50.5	53.3 (15)	46.7		
1919	49.5 (97)	50.5	61.1 (244)	38.9	66.3 (89)	33.7				
1920	52.7 (148)	47.3	64.9 (239)	35.1						

[1] The number in parentheses indicates the total number (male and female) employed.

RELATIVE ABUNDANCE OF SEXUALLY IMMATURE AND MATURE HERRING IN THE SAMPLES AND IN THE GENERAL POPULATION

In sexually immature herring the testes and ovaries consist of narrow, thin, flat strands of soft, whitish material and extend from the anterior to the posterior end of the body cavity along its dorsal wall. In the females the ovaries may contain minute eggs visible to the naked eye. When such a condition exists in a large individual at spawning time it is problematical whether the individual is actually sexually immature or whether it is simply a nonspawning mature fish; that is, a fish that had spawned before but which for some reason had failed to develop its sex products in the year of its capture. In a sexually mature herring the sex products are in an advanced stage of development; both the testes and ovaries are enlarged and partly fill the body cavity.

[5] The 1924 samples are not included in Table 49 because, having been taken late in the season, they are not comparable in this respect with the samples of the preceding years, which were taken relatively early in the season.

In a ripe fish the sex products are easily pressed out of the body. In a spent or spawned fish the gonads are soft and flaccid.

Table 50 shows the proportion of immature male and female fish found in each age group of each collection. The data of this table are arranged like those of Table 47. As the herring samples were taken on the breeding grounds, it is to be expected that a large percentage of each would consist of sexually matured fish. Only 3 per cent of all the herring taken, 1.3 per cent of all the males and 3.3 per cent of all the females, were sexually immature or nonspawning fish. The percentage of nonspawning males varied from 0 to 4.3 per cent in the four collections and females from 1.7 to 7.8 per cent. The higher percentages of both sexes occurred in the year 1922.

TABLE 50.—*Relative abundance of immature and sexually mature males and females in samples of lake herring taken 1921, 1922, 1923, and 1924 at Bay City, Mich.*

Fish captured	Individuals in year—															
	II				III				IV				V			
	Immature		Mature		Immature		Mature		Immature		Mature		Immature		Mature	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Number:																
1921	1	1	1	1	2	3	40	44	1	4	138	103	0	2	82	66
1922	1	2	1	0	7	4	71	66	3	10	146	85	1	1	46	47
1923	0	0	0	2	0	3	118	49	0	0	155	84	0	0	59	30
1924 [1]					2	12	130	255	0	6	256	398	0	0	48	102
Total	2	3	2	3	11	22	359	414	4	20	695	670	1	3	235	245
Total [2]	9		5		48		773		25		1,365		4		480	
Percentage:																
1921	50.0	50.0	50.0	50.0	4.8	6.4	95.2	93.6	0.7	3.7	99.3	96.3	0.0	2.9	100.0	97.1
1922	50.0	100.0	50.0	.0	9.0	5.7	91.0	94.3	2.0	10.5	98.0	89.5	2.1	2.1	97.9	97.9
1923		.0		100.0	.0	5.8	100.0	94.2	.0	.0	100.0	100.0	.0	.0	100.0	100.0
1924 [1]					1.5	4.5	98.5	95.5	.0	1.4	100.0	98.6	.0	.0	100.0	100.0
Average	50.0	50.0	50.0	50.0	3.0	5.0	97.0	95.0	.6	2.9	99.4	97.1	.4	1.2	99.6	98.8
Average	64.3		35.7		5.8		94.2		1.8		98.2		.8		99.2	

Fish captured	Individuals in year—											
	VI				VII				All years, II to VII			
	Immature		Mature		Immature		Mature		Immature		Mature	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Number:												
1921	0	0	30	21	0	0	6	3	4	10	297	238
1922	0	0	5	4					12	17	269	202
1923	0	0	8	7	0	0	1	1	0	3	341	173
1924 [1]	0	0	12	21	0	0	2	3	2	18	448	779
Total	0	0	55	53	0	0	9	7	18	48	1,355	1,392
Total [2]	0		108		0		16		86		2,747	
Percentage:												
1921	0.0	0.0	100.0	100.0	0.0	0.0	100.0	100.0	1.3	4.0	98.7	96.0
1922	.0	.0	100.0	100.0					4.3	7.8	95.7	92.2
1923	.0	.0	100.0	100.0	.0	.0	100.0	100.0	.0	1.7	100.0	98.3
1924 [1]	.0	.0	100.0	100.0	.0	.0	100.0	100.0	.4	2.3	99.6	97.7
Average	.0	.0	100.0	100.0	.0	.0	100.0	100.0	1.3	3.3	98.7	96.7
Average	.0		100.0		.0		100.0		3.0		97.0	

[1] The following immature fish are not included: 1 female (?) and 3 individuals, sex undetermined, of age group II; 2 males (?), 2 females (?), and 11 fish, sex undertermined, of age group III; 1 fish, sex undetermined, of age group IV.
[2] The fish mentioned in footnote 1 included.

As a rule, in a long-lived species of fish the year of age at which sexual maturity is first attained varies more and has a greater range than in a short-lived species. Thus, Thompson (1914) found that about 5 per cent of the 7-year female halibut of the Pacific were sexually mature and that at 12 years of age 50 per cent were mature, while at 15 years 10 per cent were still immature. In my herring samples 94.2 per cent of the fish in their third year, 98.2 per cent in their fourth year, 99.2 per cent in their fifth year, and all older fish were sexually mature. Thus, many of the relatively short-lived Bay City lake herring reach maturity in the third year. Fourteen 2-year fish were taken in my samples. This number is too small to show the percentage of fish that reach sexual maturity in their second year. It indicates, however, that a few fish do so mature and join the schools of breeding fish in this year. A small percentage (0.8) of herring is still sexually immature or at least nonspawning in the fifth year. In the sample of 1923 no immature herring are present in the fourth and older age groups.

It should be emphasized that because the collections were made during the spawning run, the percentages of Table 50 do not show the actual proportion of mature and immature individuals in the general population in all age groups. They show these proportions only for the fish that take part in the spawning run. In this run only about 6 per cent of the 3-year fish were immature. Inspection of Table 30 shows that the percentage of immature herring of the third year must have been much larger than this. It there appears that the fourth age group predominates in each sample for four consecutive years. This can not be due to selective action of the pound nets on fish of the 4-year lengths, for these differ in length by only about 7 millimeters (Table 34) from the 3 and 5 year fish. If we assume that the 3 and 4 year fish captured in 1921 were in all respects representative samples of the general population and that there is no selective death rate, they should have reappeared as 4 and 5 year fish in the catch of 1922 in the same proportion as they occurred as 3 and 4 year fish in that of 1921. In that case the 5-year class of 1922 would have been larger than the 4-year class. It is, in fact, much smaller. It seems, then, that before the 3-year fish of the spawning run of 1921 entered the run of 1922 their number was greatly augmented. That is, many immature fish from the general population of the 3-year class of 1921 were added to the spawning run of 1922 as mature 4-year fish. It is this annual addition that results in the predominance of the 4-year fish in the samples of all years. As fewer fish attain sexual maturity for the first time in their fifth year than in their fourth, the 5-year group would be composed chiefly of fish that escaped the nets or death from other causes in their fourth year, and this would then result in the consistant smaller representation of the 5-year group each year. That some individuals attain sexual maturity for the first time in their fifth year seems probable from the fact that the 4 and 5 year herring do not reappear as 5 and 6 year fish, respectively, in the same relative abundance. Unless we postulate, as we did with the 3 and 4 year fish, that the 5-year class is augmented by individuals that were sexually immature in their fourth year, we can hardly explain why the 4-year fish are, on the average, about twice (2.2 times) as abundant as the 5-year fish, but when reappearing as 5-year individuals the former are about seven times as abundant as the latter, which reappear as 6-year fish. (Compare the number of individuals of the lower half of Table 30.) Table 30 shows, further, that the 5 and 6 year fish reappear as 6 and 7 year fish, respectively, in approximately the same relative abundance, which indicates that virtually no herring reach sexual maturity for the first time in the sixth year of life. (The general conclusion that the percentage of imma-

ture herring in the third and older age groups is greater than that suggested in Table 50 seems substantiated by the data of the Oscoda herring, page 388, Table 55. The percentages of immature fish, especially for age Groups III and IV, are considerably larger in the Oscoda sample than in any of the samples taken at Bay City. The Oscoda herring apparently had not yet been completely segregated into spawning and nonspawning fish.) To obtain accurate values for the relative abundance of sexually immature and mature fish of the general population in an age group we must determine the component year classes and age groups of schools of immature fish and follow them for several consecutive years.

COMPARISON OF SAMPLES OF HERRING TAKEN IN 1924 AT THE SAME LOCALITY IN SAGINAW BAY BUT ON DIFFERENT DATES

In Tables 51 and 52 the individual herring samples of a single locality in Saginaw Bay are compared, one with the other, in order to ascertain if possible whether the characteristics of a sample vary in any one direction with the advance of the season; that is, to determine whether samples taken on different dates are comparable. In Table 51 the range in length, the modal length, the average length of the sample, the average actual length of each age group, and the relative abundance of each age group are compared; in Table 52 the computed lengths for each year of life of corresponding age groups are compared. The Tobico samples show virtually no differences in the range in length or the average size of the sample, and while the actual and the computed lengths of the age groups and the percentages of abundance vary with the samples, these variations are not consistent. The range in length and the age composition are virtually the same in the two Nayanquing samples. The herring taken on November 27 tend to average somewhat less in length than those taken on November 24, although the computed growth rates of the two series of fish are virtually identical (Table 52). In the two Gravelly Point samples the age composition is very similar; the range in length is considerably less in the herring taken December 4 than in those taken November 30. The modal length and the average size of the former fish exceed those of the latter. This, however, is due entirely to the small 3-year fish taken on November 30. The growth rates of the 4 and 5 year fish are virtually identical for corresponding years of life.

TABLE 51.—*Range in length, modal length, average length of sample, average actual length of each age group, and percentage of abundance of each age group for each individual sample of herring taken in 1924 on different dates at Tobico, Nayanquing, and Gravelly Point in Saginaw Bay* [1]

Locality in Saginaw Bay	Date of capture in 1924	Range in length	Modal length	Average length, in millimeters, of sample	Average actual length, in millimeters, of age group				Percentage of sample in age group					
					III	IV	V	VI	II	III	IV	V	VI	VII
Tobico	Nov. 23	215-299	[2] (?)	244(109)	231 (27)	246 (69)	258 (9)	264 (4)	0.0	24.8	63.3	8.3	3.7	----
Do	Nov. 25	211-296	(?)	245(156)	237 (50)	244 (83)	252(21)	256 (2)	.0	32.1	53.2	13.5	1.3	----
Do	Nov. 27, 28	220-306	(?)	243 (94)	237 (21)	239 (52)	254(15)	269 (6)	.0	22.3	55.3	16.0	6.4	----
Difference between extremes				2	6	7	6	13	----	9.8	10.1	7.7	5.1	----
Nayanquing	Nov. 24	215-304	(241-245)	244(143)	239 (38)	243 (89)	259(13)	283 (3)	.0	26.6	62.2	9.1	2.1	----
Do	Nov. 27	210-295	(231-235)	241(108)	233 (26)	242 (63)	250(16)	257 (3)	.9	23.9	57.8	14.7	2.8	----
Difference between extremes				3	6	1	9	26	----	2.7	4.4	5.6	.7	----
Gravelly Point	Nov. 30	160-361	(231-235)	238(367)	225(144)	242(164)	266(39)	261(11)	1.1	39.2	44.7	10.6	3.0	1.1
Do	Dec. 4	208-365	(241-245)	244(175)	234 (57)	243 (84)	260(30)	267(3)	.0	32.6	48.0	17.1	1.7	.0
Difference between extremes				6	9	1	6	6	----	6.6	3.3	6.5	1.3	----

[1] The number of specimens employed is shown in parentheses.
[2] The mode could not be determined for the Tobico samples as in each sample two or three size classes included the greatest number of individuals.

TABLE 52.—*Comparison of computed lengths of each year of life of corresponding age groups of herring collected at same locality but on different dates*

Locality in Saginaw Bay	Date of capture in 1924	Age group	Number of fish	Average computed length, in millimeters, for year of life				
				I	II	III	IV	V
Tobico	Nov. 23	III	27	145	202	[1] 231		
Do	Nov. 25	III	50	143	204	237		
Do	Nov. 27, 28	III	21	142	201	237		
Do	Nov. 23	IV	69	138	194	226	246	
Do	Nov. 25	IV	83	134	191	224	244	
Do	Nov. 27, 28	IV	52	139	191	221	239	
Do	Nov. 23	V	9	116	178	214	239	258
Do	Nov. 25	V	21	116	177	210	235	252
Do	Nov. 27, 28	V	15	119	179	212	238	254
Nayanquing	Nov. 24	III	38	144	202	239		
Do	Nov. 27	III	26	142	201	233		
Do	Nov. 24	IV	89	137	192	225	243	
Do	Nov. 27	IV	63	136	191	222	242	
Do	Nov. 24	V	13	118	178	212	238	259
Do	Nov. 27	V	16	118	175	209	233	250
Gravelly Point	Nov. 30	III	144	138	193	225		
Do	Dec. 4	III	57	144	201	234		
Do	Nov. 30	IV	164	133	190	221	242	
Do	Dec. 4	IV	84	133	191	224	243	
Do	Nov. 30	V	39	120	183	218	244	266
Do	Dec. 4	V	30	123	183	220	242	260

[1] The last value of each horizontal row represents actual measurements of fish.

The data of Tables 51 and 52 indicate that no consistent differences in size, rate of growth, and age composition occurred in the 1924 herring samples taken at the same locality but on different dates. There are no indications in these tables that the character of the herring stock of one locality changed during that period of the spawning run under consideration. The computed values of length of Table 52 furnish the most convincing evidence. The fluctuating differences that do occur may, no doubt, be attributed to random sampling.

COMPARISON OF SAMPLES OF HERRING TAKEN IN 1924 AT DIFFERENT LOCALITIES IN SAGINAW BAY

Since the 1924 samples of herring taken at one locality in Saginaw Bay are comparable, they may be treated as a unit collection. Are the samples taken in different parts of Saginaw Bay also comparable? Or is the Saginaw Bay herring population composed of various races, each of which remains segregated and spawns on its own particular breeding grounds in the bay? To obtain some light on this subject Tables 53 and 54 were constructed. In these the data of the herring of a given locality in the bay, shown in the two preceding tables, are combined, Table 53 summarizing the data of Table 51 and Table 54 those of Table 52 on computed lengths.

TABLE 53.—*Range in length, modal length, average length of samples, and average actual length of each age group for the combined samples of herring taken at Tobico, Nayanquing, Au Gres, and Gravelly Point in Saginaw Bay* [1]

Locality in Saginaw Bay	Dates of capture in 1924	Range in length	Modal length	Average length, in millimeters, of samples	Average actual length, in millimeters, of age group—			
					III	IV	V	VI
Tobico	Nov. 23, 25, 27, 28	211–306	(?)	244 (359)	236 (98)	243 (204)	254 (45)	267 (15)
Nayanquing	Nov. 24, 27	210–304	(241–245)	243 (251)	237 (64)	243 (152)	254 (29)	
Au Gres	Nov. 21	210–295	(236–240)	240 (119)	233 (53)	243 (57)	255 (7)	
Gravelly Point	Nov. 30, Dec. 4	160–365	(231–235)	240 (542)	227 (201)	243 (248)	264 (69)	262 (14)
Difference between extremes				4	10	0	10	5

[1] The number of specimens employed is shown in parentheses.

TABLE 54.—*Comparison of computed lengths of each year of life of corresponding age groups of herring collected at various localities in Saginaw Bay*

Locality in Saginaw Bay	Dates of capture in 1924	Age group	Number of fish	Average computed length, in millimeters, for year of life—					
				I	II	III	IV	V	VI
Tobico	Nov. 23, 25, 27, 28	III	98	144	203	[1] 236			
Nayanquing	Nov. 24, 27	III	64	143	202	237			
Au Gres	Nov. 21	III	53	140	200	233			
Gravelly Point	Nov. 30, Dec. 4	III	201	140	196	227			
Tobico	Nov. 23, 25, 27, 28	IV	204	136	191	223	243		
Nayanquing	Nov. 24, 27	IV	152	136	192	224	243		
Au Gres	Nov. 21	IV	57	131	188	223	243		
Gravelly Point	Nov. 30, Dec. 4	IV	248	133	190	222	243		
Tobico	Nov. 23, 25, 27, 28	V	45	117	178	212	237	254	
Nayanquing	Nov. 24, 27	V	29	118	177	210	235	254	
Au Gres	Nov. 21	V	7	117	171	202	233	255	
Gravelly Point	Nov. 30, Dec. 4	V	69	121	183	218	243	264	
Tobico	Nov. 23, 25, 27, 28	VI	15	117	174	206	233	253	267
Gravelly Point	Nov. 30, Dec. 4	VI	14	112	166	200	227	248	262

[1] The last value of each horizontal row represents actual measurements of fish.

Examination of Tables 53 and 54 shows that beyond any question the Tobico and Nayanquing herring belong to the same general population. The range in length, the average size of the sample, and the average actual and computed lengths of the age groups are virtually identical in the two collections. The modal and the average length of the Au Gres and the Gravelly Point herring are somewhat less than those of the Tobico and the Nayanquing fish. Examination of the actual lengths of Table 53, however, shows that this decrease in size is due entirely to the small average size of the 3-year fish. Those of Gravelly Point are noticeably small. As stated on page 385 the small size of these fish is due to the 3-year individuals taken November 30 (Table 51). The 3-year herring taken at Gravelly Point on December 4 reached about the same average length as those taken at Tobico, Nayanquing, and Au Gres (Tables 51 and 53). Mr. Brackenbury, a fisherman who has fished at Gravelly Point for the last 32 years, states that large numbers of small herring come on late in the fall after the main run of herring is over. This late run, he states, is composed principally of males. Our November 30 sample may include part of such a late run, although the 3-year fish of this sample are mostly females (75.6 per cent). The differences in length between the 3-year herring from Gravelly Point and those from the other localities considered are no greater than these differences between the 3-year fish taken at Gravelly Point on different dates.

No striking differences exist in the computed growth rates and lengths of the 4-year fish of the four localities under consideration; but the 5-year herring from Gravelly Point seemed to have had a faster rate of growth than those from the three other localities, while the 6-year fish from Gravelly Point appeared to have grown less rapidly than those from Tobico. The differences are not consistent.

The data of Tables 53 and 54 show that the Tobico, Nayanquing, and Au Gres herring undoubtedly belong to the same general population. The data of the Gravelly Point herring are not conclusive but they suggest that in all probability the Gravelly Point fish are not different from those taken farther south in the bay. On the basis of growth rate we apparently can not separate the herring population of Saginaw Bay into distinct races.

VARIATIONS IN RATES OF GROWTH OF HERRING FROM DIFFERENT LOCALITIES IN LAKE HURON

The discussion so far has involved only the herring taken in Saginaw Bay, the principal herring grounds of Lake Huron; but it is of extreme interest and of economic importance to compare the Saginaw Bay herring with those of other localities, especially as regards their rate of growth, for a difference in rate of growth of herring in different localities might afford evidence of local races. The only material at present available for this comparative study is that collected by Doctor Koelz in 1917 and 1919 and by me at Oscoda, Mich., in 1922. This material does not include, for the present study, an adequate number of individuals for all the localities at which collections were made. (See Table 1.)

TABLE 55.—*Range in length, modal length, average length of sample, percentage of abundance of each age group, percentage of males and females in each age group, and percentage of immature and mature fish in each age group for herring taken November 1, 1922, at Bay City, and November 2, 1922, at Oscoda, Mich.*[1]

Locality	Range in length	Modal length	Average length of sample in millimeters	Percentage of abundance of age group					Percentage of males and females in age group—							
				II	III	IV	V	VI	III		IV		V		VI	
									Male	Female	Male	Female	Male	Female	Male	Female
Bay City	201–285	236–40	235 (501)	0.8	29.5	48.9	19.0	1.8	52.7	47.3	61.1	38.9	49.5	50.5	55.6	44.4
Oscoda	176–295	231–35	228 (362)	5.2	39.5	42.3	11.9	1.1	30.6	69.4	37.1	62.9	27.9	72.1	50.0	50.0

Locality	Percentage of immature and mature fish in age group—											
	II		III		IV		V		VI		II–VI	
	Immature	Mature	Immature	Mature	Immature	Mature	Immature	Mature	Immature	Mature	Immature	Mature
Bay City	75.0	25.0	7.4	92.6	5.3	94.7	2.1	97.9	0	100	5.8	94.2
Oscoda	94.7	5.3	39.4	60.6	12.3	87.7	4.7	95.3	0	100	26.4	73.6

[1] The number of specimens employed is shown in parentheses.

TABLE 56.—*Comparison, for corresponding age groups, of computed lengths and increments in length of each year of life of Bay City (Tobico) herring collected November 1, 1922, with those of Oscoda herring taken November 2, 1922*

Locality	Year class	Age group	Number of fish	Average computed length, in millimeters, of year of life—						Average computed increment, in millimeters, for year of life—					
				I	II	III	IV	V	VI	I	II	III	IV	V	VI
Bay City	1917	VI	9	117	161	198	224	242	[1] 252	117	44	37	26	18	10
Oscoda	1917	VI	4	99	138	167	194	212	235	99	39	29	27	18	23
Bay City	1918	V	95	114	171	205	229	241	-----	114	57	34	24	12	-----
Oscoda	1918	V	43	113	166	198	223	239	-----	113	53	32	25	16	-----
Bay City	1919	IV	245	122	183	217	236	-----	-----	122	61	34	19	-----	-----
Oscoda	1919	IV	153	114	175	210	231	-----	-----	114	61	35	21	-----	-----
Bay City	1920	III	148	139	200	229	-----	-----	-----	139	61	29	-----	-----	-----
Oscoda	1920	III	143	127	192	225	-----	-----	-----	127	65	33	-----	-----	-----
Bay City	1921	II	4	141	217	-----	-----	-----	-----	141	76	-----	-----	-----	-----
Oscoda	1921	II	19	140	203	-----	-----	-----	-----	140	63	-----	-----	-----	-----

[1] The last total length of each horizontal row is based on direct measurements of fish.

The Oscoda sample taken in 1922, however, is fairly representative, and it is of interest to compare this sample somewhat in detail with the one taken at approximately the same time at Bay City (Tobico). Table 55 compares the two samples with respect to range in length, modal length, average length of the sample, percentage abundance of each age group, percentage of males and females in each age group, and percentage of immature and mature fish in each age group, while Table 56 compares the computed and actual total lengths and the computed increments of length of corresponding age groups of the two samples. The first striking difference between the two series of herring to be noted in Table 55 is in the age composition. The 2 and 3 year fish (especially the former) are much better represented in the Oscoda collection (5.2 and 39.5 per cent) than in the Bay City sample (0.8 and 29.5 per cent). The second marked difference is in the relative abundance of males and females. In every age group the males are relatively much more numerous in the Bay City sample than in that from Oscoda. The males preponderate in the former collection, the females in the latter. The third noticeable difference is in the percentage of immature and mature fish. The percentages of immature fish in age groups II to V, inclusive, in the Bay City herring are, respectively, 75, 7.4, 5.3, and 2.1; in the Oscoda fish 94.7, 39.4, 12.3, and 4.7, respectively. In general, 5.8 per cent of all the Bay City herring under consideration were nonspawning or sexually immature, while, 26.4 per cent of all the Oscoda fish were nonspawning. This third difference is especially significant as it probably accounts for all the other differences that may exist between the two samples of herring compared.

The Oscoda sample evidently represents an earlier stage in the spawning run than does the sample from Bay City, although both collections were made at approximately the same time. The schools of herring at Oscoda apparently had not yet been as completely segregated into spawning and nonspawning fish by November 1 as those found at Tobico. On this basis it is to be expected that the 2 and 3 year fish would be more abundant in the Oscoda collection than in the Tobico sample. Most of the Oscoda nonspawning fish whose sex could be determined were females (70.8 per cent). This probably explains, at least in part, why the females were so preponderant in the Oscoda age groups. Computations show that the nonspawners of an age group average less in length than the spawners of that age group. I found for the Oscoda herring that in the third age group 54 immature individuals averaged 222 millimeters in length, while 83 mature specimens averaged 228 millimeters, and that in the fourth age group 18 nonspawning fish averaged 220 millimeters in length, while 131 spawners averaged 233 millimeters. A priori, the Oscoda herring should then have a greater range in length but smaller average lengths than the Tobico fish. Tables 55 and 56 show this to be true. In the Oscoda fish the range in length is greater, but the modal and average lengths of the sample as well as the average actual and computed lengths of the age groups are less than in the Tobico fish. The increments of Table 56 show that these smaller total lengths of the Oscoda herring are due to the growth rate of either the first or second year of life. The 5-year specimens of the two samples did not grow at very different rates (the 6-year fish are too few in number to be considered). The nonspawners were too few in number to affect the growth rates of these age groups. The 4 and 3 year fish of Oscoda grew less in the first year of life but as rapidly as or faster in the later years of life than the corresponding age groups from Tobico. The 2-year herring, which in both samples were principally immature fish, grew at the same rate in the first year; in the second year the Oscoda fish grew the more slowly.

TABLE 57.—*Average actual and computed total lengths and average computed increments of length for sexually mature III and IV year herring taken in 1922 at Bay City and Oscoda, Mich.*[1]

Locality	Year class	Age group	Number of fish	Average computed length, in millimeters, of year of life—				Average computed increment, in millimeters, for year of life—			
				I	II	III	IV	I	II	III	IV
Bay City	1919	IV	230	123	183	218	237	123	60	35	19
Oscoda	1919	IV	128	113	175	211	233	113	62	36	22
Bay City	1920	III	137	141	201	230	-------	141	60	29	-------
Oscoda	1920	III	83	131	196	228	-------	131	65	32	-------

[1] The last total length value of each horizontal row is based on direct measurements of fish.

As many more nonspawners are included in the third and fourth age groups of the Oscoda sample than in those of the Bay City collection, the corresponding growth rates for these age groups, shown in Table 56, are not strictly comparable. Table 57, therefore, compares these rates of growth for the mature fish only. The results are not radically different from those obtained above. In both age groups (Table 57) the Bay City herring exceed the Oscoda fish in size. In both age groups this is due solely to the growth rate of the first year of life. In the later years of life the Oscoda herring grew faster than those from Bay City.

The samples of herring from the other localities on Lake Huron are too small in any single year to permit of detailed comparisons. However, they may furnish some information on the general growth rates of the herring of these localities. To give a greater number of specimens from each locality, collections made at the same locality in different years are combined and treated as a unit. Table 58 shows the average length in millimeters as determined by actual measurements of fish, of the individuals of each of the age groups comprising the samples taken at 12 localities. Of these 12 localities, Bay City and Oscoda alone are adequately represented by sufficient material. The Alpena, St. Ignace, Killarney, Wiarton, and possibly East Tawas samples may be adequate for a comparative study of growth. Especially may this be true when

the calculated lengths of these fish, as shown in Table 59, are employed. In Table 59 are given the computed average lengths, as determined from measurements of scales, for each year of life. To obtain these averages, I computed the lengths for each year of life of all the year classes of a sample and then averaged these lengths of corresponding years of all year classes. In this way some comparable general norms of growth of the herring of the several localities are obtained. A variable error, due to the "apparent change in growth rate," is introduced into the averages by this method; but as each sample considered consists of approximately the same age groups, the

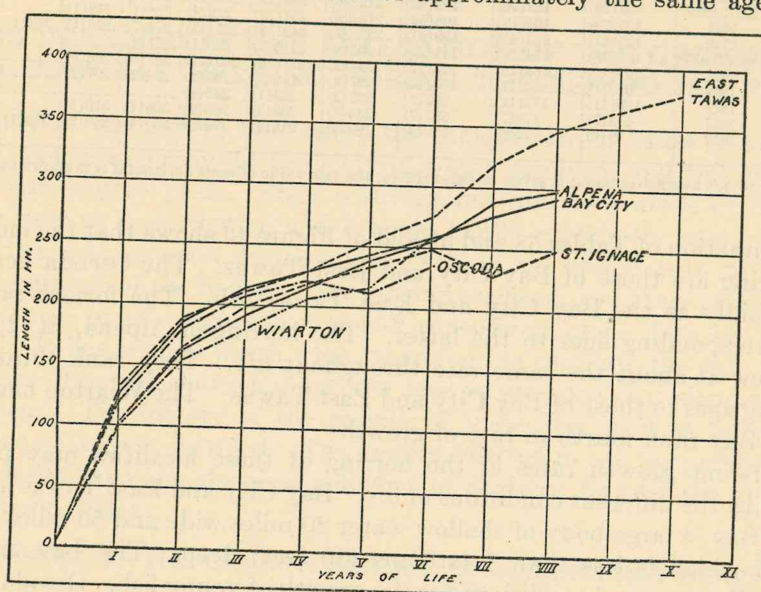

FIG. 43.—Showing the total length attained at the end of each year of life by lake herring taken at various ports on Lake Huron. The curves are plotted from the computed lengths of Table 59

averages are still roughly comparable. Considering the number of specimens employed for each locality, the averages of length are at best approximate. The computed total lengths of the herring of the above-mentioned localities are plotted in Figure 43. (For location of each port see fig. 1.)

TABLE 58.—*Average total length, as determined by actual measurements of fish, attained at end of each year of life by lake herring collected at various ports on Lake Huron* [1]

Locality	Year of capture	Number of individuals	Average length, in millimeters, of fish at end of year—										
			I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Bay City	1921–1924	2,321	------	202(16)	231(577)	239(1,132)	245(464)	257(109)	275(18)	309(5)	------	------	------
East Tawas	1917	25	------	------	230(8)	233(9)	250(6)	------	270(1)	------	------	377(1)	------
Oscoda	1922	362	------	203(19)	225(143)	231(153)	239(43)	235(4)	------	------	------	------	------
Alpena	1917, 1919	74	108(1)	167(3)	208(12)	215(19)	237(15)	257(14)	262(7)	296(3)	------	------	------
St. Ignace	1917	70	------	------	206(18)	219(23)	233(17)	246(8)	268(3)	249(1)	------	------	------
Killarney	1919	41	------	------	------	217(14)	243(9)	257(5)	275(6)	284(6)	302(1)	------	------
Wiarton	1917, 1919	33	------	161(4)	197(6)	203(15)	223(5)	219(2)	277(1)	------	------	------	------
Mindemoya	1917	12	------	------	------	------	------	287(1)	296(6)	296(5)	------	------	------
Duck Islands	1919	11	------	------	195(1)	208(1)	241(5)	256(2)	------	291(2)	------	------	------
Harbor Beach	1917	11	------	------	215(2)	225(7)	208(1)	245(1)	------	------	------	------	------
Cheboygan	1917	7	------	------	------	233(1)	268(3)	219(1)	284(1)	310(1)	------	------	------
Blind River	1917	6	------	------	------	------	------	------	258(2)	268(2)	264(1)	------	269(1)

[1] Number upon which an average is based is shown in parentheses. Some of the averages may be a little too low, as some of the fish were captured in late summer or early fall and therefore did not complete their last growth year. See Table 1 for the dates of capture.

TABLE 59.—*Total length attained at end of each year of life by lake herring taken at various ports on Lake Huron. Each average is based on uncorrected computed lengths of several year classes* [1]

Locality	Year of capture	Calculated length, in millimeters at end of year—										
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Bay City	1921–1924	127 (2, 313)	185 (2, 302)	213 (1, 725)	228 (593)	243 (129)	258 (17)	277 (3)	292 (3)	------	------	------
East Tawas	1917	131 (25)	188 (25)	211 (17)	228 (8)	255 (2)	275 (2)	320 (1)	347 (1)	364 (1)	377 (1)	------
Oscoda	1922	120 (362)	180 (343)	207 (200)	220 (47)	212 (4)	235 (4)	------	------	------	------	------
Alpena	1917, 1919	103 (73)	163 (70)	192 (58)	215 (39)	238 (24)	255 (10)	288 (3)	296 (3)	------	------	------
St. Ignace	1917	103 (70)	165 (70)	198 (52)	218 (29)	234 (12)	249 (4)	228 (1)	249 (1)	------	------	------
Killarney	1919	105 (41)	163 (41)	199 (41)	225 (27)	242 (18)	261 (13)	274 (7)	296 (1)	302 (1)	------	------
Wiarton	1917, 1919	101 (33)	154 (29)	181 (23)	205 (8)	216 (3)	259 (1)	277 (1)	------	------	------	------
Mindemoya	1917	107 (12)	188 (12)	223 (12)	254 (12)	271 (12)	282 (11)	287 (5)	296 (5)	------	------	------
Duck Islands	1919	92 (11)	154 (11)	193 (10)	227 (9)	248 (4)	267 (2)	281 (2)	291 (2)	------	------	------
Harbor Beach	1917	120 (11)	173 (11)	203 (9)	201 (2)	223 (1)	245 (1)	------	------	------	------	------
Cheboygan	1917	113 (7)	170 (7)	207 (7)	235 (6)	238 (3)	285 (2)	308 (1)	310 (1)	------	------	------
Blind River	1917	98 (6)	142 (6)	170 (6)	199 (6)	218 (6)	235 (6)	245 (4)	249 (2)	252 (1)	260 (1)	269 (1)

[1] Number upon which average is based is given in parentheses; the last value of each horizontal row shows the actual length when captured.

An examination of Tables 58 and 59 and of Figure 43 shows that the most rapidly growing herring are those of Bay City and East Tawas. The Oscoda herring grew nearly as rapidly as the Bay City and East Tawas fish. The former rank second in size at corresponding ages to the latter. The herring of Alpena, St. Ignace, and Killarney grew at about the same rate throughout life. They rank third in size at corresponding ages to those of Bay City and East Tawas. The Wiarton herring taken in Georgian Bay rank fourth in rate of growth.

The different growth rates of the herring of these localities may possibly be correlated with the different conditions of life. Bay City and East Tawas are situated on Saginaw Bay, a large body of shallow water 20 miles wide and 50 miles long, more than half of which is less than 5 fathoms (30 feet) deep. The bay undoubtedly provides excellent natural conditions for the growth of young fish. Oscoda is situated about 15 miles north of East Tawas just outside of Saginaw Bay. The herring of Alpena, situated on Thunder Bay, presumably are confined in early life to a much smaller area of shallow water than those of Saginaw Bay and are more exposed to the colder waters of the lake proper. In fact, many of the Alpena herring spawn and live in the unprotected waters of Lake Huron. St. Ignace, on the Straits of Mackinac, and Killarney, on the North Channel, are situated in the most northern part of Lake Huron. Herring of these localities probably are subjected to colder waters than are those of Saginaw Bay; the growing season of the former may also be shorter. The Wiarton herring presumably are most restricted in their range. As may be seen from the map (fig. 1), the 20-fathom contour line, beyond which herring seldom occur near the bottom, lies very near the shore line along the entire west coast of Georgian Bay from Owen Sound north to Tobermory Light. A study, then, of the general hydrographic features of each of the above localities alone would lead us to expect that Saginaw Bay would produce the fastest growing herring and Wiarton the slowest growing.

This incomplete comparative study shows at least two things: (1) That there may be distinct races of herring in Lake Huron or, at any rate, that there are distinct differences between the growth rates of the herring of certain localities in Lake Huron, and (2) that Saginaw Bay produces, so far as known, the most rapidly growing herring in Lake Huron.

The above data suggest that the migrations of the herring are more or less local. If the lake herring of two localities intermingled, their growth rates should be the same. The different growth rates indicate that at least the majority of the herring of the Saginaw Bay district keep apart from those of the Alpena district, and vice versa, and that the Wiarton herring do not intermingle with those of Killarney in Georgian Bay.

FACTORS INVOLVED IN THE ALTERATION OF THE GROWTH RATE OF SAGINAW BAY HERRING DURING THE PERIOD 1915 TO 1923

A study of the factors that affect the growth rate of fishes in nature usually requires a biological survey of the body of water involved, and this should cover a period of consecutive years. Such a survey has not been made of Saginaw Bay, and if one were to be carried on now it could hardly explain the past growth history of its herring; but we know during which years of the period 1915 to 1923 acceleration in the growth of the Saginaw Bay herring occurred, and there are certain factors that are known to affect growth rate and concerning which data are available for the period. It has seemed worth while, therefore, to correlate the data on these factors with the observed changes in growth rate in the hope that significant relations would appear. The history of the growth of these herring is so unique that any attempt to explain it is justified. The factors referred to are temperature and light, fishing intensity, and the chemical pollution of Saginaw Bay by the Dow Chemical Co. of Midland, Mich.

RÉSUMÉ OF THE GROWTH HISTORY OF SAGINAW BAY HERRING

The significant facts of growth already discussed are the following: [6]

1. In each of the years 1915 to 1918, inclusive, the rate of growth of herring in the first year of life was the same.

2. In the year 1919 the growth rate was increased in herring 1, 2, and 3 years of age.

3. Neither in 1919 nor subsequently did the growth rate of fish older than 3 years increase.

4. The acceleration of growth rate initiated in 1919 in fish 3 years of age and younger continued in the years 1920, 1921, and 1922.

5. In the period 1919 to 1922, inclusive, fish in their first year of life, in general, grew more rapidly each successive year. During this period there was progressive increase of growth rate in 1-year fish, although in 1922 the increase was very slight (1 millimeter).

6. During the period 1919 to 1923, inclusive, the growth rate of the second and third year fish did not increase in successive years but remained virtually constant at the increased rate attained in 1919.

7. The growth rate for the fourth and later years likewise tended to remain constant in the years 1919 to 1924, inclusive.

[6] For each statement refer to Table 39.

The accelerated growth rate of young fish in 1919 and later years presumably was due to some improvement in growth conditions. Conditions relatively unfavorable to the growth of fish of the first three years apparently were present during the years 1915 to 1918, inclusive, and conditions became favorable during the years 1919 to 1922 (1923?), inclusive.

Why were only the herring of years I to III affected by alteration in growth conditions? From the fact that Hankinson (1914) found herring of the first year in shallow water in Lake Superior it is reasonable to believe that herring hatched in Saginaw Bay remain there during the first year of life, or at least during the major part of their first growing season, and this in spite of the fact that none have been taken in the bay. It is not probable that upon hatching the young immediately move out of the bay. If any of the older fish (age groups II and older) remained in Saginaw Bay throughout the summer they would certainly be taken by the commercial nets, which have been set in all parts of the bay without taking them in commercial quantities; but no herring are taken in the bay after the big run in the spring, which may continue until June in the vicinity of Bay Port, although it lasts about one week only in April along the west shore of the bay. Yet each fall large numbers of sexually mature herring (age groups II and above) may be taken almost anywhere in Saginaw Bay.[7] The available evidence, then, indicates that the older Saginaw Bay herring, both immature and mature (age groups II and above), spend the greater part of their growing season in Lake Huron proper. The immature fish older than 1 year may or may not migrate far into the bay with the spawners. Very few of years II to V (Table 50) were taken in my Tobico samples. It appears, then, that herring hatched in Saginaw Bay very probably spend their first growing season in the bay, and that herring older than 1 year spend only the early part of the growing season there. The following discussion assumes the correctness of this conclusion, and the conclusion itself is reinforced by the fact that it permits a consistent interpretation of the growth-rate data.

If the same changes in growth conditions occurred throughout Lake Huron, all the affected age groups collected in one locality should show the same kind of alteration in growth rate in the same calendar years. Further, the herring taken at localities on Lake Huron remote from Saginaw Bay should show, for the same calendar years, a history of growth similar to that of herring taken in Saginaw Bay. The first expectation does not appear to be substantiated by the fact (p. 393), as the 1-year herring of Saginaw Bay grew progressively larger each year during the period 1919 to 1922, while the 2 and 3 year herring (which do not remain in the bay) each maintained a constant growth rate throughout these years. No suitable data are available by which to test the validity of the second expectation. As the effect on Saginaw Bay herring in one locality is greatest in that year of life that, presumably, is spent wholly in the bay, and as the alteration in the growth rate of age groups I to III did not occur in the same manner in the same calendar years, we may conclude that the alteration in the rates of growth of the Saginaw Bay herring under consideration was due primarily to some local changes in the environment of Saginaw Bay.

[7] Whether the main body of herring remains in the bay during the winter after having spawned is not known. In general, relatively few herring are taken from the bay through the ice. As virtually no growth occurs in the winter, the whereabouts of the herring during this season has no bearing on the present inquiry into the alteration of growth rate.

Alterations in the conditions of growth in the bay would affect the growth rate of the 1-year herring more than that of the older groups. The growth rate of the 1-year fish would not be altered necessarily in the same way from year to year as that of the older fish, as the environmental growth conditions (bay and open lake) may not have been the same for the two groups; but if the environment of the second and older age groups was virtually the same in any one calendar year why did the 2 and 3 year fish show alterations in their growth rate while the older herring did not? Or, in other words, if the second and older age groups had been subjected to the same environmental conditions, as I believe, would not these age groups show the same kind of changes in their growth rates? There are at least two probable reasons why they would not: (1) The younger (2 and 3 year) herring may commence the new year's growth earlier in the spring than the older fish. This was found to be true in the marine herring (*Clupea harengus*) by Dahl (1907), in the lemon dab (*Pleuronectes microcephalus*) by Storrow (1916), in the haddock (*Gadus æglefinus* L.) by Sæmundsson (1925), and in the Atlantic salmon by Menzies and Macfarlane (1926). In that case changes in the conditions of growth in the bay would affect the growth of the younger herring more than that of the older. (2) In general, the total amount of annual growth becomes progressively less with age. Slight alterations (inasmuch as these older herring remained in the bay for a short period, most of it when growth is not taking place, alterations in conditions could have affected growth only slightly) in growth rate can not be detected as readily in the average measurements of the older fish as in those of the younger. Thus, even though the growth rates of all the age groups (II and above) of the Saginaw Bay herring were affected by changed environmental conditions of growth, the measurable effect would become progressively less with each older age group and finally disappear. I believe that for these reasons the alterations in the growth rates of the 2-year herring (Table 39) were more noticeable than those of the 3-year fish, and that no consistent changes in growth rates occurred in the older fish. As the 2 and 3 year herring had lived under similar conditions of growth in any one calendar year, it is to be expected, as was actually found to be true, that the kind of changes in growth for the same calendar years would be identical in these two age groups.

We may now ask, What affected the growth rate of herring of years I to III in Saginaw Bay? As it has been shown that a low growth rate of fish 1 to 3 years of age prevailed in the bay in the years 1915 to 1918, inclusive, as compared with that of the years 1919 to 1922, inclusive, two alternatives are possible: (1) The low rate of growth of 1915 to 1918 is the normal or usual one and prevailed before 1915. In that case something happened in 1919 to better hitherto prevailing normal growth conditions. (2) The growth rate of 1915 to 1918 was abnormally low; a higher rate prevailed before 1915 and was resumed in 1919. In that case some factor unfavorable to growth was effective in the years 1915 to 1918 but not before or after those years.

COMPARISON OF GROWTH RATES EXISTING BEFORE AND AFTER THE PERIOD 1915 TO 1918

To decide between these alternatives it is necessary to compare the growth rates of the Saginaw Bay herring existing before and after the period 1915 to 1918. Was the growth rate of 1919 to 1922 merely a resumption of that prevailing before 1915?

The only material available for the period before the year 1915 is the sample of 17 herring collected by Doctor Koelz in 1917 at Bay City, Mich. Doctor Koelz made no effort to take unusually large herring. His only precaution was to take nothing but perfect representative specimens.

TABLE 60.—*Actual lengths of Saginaw Bay herring captured in 1917 compared with those of herring captured in 1924 for corresponding years of life* [1]

Date of capture	Actual length, in millimeters, at end of year—				
	III	IV	V	VI	VII
Oct 25, 1917	235 (3)	246 (6)	271 (4)	293 (2)	311 (2)
Nov.-Dec., 1924	236 (162)	243 (356)	254 (74)	267(18)	280 (4)

[1] The number of specimens employed is given in parentheses.

TABLE 61.—*Comparison, for the first 3 years of life, of average computed increments of length of herring taken in 1917 with those of herring taken in 1921, 1922, 1923, and 1924. The increments of corresponding years of 1921, 1922, 1923, and 1924 fish were combined and were derived from Table 43* [1]

Year of life	Year of capture	Average computed length increment, in millimeters, attained during the year—													
		1911	1912	1913	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924
I	1917	136 (2)	127 (2)	119 (4)	135 (6)	129 (3)	-----	-----	-----	-----	-----	-----	-----	-----	-----
	1921, 1922, 1923, 1924	-----	-----	-----	107 (3)	116 (12)	115 (67)	115 (216)	115 (401)	122 (450)	132 (467)	138 (530)	143 (164)	113 (5)	-----
II	1917	-----	48 (2)	39 (2)	55 (4)	58 (6)	60 (3)	-----	-----	-----	-----	-----	-----	-----	-----
	1921, 1922, 1923, 1924	-----	-----	-----	-----	42 (3)	45 (12)	46 (67)	49 (216)	62 (401)	61 (450)	60 (467)	57 (530)	60 (164)	77 (5)
III	1917	-----	-----	28 (2)	43 (2)	41 (4)	31 (6)	46 (3)	-----	-----	-----	-----	-----	-----	-----
	1921, 1922, 1923, 1924	-----	-----	-----	-----	-----	27 (3)	30 (12)	31 (67)	34 (216)	34 (401)	34 (450)	32 (467)	31 (530)	33 (164)

[1] The number of specimens employed is given in parentheses.

In Table 60 the average lengths, as determined from direct measurements of fish, of the herring of Koelz's sample are compared with those of the herring taken at Bay City in 1924 for corresponding age groups. That is, the fish taken in 1917 are compared with the largest taken subsequent to the year 1918. From the table it may be seen that all fish taken in 1917 are longer, on the average, for their respective age groups than those taken in 1924. The averages of the age groups of the 1917 sample are based on too few specimens, to be sure, but their significance lies largely in the fact that they are consistently larger throughout than those of 1924 for corresponding age groups.

In Table 61 a comparison is made between the average computed increments of length of the herring taken by Koelz in 1917 and those of the herring taken in 1921, 1922, 1923, and 1924 for the first three years of life. In order to have as large numbers of specimens in each group as possible, the computed increments of corresponding years of life of the 1921, 1922, 1923, and 1924 fish were combined and were derived

from the total lengths of Table 43. (For the individual average length increments of each year of these fish see Table 39.) By this method of combination more than one age group is involved in most of the averages of the calculated increments. To each younger year class, beginning with that of 1917, a younger age group is added in the table. Obviously the progressive increase in the averages of the first year of life after 1918, as shown in Table 61, may be due in part to Lee's "phenomenon" and not entirely to an acceleration in growth rate. However, the values for the year classes older than 1917 may involve Lee's "phenomenon" also, so in this respect the two series of averages are comparable. Even so, we are not attempting to compare here the corresponding averages of each year class separately. As was the case in Table 60, the averages of the herring taken in 1917 are based on too few specimens to be accurate, but here again their significance lies partly in the consistency of the results based on them. We point out merely that the increment averages for the calendar years preceding 1915 and succeeding 1918 are greater, on the whole, than those for the years 1915 to 1918. Whether or not the progressive increase in the growth rate of the 1-year fish after 1918 is due partly to Lee's "phenomenon" seems to me to be immaterial in the present discussion. That the fish actually grew faster subsequent to 1918 than during the period 1915 to 1918 has been shown in the discussion of Tables 35 to 39 (pp. 363 to 369). It is to be noted that for some years two averages that are widely divergent are given for fish of the same year class. In such case that average based on the larger number of specimens presumably is the more accurate and is so considered throughout this discussion.

An examination of the growth rates of the first year of life, as given in Table 61, shows that those of the years 1911 to 1914, inclusive, were higher in general than those of the years 1915 to 1918, inclusive, and as high as those of the years 1919 to 1922, inclusive. The growth rates of the second year of life of the years 1914 and 1915 exceeded those of the years 1916 to 1918, inclusive, but were less than those of the years following 1918; those of the years 1912 and 1913 were about the same as those given for the period 1916 to 1918. The rates of growth of the third year of life of the years 1914 and 1915 exceeded those of any succeeding years, while those of the years 1913 and 1916 were about the same as those of the years 1917 and 1918. The data suggest that 1913 was an unfavorable year for the growth of the herring considered, and that 1915 was unfavorable for the growth of the 1-year herring but favorable for that of herring of years II and III. If the latter statement be true, our previous statements that the period of low growth rates included the years 1915 to 1918 must be modified somewhat, as follows: Low growth rates prevailed among the herring of year I during the period 1915 to 1918, and among those of years II and III during the period 1916 to 1918. It appears valid to conclude now that the data of Tables 60 and 61 indicate that the low growth rates prevailing among the herring of Saginaw Bay during the period 1915 (1916) to 1918 were abnormal; that, in general, higher rates prevailed before 1915 (1916) and were resumed in 1919. Apparently, then, the growth rates prevailing among the herring in Saginaw Bay before 1915 (1916) were in some way inhibited during the period 1915 (1916) to 1918 and restored or partly restored in 1919. Growth conditions in the bay were unfavorable during the years 1915 (1916) to 1918, inclusive.

Further evidence that the lengths reached by the herring in 1924 were not unusual may be found in the statements of Jordan and Evermann (1911), who visited Bay Port, on Saginaw Bay, in 1908 or 1909. They write (p. 6): "The herring of Saginaw Bay is also in all respects identical with the specimens from Collingwood [Georgian Bay]. It is not only slender, as usual in this species, but reaches *only a small size,*[8] the average weight when mature being 6 ounces, those examined by us, from Bayport, ranging from 2.5 to 9.5 ounces. The maximum length is 12 inches and the usual from 9 to 10." I found that 500 mature herring taken in 1922 averaged only 5.2 ounces in weight, and that my herring taken in 1924 averaged 242 millimeters or 9.5 inches, in length. The above authors do not give their standard for comparison, but it is at least evident that their specimens were as large as if not larger than mine.

TEMPERATURE AND SUNSHINE AS FACTORS

If I am right in concluding that factors that affected growth in Saginaw Bay in 1915 to 1918 were local and not general over Lake Huron, we may ask what they were. What growth-controlling factors operated in Saginaw Bay during the period 1915 (1916) to 1918 that were absent in the open lake. Did these factors exist, also, before the period 1915 (1916) to 1918 and were they absent or reduced subsequent to it?

The first compound factor that suggests itself is that of temperature and light. Temperature may be considered first. Inasmuch as it was concluded that the unfavorable conditions of growth were restricted to the Saginaw Bay region, fluctuations in the mean temperature of the growing season probably may be excluded, for temperature presumably should affect the growth rate of herring of all age groups and of all localities on Lake Huron; but as reliable statistics of the air temperatures of the Saginaw Bay region are available it is of interest to compare those of different years with ascertained growth rates to see whether any relation is discoverable. The temperatures of the water of Saginaw Bay for past years are not known. Neither do we know the exact relation between these temperatures and those of the air. If the temperatures of the air are to be used, we must assume that, in general, the temperature of the water of Saginaw Bay is dependent on that of the air. That is, if the air temperatures of the Saginaw Bay region show that a certain year was a relatively cool one we must assume that the water of Saginaw Bay was, on the whole, relatively cool in that year. The critical temperatures are presumably those of the growth season, which for the young herring of Saginaw Bay very probably extends from April to November. According to the fishermen, the bay is generally not free from ice until April, while according to hatchery employees at Bay City, herring eggs collected by them hatch some time in April. It is very probable, then, that the wild immature herring begin their growth in April. It is not known how long growth continues in the fall or whether it ceases entirely in the winter, though it is virtually certain that growth is considerably retarded during the winter period. However, irrespective of whether we select as the growth season the period March to November, April to November, or April to October, the conclusion derived from

[8] Italics are mine.

a study of the air temperatures remains the same. Table 62 shows, in degrees Fahrenheit, for the months of April to November, inclusive, for the years 1913 to 1922, the mean monthly air temperatures at Saginaw, Mich. They were taken from the various reports of the chief of the United States Weather Bureau. The mean of the monthly averages of each year is shown in the last column of the table, while the mean of each month of the several years is given at the bottom of each column. To make comparison of these temperature data easier and more accurate, I determined, by means of a polar planimeter, the area inclosed by each curve plotted from the monthly averages for each year, employing as the base line a line drawn through 39.2° F., the temperature at which water reaches its maximum density. The resultant values express roughly the relative amount of heat available from the air for each year for the months April to November, inclusive. These values are arranged in Table 63 in order of size. It may be noted, when a comparison is made, that the order of the years, based on the size of the planimeter measurements differs only slightly from that based on the magnitude of the annual averages of the mean monthly temperatures.

TABLE 62.—*Mean monthly air temperatures, in ° F., of April to November, 1913 to 1922, inclusive, taken at Saginaw, Mich., by the United States Weather Bureau*

Year	April	May	June	July	August	September	October	November	Averages, April to November, inclusive
1913	45.8	56.4	68.0	70.2	69.6	60.5	50.2	41.6	57.8
1914	43.5	58.8	65.6	70.8	68.7	60.6	54.6	37.4	57.5
1915	51.6	51.6	61.5	68.8	64.0	62.8	51.0	40.2	56.4
1916	45.5	56.4	62.2	76.8	71.9	60.8	50.0	38.4	57.8
1917	41.4	50.0	61.9	71.4	67.4	58.8	42.1	35.6	53.6
1918	42.2	59.9	64.3	69.4	72.3	54.9	53.0	41.1	57.1
1919	44.2	54.8	73.6	72.6	67.4	64.0	52.8	35.2	58.1
1920	39.2	54.7	67.5	67.2	67.4	63.6	57.4	36.6	56.7
1921	51.7	59.6	69.9	77.5	68.8	66.8	50.4	35.5	60.0
1922	45.7	62.6	67.0	69.4	68.5	63.4	51.0	40.4	58.5
Grand average	45.1	56.5	66.2	71.4	68.6	61.6	51.3	38.2	57.4

TABLE 63.—*Area included in curve based on average monthly air temperatures of Saginaw, Mich., for period April to November, 1913 to 1922, inclusive (Table 62). The base line employed is the line drawn through 39.2° F.*

Year	Area within curve	Year	Area within curve
1921	1.10	1914	0.90
1919	.96	1918	.88
1922	.93	1920	.88
1916	.905	1915	.815
1913	.90	1917	.725

We know nothing specifically about the relation of temperature to growth rate in the herring or about optimum temperatures for the growth of the herring; but if we assume that, other factors remaining constant, the year with the warmest growth season produces the largest and fastest growing fish, we ought, then, to find that the herring in Saginaw Bay grew most rapidly in 1921 and least rapidly in 1917, and that the growth rates of the other years fluctuated in general as the average temperatures or heat budgets (Table 63) of these years; that is, that the growth rates of a relatively cool year were lower than those of a relatively warm year, and vice versa. At first glance there appears to be some correlation between temperature and the growth rate of the Saginaw Bay herring. We see from Tables 62 and 63 that the years 1919, 1921, and 1922 were the warmer years of the series, and from Table 39 that during these years and 1920 growth was more rapid than during the years 1915 to 1918. In the years 1915 to 1918 chemical substances undoubtedly were present in Saginaw Bay water that were not present before or after that period. Their effect on growth rate is discussed in another place. Assuming that they had an effect, the relation of temperature and growth rate might be obscured by it if years when the chemicals were present were compared with other years. It is best, therefore, to compare the years 1915 to 1918 one with another and the years subsequent to 1918 one with another to see whether in either period any relation is revealed between fluctuations in temperature and those in growth rate.

We may then consider the 1-year fish of each year class separately and compare, year for year, their growth rate with temperature. We find, then (Table 39), that the 1-year fish grew approximately at the same rate during 1915 to 1918 apparently uninfluenced by the fact that the average annual air temperature dropped 4.2° F. in 1917 and rose 3.5° F. in 1918 (Table 62), or, otherwise stated, that the average temperature was decreased about 20 per cent in 1917 and increased about 18 per cent in 1918 (Table 63). Yet in 1919, with an increase in the average air temperature of only 1.0° F., or about 8 per cent, the growth rate of the 1-year fish increased (113–116 to 116–127 millimeters); and with a decrease of 1.4° F. in the average air temperature (8 per cent) in 1920, the growth rate of these fish increased above that of 1919 (116–127 to 117–139 millimeters). With an increase of 3.3° F. in the mean air temperature in 1921 (roughly 20 per cent), the growth rate increased only slightly above that of 1920 (133 and 139 to 136 and 142 millimeters, respectively); and with a decrease in temperature of 1.5° F. (15 per cent) in 1922 there was a slight increase in rate of growth. Apparently, so far as these data show, there was little correlation between the growth rate of the 1-year herring of Saginaw Bay and temperature during either the period 1915 to 1918, or, in that following 1918. We conclude that the evidence does not show that temperature was the controlling factor in the alteration in the growth rate of the herring of Saginaw Bay during the period 1915 (1916) to 1922.

The amount of sunshine determines the rate of growth of phytoplankton and consequently that of the zooplankton, on which herring feed; but the relation of sunshine to both air and water temperatures is such that probably mean air temperatures afford a good index to both. It has not been thought necessary, therefore, to study the data for the purpose of determining whether any relation exists between the average number of sunshine hours in various seasons and the rate of growth of the 1-year herring.

FISHING INTENSITY AS A FACTOR

One of the best and most convincing demonstrations of the effect of intensive fishing on the rate of growth of fishes is that afforded by the work of the Danish biological station at Copenhagen, carried on under the direction of Doctor Petersen (1922). In his survey of the plaice fisheries, covering the years 1893 to 1922, Doctor Petersen reports some interesting facts on the relation between these fisheries and the stock of plaice. I can do no better than quote him verbatim. On page 9, he writes:

> In 1899, I introduced fishing by Snurrevaad in Great Belt and this kind of fishing soon had a rapid growth. (See Report XXVII, 1920.)
>
> The old dense stock, consisting chiefly of small, old plaice, was fished up so that the stock became much less dense; but gradually the plaice got bigger, on the average, though much younger.
>
> Now, the fishing is pursued chiefly on younger plaice but formerly mostly on older plaice. The density of the stock is now very sparse; where in former years we took 200 to 300 plaice in one haul, with Snurrevaad we can now take but one plaice or two or none at all. Here, I have virtually seen an accumulated stock fished up and replaced by a new one of younger but bigger fishes; to be sure not nearly as numerous pr. ha., but it is obvious that the stock is quickly renewed, so that the statistics have been able to note good progress since 1899 in total production in kg., and the production has been kept up until this day in spite of great fluctuations from one year to another.

Again, page 18:

> It is thus beyond doubt that the intensity of fishing, while diminishing the density of the stock in most of the Danish seas, has increased the growth rate of the individuals, so that the productivity as a whole has been kept up, and the average size of the plaice in our southern waters is therefore larger than formerly.
>
> Heincke has already called attention to the fact that in the age of the plaice we have a kind of measurement of the fishing intensity, the age will always decrease with a growing fishing intensity; and I shall add that in the growth rate we have another means of measuring the fishing intensity, about which I shall give further particulars in the following. [See, also, Garstang, 1926.]

Is the acceleration in the growth of the Saginaw Bay herring due to intensive fishing perhaps? It is true that the adult plaice differ greatly in their mode of life from the lake herring. Adult plaice are bottom forms and bottom feeders. They migrate, but very slowly. As the amount of food found on the bottom is strictly limited the rate of growth of the plaice depends directly on the amount of space and food that is available for each individual. The lake herring, however, are pelagic plankton feeders. Intense fishing would reduce the number of spawners, the number of eggs laid in the fall, and the number of fry hatched in the following spring. The fingerlings are known to occur in immense schools (Hankinson, 1914) and the fry may have the same habits. The amount of food that each obtains may depend on their number. In any season in which their number had been reduced greatly by overfishing there would then be less crowding of the growing fry and more food available for each individual, a lessened competition. This might increase the growth rate.

It seems unlikely, however, with the abundance of plankton organisms and their rapid rate of reproduction, that plankton-feeding forms can so far reduce their food supply as to affect their own growth rate. However, if we are to explain the increased growth rate of the Saginaw Bay herring of the 1919 hatch on the basis of lessened competition due to heavy fishing we must suppose that the number of spawners in the fall of 1918 was so reduced by fishing that the number of fry hatched in the spring of 1919 fell below the usual number so far that an increase in their growth rate above the normal took place. We are not concerned here as to whether the lessened number of spawners in the fall of 1918 may have resulted from extremely heavy fishing in 1918 or gradually due to continued heavy fishing in the several years preceding 1918. All we need to assume is that intense fishing had reduced the number of spawners in the fall of 1918.

I have shown (Table 39) that the 1-year herring showed a progressive increase in growth rate in 1920, 1921, and 1922. To explain this progressive increase in growth rate on the basis of heavy fishing we must believe that the number of surviving spawners became progressively less each successive fall below the normal during the period 1918 to 1921, and that consequently competition for food among the young herring grew progressively less severe during the period 1919 to 1922. That is, fishing intensity must either have remained constant after 1918 or have become more severe. This may or may not have occurred, we do not know; but in order to explain the growth data of the 1-year herring on the basis of overfishing we must accept this postulation as a fact. If fishing intensity had diminished after 1918, the surviving spawners of each fall, and consequently the resultant fry, would have increased in number and competition for food among the fry would have become more severe. In that case the growth rate of the 1-year herring would then either have remained constant or have decreased after 1918.

What effect should such a constant or increased fishing intensity after 1918 have had on the growth rate of the 2 and 3 year herring? If competition for food amongst the older herring (2 years and older) in the open lake is not severe, fishing intensity should not be a significant factor in the growth rate of these fish while in the open lake. If, on the other hand, competition in the open lake is severe, fishing intensity should be a factor. Competition may be an important factor in the early growth of these fish in spring when they are in Saginaw Bay. In either case, whether competition occurs in the open lake and in Saginaw Bay or in Saginaw Bay only, if the number of surviving spawners each successive year fell more and more below the usual number, competition among the older age groups in the open lake or in Saginaw Bay would become less severe each year, and accordingly their rate of growth while in the open lake or in Saginaw Bay would become progressively larger each year. The second and third age groups should then show a progressive increase in growth rate after 1918. This we know was not the case.

It seems, then, that our data on the growth of the herring can not be explained by overfishing or intense fishing. If we interpret the growth history of the 1-year herring on this basis, that, if we are consistent, of the 2 and 3 year fish must remain inexplicable. If, on the other hand, we explain the growth data of the 2 and 3 year herring on the basis of heavy fishing, those, if we are consistent, of the 1-year fish must remain unexplainable. Intense fishing would alter the growth rate of all three age groups in the same fashion.

TABLE 64.—*Statistics of catch of herring for Saginaw Bay for the years 1916 to 1925, inclusive. The statistics were furnished by the Department of Conservation of the State of Michigan*

Year	Pounds	Value [1]	Average price per pound	Year	Pounds	Value [1]	Average price per pound
1916	5,321,542			1922	3,002,784	$64,582	$0.022
1917	2,819,948			1923	1,830,398	41,203	.023
1918	3,847,065			1924	1,713,693	35,471	.021
1919	3,882,570			1925	3,736,472	80,847	.022
1920	2,441,750	$80,761	$0.033	Average	2,993,002		.026
1921	1,333,793	48,964	.037				

[1] Taken from the biennial report of the Department of Conservation of the State of Michigan.

Suitable statistics would reveal whether or not fishing was intense in a certain year. The statistics shown in Table 64, even though we assume that they represent the actual quantity of fish taken each year, are not adequate to show the intensity of fishing in the herring industry of Saginaw Bay. In order to determine this from the data of Table 64, we must know the size of the herring population in the lake for the year considered. A big catch in one year—as, for example, 1916—may in reality represent less intense fishing than a small catch in another year, such as 1921. If in spite of this we wish to assume that a catch of a year and the growth rate of the fry hatched the year following are more or less closely correlated (that is, that fry of a year following one in which the catch was relatively large grow relatively fast, and fry of a year following one in which the catch was relatively small grow relatively slowly), we should, then, on the basis of the statistics of Table 64, expect the growth of the herring fry hatched in Saginaw Bay in 1917, 1919, 1920, 1923, and 1926 to be relatively large, and that of those fry hatched in 1918, 1921, 1922, 1924, and 1925 to be relatively small. These expectations, however, do not agree with the fact (Table 39) that the fry hatched in 1917 and 1918 grew comparatively slowly while those hatched in the years 1919 to 1922 grew progressively faster each year.

It appears, then, that in all probability fishing intensity was not the controlling factor in the acceleration in the rate of growth of the herring of Saginaw Bay.

The discussion of the possible effects of temperature and light and fishing intensity is incomplete and inadequate because of lack of suitable data. It can not be said that no correlation exists between these factors and growth rate, but that these factors very likely did not control the growth rate. It is altogether more probable that a third factor was the really effective one. This third factor is the temporary chemical pollution of Saginaw Bay. The history of this pollution, so far as I have been able to obtain it, is given below.

TEMPORARY CHEMICAL POLLUTION OF SAGINAW BAY AS A FACTOR

During the World War (1915 to 1918) the Saginaw Bay fishermen received many complaints relative to the odor and taste of their products, especially perch, suckers, and pickerel, taken from the bay. At the same time the city chemist of Bay City, Louis P. Harrison, received similar complaints about the city water, which at the time was taken from the Saginaw River. The fishery interests procured the services of Dr. Herbert W. Emerson, of the University of Michigan, who, independently with Mr. Harrison, investigated the obnoxious pollution. By various and repeated analyses of the waters of the bay and the Saginaw River system the trouble was traced to the plant of the Dow Chemical Co. at Midland, Mich., about 40 miles above the mouth of the river. It was discovered that the company was dumping its chemical wastes directly into the river and that the objectionable taste and odor of the fish and water were due to the presence of dichlorobenzol, a heavy, clear, oily liquid.

According to Mr. Dow, the marked pollution was due to an explosion in one of his chemical plants whereby a large amount of paradichlorobenzol, a useless by-product at that time, was suddenly dumped into the river.

Paradichlorobenzol ($C_6 H_4 Cl_2$), a white crystal, is derived from chlorobenzene ($C_6 H_5 Cl$), a heavy, clear liquid, and, unlike the latter, is very soluble in water. "The benzene hydrocarbons have a paralyzing action on the motor nerves and a more noteworthy action on the brain and cord, causing lethargy and somnolence. Bromobenzene and chlorobenzene act in the same way as benzene itself." (May, 1921, p. 19.) As the physiological action or effect of a chemical depends largely upon its ionization, and this again depends chiefly on its solubility, it is conceivable that paradichlorobenzol is much more toxic than chlorobenzene. It is also known that an increase in the halogen radical enhances the toxicity of chlorobenzene. As we shall see later, Mr. Harrison found that the effluent of the Dow chemical plants actually killed perch immersed in it. There can be no doubt, then, that the dichlorobenzol solutions may act upon the fish either directly by killing them outright or by acting as a depressant, or indirectly by destroying the plankton food of herring or by decreasing its reproductive activity. I obtained the significant details of the history of this pollution from the various principals involved. For this history I am indebted mostly to Herbert H. Dow, of the Dow Chemical Co.; W. P. Kavanaugh, of the Michigan Fisherman's Association; Louis P. Harrison, Bay City chemist; and to Dr. Herbert W. Emerson, of the University of Michigan.

The principal products manufactured by the old Midland Chemical Co., the predecessor of the Dow Chemical Co., were bromine and salt derived from the brine of salt mills. This company did not extract the calcium and magnesium chlorides from the brine but dumped them, with the bittern water, into the Saginaw River. This bittern water derived from the Saginaw salt blocks and dumped into the river contained on an average 50 per cent more salt (NaCl) than calcium chloride and magnesium chloride combined. The Midland Chemical Co. "took only about a tenth of 1 per cent of the material out of the brine—the balance of it went into the river." (Dow.) As time went on one product after another was extracted from the brine, until at the present time salt is produced only as a by-product for the purpose of recovering other constituents in the brine.

Upon the outbreak of the war in Europe (fall of 1914) the Dow Chemical Co. began to save virtually all their by-products. During the war it manufactured a number of chemicals not made theretofore. Thus, it began the manufacture of chlorbenzol in the spring of 1915. The useless by-products were run into the river. In the fall of 1916 an explosion in the chlorbenzol plant suddenly released into the river a large amount of paradichlorobenzol, a useless by-product at that time. It was also in the fall of this year that the water and fish of the Saginaw Bay and the Saginaw River acquired their obnoxious taste and that Doctor Emerson and Mr. Harrison commenced their investigations.

After the source of the pollution had been discovered the investigators found that large amounts of chlorbenzol or its derivatives were being dumped daily into the river by the chemical plant. The explosion was obviously, then, not the only cause of the trouble. It appears that the by-products of chlorbenzol had always been dumped into the river since the beginning of its manufacture in 1915, and that the sudden release of an enormous quantity of the by-product at one time tainted the fish and water to such an extent as to focus public attention upon this pollution and bring it to a crisis. The investigation culminated in the issuance of an injunction against the chemical company, secured through the State's attorney general in April, 1917. Shortly thereafter the chemical company constructed an artificial pond

or settling basin at the rear of the chemical plants. Into this basin the chemical wastes were diverted. The overflow of the pond, however, ran directly into the river.

The testimony of the investigators indicates that the pond was not very effective in relieving the situation. Mr. Harrison determined, by a controlled experiment conducted after the issuance of the injunction, that a solution of 10 drops of the chemical company's waste from the settling basin in 15 gallons of water killed perch in 24 hours. The control fish remained alive during the experiment. As the plant was under the supervision of the Federal Government and the products were necessary for the prosecution of the war, very restrictive measures could not be enforced. According to Mr. Dow, the manufacture of chlorbenzol was discontinued at Midland in November, 1917.

The Bay City tap water retained its obnoxious qualities for some time after November, 1917. Even in the spring of 1918 with each stirring up of the water in the Saginaw River the characteristic odor and taste recurred. Mr. Kavanaugh testifies that the fish of the bay also remained tainted until the early spring of 1918 to such an extent as to make many unsalable. The pollution, though less severe, undoubtedly continued into the summer of 1918. With the resumption of fishing in the fall all traces of the disagreeable odor and taste had disappeared. So far as we know, the year 1919, then, was the first after 1915 in which the waters of the bay were entirely free from the Dow chemical pollution.

According to Doctor Koelz's field notes taken in 1917, the complaints of the fishermen relative to the unsalability of fish involved principally the perch (*Perca flavescens*) taken in the bay. Many individuals of the other species taken in Saginaw Bay were tainted also, and according to one fisherman many fish were afflicted with sores on the body and had to be discarded. Norman Macaulay, manager of the Booth fisheries at Bay City, informed me that the offensive taste and odor were most noticeable in the yellow perch, the suckers, and the yellow pickerel, especially in the spring shortly after the ice broke up. These Saginaw Bay fish were so tainted at this time of the year that it was utterly impossible to use them as food. The herring and other fish taken in the fall were not so noticeably affected by the pollution; they did not lose their salability. Testimony of B. Brackenbury, of Au Gres, substantiates that of Mr. Macaulay. Mr. Brackenbury states that the pollution did not taint the fish taken at Au Gres. So far as he knew the pollution was noticeable as far as Sebewaing on the east shore of Saginaw Bay, about 25 miles direct by water from the mouth of the Saginaw River. Mr. Macaulay states that the Dow Chemical Co.'s pollution affected the taste of fish taken as far as the Charity Islands at the mouth of Saginaw Bay, about 35 miles due northeast from the mouth of the Saginaw River. Whitefish received by him and taken at the Charities were noticeably tainted.

According to the fishermen, then, Saginaw Bay herring taken in the fall of the year were not noticeably affected in taste and odor by the pollution of the Dow Chemical Co.; only those taken in the spring were tainted.

The period (1915 to 1918) during which the dichlorobenzol wastes of the Dow Chemical Works polluted Saginaw River and Bay is seen to be precisely that during which the growth rate of the herring was reduced. Before that period and subsequent to it the growth rate was higher than during the period and presumably normal.

As the 1-year herring hatched in Saginaw Bay remain there longer than the older fish that migrate into the bay, the former were already subjected to the pollution in 1915 while the latter were first subjected in the fall of 1915 or the spring of 1916. This would explain why the growth rate of the 1-year fish was first reduced in 1915 and that of the older groups in 1916. (See p. 397.) All age groups in Saginaw Bay were subjected to the chemical pollution in 1916, 1917, and 1918—the 1-year group presumably throughout the growing season, the older age groups in the fall and also in the spring, when the pollution was most concentrated and most severe. By the spring of 1919 the pollution had abated to such an extent as to permit the 1-year herring to return partly to their normal rate of growth. The absence of the concentrated pollution in the spring of 1919 allowed the older age groups to return to their normal growth rate. It was not until 1921 that the 1-year herring apparently regained their normal rate of growth. This may be accounted for in two ways: (1) According to Mr. Harrison, Bay City chemist, the dichlorobenzol, which is a heavy liquid, could be seen to lie as a separate layer on the bottom of the river in various places. It is plausible to believe that this deposit was dissipated gradually by solution into the river water and by current and wave action, so that normal conditions in the bay were restored slowly. (2) The chemical pollution may have reduced the abundance of plankton, the food of the herring. The restoration of the normal supply in all probability would be gradual. It is not surprising, therefore, that the normal growth rate of the 1-year herring returned slowly. Neither does it seem remarkable that normal growth rate returned suddenly in the older fish. They were subjected only for a short period each year at a time when the pollution was most concentrated. When this severe pollution ceased the period of exposure was too brief to allow the relatively mild pollution to retard the growth of these fish.

It is realized that there were various other industrial wastes that entered the Saginaw River and found their way into the bay. The wastes from some of these industries doubtless were increased as production grew during the war period; but with the close of the war, industries in general continued to operate by the same methods. They produced other materials of similar kind, sometimes in reduced quantities. There is no reason to suppose that the quality of their wastes changed when the war closed, although the quantity may have been somewhat less; but the waste of the Dow chemical works was qualitatively different during the war period from what it was before or after, in that it contained dichlorobenzol.

The growth alteration of the Saginaw Bay herring appears, then, to be correlated with the temporary pollution by the Dow Chemical Co. by wastes containing dichlorobenzol. The period of retarded growth coincides exactly with the period of the pollution. The presence of this pollution explains all the facts in the growth history of the herring, and no known fact is inconsistent with this explanation. If this chemical pollution is not responsible, then the coincidences of the critical dates and data are truly remarkable.

INDIRECT ECONOMIC LOSSES IN THE HERRING FISHERIES DUE TO CHEMICAL POLLUTION OF 1915 TO 1918

The loss to the fisheries during 1915 to 1918 must have been considerable. Not only did the fishermen lose through the unsalability of part of their products but also through the deleterious effect of the pollution upon the growth rate of the fishes. The indirect loss occasioned by the latter factor is passed by commonly as of little consequence, not only by the general public but by the fishermen themselves. This attitude can be accounted for by the fact that in most cases the magnitude of these indirect losses must be left to the imagination or be stated in terms of description instead of dollars and cents. In order, then, to stress as emphatically as possible the importance of the indirect effect of pollution upon fish life and industry, I have computed roughly from my growth data and herring statistics the indirect financial losses suffered by the herring industry of Saginaw Bay during 1917 to 1923.

To obtain such estimates for a certain year, I proceeded as follows: The age composition of the annual catch of the year, as shown by a representative sample, was determined first. Then the average length of the individuals of each age group being known, the theoretical average weight of these individuals was computed by means of the length-weight formula, $W=k.L^3$ (p. 379). Next, the theoretical average weight of each age group was multiplied by the number of the individuals found in each corresponding age group of the sample and the total weight of the whole sample ascertained. From these values the percentage, expressed in terms of weight, contributed to the sample by each age group was determined. Applying these percentages to the total catch of the year (Table 64), the portion of the annual yield furnished by each age group was ascertained. Next, the percentage under normal weight of each age group exposed to the pollution was found by comparing the theoretical weight of that age group with that of a corresponding age group not exposed to the pollution. From these percentages and the total production contributed by each age group to the annual catch the total number of pounds under the normal was computed for each age group. The summation of these pounds gave, then, the total number of pounds under the normal for the year. The multiplication of this annual total by the average price of the herring showed the monetary loss for the year.

The above process was carried out only for the herring taken in 1921, 1922, and 1923. As no representative samples were available for the years preceding 1921, the actual age composition of the catches for these years could not be determined. As the age composition varies little from year to year, no good reason exists why the average age composition derived from the four samples collected in the years 1921 to 1924, inclusive, can not be employed here. The combined sample of 2,311 fish would then serve as the standard for each year. The loss in weight, however, would still be determined by the actual loss suffered during the particular year considered, as shown by the uncorrected computed lengths. For some years the average weights of the old fish are unavailable. In such cases the averages of fish of corresponding ages of the following year are then employed. It is realized, of course, that none of the calculated losses are absolutely accurate; they are rough estimates only, but are far better than no estimates at all.

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Table 64 shows that the Saginaw Bay fishermen caught 1,333,793 pounds of herring in 1921, valued at $48,964. In 1922 they took 3,002,784 pounds, valued at $64,582, and in 1923 some 1,830,398 pounds, valued at $41,203. The actual age composition of the catches of these years, as taken from Table 29, follows:

Sample taken	Number of individuals in each age group						
	II	III	IV	V	VI	VII	Total
1921	5	97	291	205	67	12	677
1922	4	148	245	95	9	0	501
1923	2	170	240	90	15	2	519

The actual average length of each age group of these herring is shown in Table 29 also. These lengths and the theoretical weights (in ounces) are as follows:

Sample taken	Age group											
	II		III		IV		V		VI		VII	
	Length	*Weight*	*Length*	*Weight*	*Length*	*Weight*	*Length*	*Weight*	*Length*	*Weight*	*Length*	*Weight*
1921	195	2.94	224	4.46	232	4.95	241	5.55	254	6.50	275	8.25
1922	217	4.05	229	4.76	236	5.21	241	5.55	252	6.35		
1923	221	4.28	233	5.01	243	5.69	251	6.27	263	7.21	263	7.21

The total weight of the individuals of each age group of each sample, the percentage of weight contributed by each age group to the sample, and the number of pounds contributed by each age group to the commercial catches of 1921, 1922, and 1923 are given below:

Age group	Fish taken in year—	Total weight, in ounces, of age group of sample	Per cent weight contributed to sample by age group	Pounds contributed by age group to commercial catch	Age group	Fish taken in year—	Total weight, in ounces, of age group of sample	Per cent weight contributed to sample by age group	Pounds contributed by age group to commercial catch
II	1921	14.70	0.4	5,335	V	1921	1,137.75	32.0	426,814
	1922	16.20	.6	18,017		1922	527.25	20.4	612,568
	1923	8.56	.3	5,491		1923	564.30	19.4	355,097
III	1921	432.62	12.2	162,723	VI	1921	435.50	12.2	162,723
	1922	704.48	27.3	819,760		1922	57.15	2.2	66,061
	1923	851.70	29.2	534,476		1923	108.15	3.7	67,725
IV	1921	1,440.45	40.5	540,186	VII	1921	99.00	2.8	37,346
	1922	1,276.45	49.4	1,483,375		1923	14.42	.5	9,152
	1923	1,365.60	46.9	858,457					

The sample of 1921 weighed (theoretically) 3,560.02 ounces, that of 1922 weighed 2,581.53 ounces, and that of 1923, 2,912.73 ounces. To determine the percentage of weight under normal of the herring taken in these three years, I compared the average theoretical weights of their age groups with those of corresponding age groups taken in 1924. (See figures for Tobico and Nayanquing samples combined, Table 31.) The herring captured in 1921 will be considered first. As the 2 and 3 year individuals had not been subjected to the pollution (throughout this discussion we ignore the fact that the normal growth rate did not return until 1921 in the 1-year fish) and the loss for the 7-year fish can not be ascertained, these age groups need no consideration here. It was found (see data in table below, p. 409) that the 4-year fish of 1921, which

had been exposed to the pollution during the first year of life, were 13 per cent under normal weight, that the 5-year fish were 14.6 per cent and the 6-year individuals 15.9 per cent under normal weight. These percentages represent a total loss of 184,450 pounds to the fishermen, or an average loss in pounds of 12.1 per cent. The average price of herring in 1921, as derived from Table 64, was 3.7 cents per pound; the financial loss due to the retardation in growth rate then amounted to $6,825 in 1921.

The loss must have been less in 1922 than in 1921. None of the 2, 3, or 4 year fish taken in 1922 had been subjected to the pollution. The 5-year individuals had been exposed only during their first year of life. Computations show that they were about 14.6 per cent under normal weight. The 6-year herring were 11.9 per cent under normal weight. These percentages represent a total loss of 113,648 pounds to the fishermen, or an average loss in pounds of 3.6 per cent, with a value (at 2.2 cents per pound, Table 64) of $2,500.

The loss must have been exceedingly small in 1923. The 6-year fish were found to be about 4.5 per cent under normal weight. This represented a loss of 3,191 pounds, a general loss of 0.2 per cent, valued at $73.

The data upon which the above discussion is based are summarized below:

Age group	Theoretical average weight, in ounces, of herring captured in—				Percentage under normal weight of herring taken in—			Number of pounds under the normal of herring taken in—		
	1921	1922	1923	1924	1921	1922	1923	1921	1922	1923
IV	4.95			5.69	13.0			80,717		
V	5.55	5.55		6.50	14.6	14.6		72,968	104,725	
VI	6.50	6.35	7.21	7.55	15.9	11.9	4.5	30,765	8,923	3,191
Total								184,450	113,648	3,191

As the fish that composed the catches of 1915 and 1924 had been exposed only slightly to the chemical pollution and the growth data for the fish taken in 1916 are very incomplete, the losses for these years may be ignored. The averages of the length of the old fish in the catches of some of the other years are likewise unavailable. Those of the fish of the same age in the catch of a following year then are substituted, as, due to the law of compensation in growth, the differences between the lengths of the old fish of corresponding age groups of two successive year classes would be comparatively small anyhow. To illustrate the modified procedure (see p. 407) employed for the years preceding 1921, the various data are given in detail for 1920 only. For the other years the end results alone are given.

Table 64 shows that in 1920 the fishermen of Saginaw Bay took 2,441,750 pounds of herring, valued at $80,761.

The four samples of herring taken in the years 1921 to 1924, inclusive, comprised 2,311 individuals, distributed among the various age groups, as follows: II, 12; III, 577; IV, 1,132; V, 464; VI, 109; and VII, 14.

The computed lengths attained by the herring at various ages at the end of the growth year of 1920 are shown in Table 37. Those of different age groups belonging to the same year class were combined into one average. These combined averages (see Table 43) and the theoretical average weights of the fish of each age group are given below:

At age	II	III	IV	V	VI	VII
Average length, in millimeters	183	211	224	241	260	[1] 275
Theoretical average weight, in ounces	2.43	3.73	4.46	5.55	6.97	8.25

[1] The actual length of the 7-year herring taken in 1921.

The total weight of the individuals of each age group of the sample, the percentage contributed by each age group to the combined sample, and the number of pounds contributed by each age group to the commercial catch of 1920 are as follows:

Age group	Total weight, in ounces, of age group of sample	Percentage weight contributed by age group to sample	Pounds contributed by age group to commercial catch
II	29.16	0.3	7,325
III	2,152.21	20.2	493,234
IV	5,048.72	47.3	1,154,948
V	2,575.20	24.1	588,462
VI	759.73	7.1	173,364
VII	115.50	1.1	26,859
Total	10,680.52		

In 1920 all but the 2-year herring had been subjected in varying degrees to the chemical pollution. Computations indicate that, as compared with the 3-year fish taken in 1924 (Table 31), those of 1920 were 28.4 per cent below the normal weight. In like manner the 4, 5, and 6 year fish of 1920 were found to be 21.6, 14.6, and 7.7 per cent, respectively, below normal weight. The loss to the fishermen in 1920 totaled 628,907 pounds, valued at (3.3 cents per pound, Table 64) $20,754, an average loss in pounds of 20.5 per cent. By a process similar to that employed above, the losses for the other years were computed as follows:

Year	Loss, in pounds	Price per pound [1]	Monetary loss	Average loss of weight in percentage
1917	869,124	$0.03	$26,074	23.6
1918	1,332,909	.03	39,987	25.7
1919	1,317,995	.03	39,540	25.3

[1] The financial losses for the years preceding 1920 are computed on the basis of 3 cents per pound; the average for 1920 and 1921 was 3.5 cents per pound. According to Bay City fishermen the average price of herring is usually around 3.5 cents per pound; in the fall of 1924 and of 1925 the price to the Bay City fishermen was 3.5 and 4 cents per pound.

Adding together the annual losses computed for the years 1917 to 1923, inclusive, we obtain the sum total of 4,450,224 pounds, with a value to the fishermen of $135,753. This total is a rough estimate of the indirect losses suffered by the herring industry of Saginaw Bay and is believed to have been occasioned by the pollution in 1915 to 1917 of the Dow chemical works.

Not only were the herring indirectly affected by this pollution but presumably also the pickerel, perch, suckers, carp, and all the other species of fish that grow in Saginaw Bay. The total damage done to these species involved greater financial losses than those of the herring, for they yield the bulk of the commercial catches of the bay and possess an average value greater than that of the herring.

It must now be apparent that the indirect losses occasioned by a serious pollution may assume enormous proportions, as the effects of such a pollution are spread over a series of year classes, each one of which at one time or another enters the commercial catch and becomes one of its principal components for several consecutive years.

GENERAL SUMMARY

1. This paper is based on a study of the measurements, weights, and structural features of the scales of 3,724 lake herring (*Leucichthys artedi* Le Sueur), fishes that belong to the family Coregonidæ; 321 of these specimens were taken by Dr. Walter Koelz in 1917 and 1919 at various ports on Lake Huron, and 3,403 were taken by me in 1921, 1922, 1923, and 1924 in the region of Bay City, Mich. (Saginaw Bay), and Oscoda, Mich., also ports on Lake Huron.

2. The structural features of scales employed for life-history work are well defined and easily recognized in typical coregonid scales. In this respect these scales are usable for life-history work.

3. Scales retain their identity throughout the life of the fish. The well-established facts in proof of identity are these: (*a*) That the nuclear area or central part of the scales of old fish is structurally identical with the scales of young fish; (*b*) that regenerated scales, which replace those accidentally lost, have a central portion of quite a different type from that of normal scales; and (*c*) that scales increase in size as long as the fish grows.

4. In lake herring the number of scales in the lateral line is the same for both sexes of an age group.

5. In lake herring the number of scales in the lateral line is, on the average, greatest in the large individuals of an age group, due to the fact that these fish were also the large individuals of their year class at the time of scale formation and more scales were laid down in the longitudinal rows.

6. In lake herring the number of scales in the lateral line remains constant with the year classes and with the age groups (III and older) studied.

7. An attempt has been made to review all the criticisms that have been directed against the age hypothesis and the nature and extent of all the evidences, direct and indirect, that support or contradict the hypothesis. The review indicates that the large majority of the experiments on the scales of fishes are fragmentary but favor, as far as they go, the theory that the annuli on the scales of a fish are a reliable guide to its age. This assumption has not been tested experimentally for the lake herring. I have tested it, however, by experimentation for the whitefish (*Coregonus clupeaformis*), a coregonid closely related to the lake herring. The whitefish employed were reared in the New York Aquarium and were known to be in their eighth or ninth year of life. (Van Oosten, 1923.)

8. A review of the most important papers devoted to a study of the body-scale growth relationship shows that the question of the validity of growth calculations based on the scales of fishes is still a disputed one. The direct experimental evidences are very fragmentary, but show, as far as they go, that calculated and empirical measurements of growth agree almost exactly. An attempt has been made to ascertain the exact growth relationship between the scales and the body of the lake herring, to determine the accuracy of the calculated measurements of growth, and to analyze the factors involved in the apparent discrepancies in the calculated measurements of growth.

9. In lake herring scales of the same individual may grow at different relative rates.

10. In lake herring the various areas of a single scale may increase in length at different relative rates.

11. Lake herring scales taken from the same area on the body grow more nearly at the same rate than those taken from various parts of the body.

12. The body-scale length ratios (K/V) of lake herring of age groups III and older decrease slowly but consistently with each older age group, irrespective of whether selected corresponding scales (X scales) or unselected scales (non-X scales or those actually used for the life-history work) are employed. That is, the percentage of increase in length with age is greater in the scale than in the body of the herring.

13. The decrease in the body-scale length ratios with age is not due to the age variations in head length, for the length of the head in proportion to that of the body remains virtually constant with age in herring 3 years of age and older.

14. The body-scale length ratios (K/V) of juvenile coregonids decrease very rapidly with age and growth in the first year of life.

15. The scales of lake herring increase in length comparatively faster than the body until a body length of approximately 260 millimeters (age group VI) is reached, when the scales increase proportionately more slowly. In early life the scales increase in length much faster relatively, than the body; in later life (third year and thereafter throughout the sixth year) only a little faster.

16. In both lake herring (*Leucichthys artedi*) and whitefish (*Coregonus clupeaformis*) scale formation begins when the fish has attained a length of approximately 35 to 40 millimeters.

17. The diameter of a herring scale increases in length more nearly proportional to the increase in the length of the body than does the anterior radius.

18. The diameter dimension of the scales of an individual herring varies less than the anterior radius dimension.

19. In lake herring the computed lengths based on the diameter dimension of scales are always higher for corresponding years of life than those based on the anterior radius. The difference between the two increases consistently with each earlier year of life for which calculations are made, so that the maximum average difference is found in year I.

20. In lake herring the computed lengths based on the diameter measurements of scales are in general lower than the corresponding lengths obtained from direct measurements of fish of the same year class. The differences between the actual and computed lengths are in general greatest for the early years of life.

21. The length value computed for a particular year of life generally decreases as the age of the herring whose scales are employed increases. (Lee's "phenomenon of apparent change in growth rate".)

22. The decrease with age in the computed length values of corresponding years of life (Lee's "phenomenon") occurs when the calculated length values of herring of different age groups and of different year classes are compared.

23. The decrease with age in the computed length values of corresponding years of life (Lee's "phenomenon") also occurs when the calculated length values of herring of different age groups but of the same year class are compared.

24. A phenomenon similar to that of Lee occurs when the "annular" scale-diameter measurements of herring of different age groups but of the same year class are compared. The "annular" scale-diameter measurement of a particular year of life decreases as the age of the herring whose scales are employed increases.

25. The scale (and body) increments of the first and second growth years of a year class of the lake herring generally decrease as the age of the fish whose scales are studied increases; but the scale (and body) increment of the third growth year increases or remains constant with age, while the scale (and body) increments of the fourth and fifth growth years increase with age.

26. Every factor that could possibly explain conclusions 20 to 25, inclusive, in the lake herring was critically considered. It was concluded that these facts may be interpreted best as the results of the following three natural events in the life history of the herring: (*a*) Herring that reach sexual maturity late in life are the more slowly growing individuals of their year class; (*b*) sexual maturation usually is accompanied by a retardation in the growth of body and scale; (*c*) a compensation in growth occurs in lake herring; that is, herring that grow slowly during the earliest years of life grow rapidly during the later years of life, and vice versa. According to this view, then, Lee's "phenomenon" is largely a natural event and should occur to some extent in calculations of growth based on the scales of adult herring. The disproportionate growth rate of body and scale may be an additional factor for the "phenomenon" in the computed lengths. It is believed that late scale formation, which is usually considered to be the cause of Lee's "phenomenon," is not such a factor, for (*a*) computations of growth are based on the assumption that the lengths of the body and scales maintain a fixed relationship after the first year of life; that the body-scale ratio of a fish at death is the same as it was at the time of the completion of each annulus on the scale, irrespective of the actual growth relationship during the first year or during the intervals between the periods of annuli formation, for lengths are calculated back to the periods of annuli formation (p. 320); (*b*) the rapid proportional increase in the length of the scale during the first year of life counteracts late scale formation in its effect on the computations of length (p. 340); (*c*) late scale formation can not be a factor in the "phenomenon" found in direct measurements of scale diameters (p. 341); (*d*) corrections for late scale formation do not eliminate the "phenomenon" from computations of growth; corrected computations of length tend to be too high for the early years of life (p. 339).

27. The life history of the lake herring described in this paper is based on four large collections made at Bay City, Mich., on Saginaw Bay in the fall of 1921, 1922, 1923, and 1924.

28. No 1-year herring and relatively few 2, 6, 7, or 8 year fish were found in the commercial herring catches of Saginaw Bay. The 3, 4, and 5 year fish composed 87.2 to 97.4 per cent of the commercial catches. The fourth age group was always dominant, its individuals comprising 42.8 to 58.3 per cent of the total catch. The oldest lake herring I have ever seen was in its eleventh year.

29. The percentage of 3-year herring in the commercial catches of Saginaw Bay increased each year during the period 1921 to 1923, then remained stationary in 1924. This increase in the number of 3-year fish occurred at the expense of the 5-year fish mainly, which each year became progressively less abundant.

30. A year class predominated for one year only in the commercial catches of the Saginaw Bay lake herring. Each year class dropped off rapidly in the years following the year of its dominance—the fourth.

31. The biological data suggest that commercial fishing for herring is very intense. The symptoms of heavy fishing are: The paucity of old individuals (28), the shifting in the age composition of the samples (29), and the one-year dominance of a year class (30).

32. In lake herring males and females of an age group grow at the same rate in all years of life.

33. The sexually mature female herring weigh, on the average, slightly more than the sexually mature male herring of the same age group.

34. In the Oscoda sample of 1922 the nonspawners of an age group average less in length than the spawners of that age group.

35. The lake herring grows most rapidly in length during the first two years of life; nearly 50 per cent of the length reached in the sixth year is completed at the end of the first growth year. The data indicate that the growth rate of the first year of life determined largely the size, and indirectly the weight, of most of the individuals of the commercial catches studied (p. 369). From the point of view of the fisheries, the growth history of the 1-year fish is of extreme significance. The first prominent break in the curve of total growth in length occurs in the third year—the year during which sexual maturity is first attained by many individuals. The lake herring reaches at the end of the second year nearly 50 per cent of the weight attained in the sixth.

36. From the point of view of the commercial fisheries, it is not profitable to allow the herring at their present rate of growth to become much older than 3 or 4 years, for the increase in weight in the fourth and fifth years together is less than that of the third year alone. If the nets are so regulated that they take no fish under 4 years of age (235 millimeters, or 9.3 inches long, measured snout to base of caudal, and 5.61 ounces in weight), then many herring can spawn twice and a greater number can spawn once, thus insuring the perpetuation of the species, provided the number of spawners is not reduced below the number required for the maintenance of the species.

37. In lake herring the big yearlings of a year class are, on the average, the big fish in all succeeding years of life, but the differences between the small and large yearlings diminish each year of age—that is, the small yearlings are rapid growers, the large yearlings slow growers. (Gilbert's law of growth compensation.)

38. The length-weight relationship of lake herring taken just before spawning in the fall can be expressed satisfactorily by the formula $W=k.\ L^3$, in which k has a value of 0.01126.

39. Of the 2,950 lake herring taken in Saginaw Bay 49.5 per cent were males and 50.5 per cent females.

40. The relative abundance of male and female herring varies during the course of the spawning run. Males are more numerous than females early in the season but less numerous late in the season.

41. The relative abundance of male and female herring varies with the age groups. In general the males become relatively more numerous than the females with each higher age group. It is believed that this indicates that a bigger percentage of the females than of the males of a year class reach sexual maturation for the first time in the third year—that is, the females mature earlier in life than the males.

42. About 3 per cent of all the herring taken in the samples from Saginaw Bay were sexually immature or nonspawning fish.

43. The majority of the lake herring attain sexual maturity in the third and fourth years of life. Fewer reach it in the fifth year. Very few individuals reach sexual maturity in their second year. All herring of the sixth and older age groups are sexually mature.

44. The lake herring taken in 1924 at the same locality in Saginaw Bay but on different dates show no consistent differences in size, rate of growth, and age composition. These facts indicate that the character of the herring stock of one locality in the bay does not change during the spawning run.

45. The herring population of Saginaw Bay can not, on the basis of growth rate, be separated into distinct races.

46. Distinct differences exist between the growth rates of the herring of some localities in Lake Huron. This suggests that there may be distinct races of herring in Lake Huron and that the migrations of the herring are more or less local.

47. Saginaw Bay produces, so far as known, the most rapidly growing herring in Lake Huron. Of the various localities in Lake Huron considered, the herring of Oscoda rank second in rate of growth, those of Alpena, St. Ignace, and Killarney third, and those of Wiarton fourth. The different growth rates of the herring of these localities possibly may be correlated with the different conditions of life.

48. The average measured length of the herring schools of Saginaw Bay tended to increase each year during the period 1921 to 1924.

49. The average measured length and weight of herring of corresponding age groups increased progressively each year during the period 1921 to 1924.

50. A study of the computed lengths and increments of the Saginaw Bay herring shows: (*a*) that in each of the years 1915 to 1918, inclusive, the rate of growth of herring in the first year of life was the same; (*b*) that in the year 1919 the growth rate was increased in herring 1, 2, and 3 years of age; (*c*) that neither in 1919 nor subsequently did the growth rate of fish older than 3 years increase; (*d*) that the acceleration of growth rate initiated in 1919 in fish 3 years of age and younger continued in the years 1920, 1921, and 1922; (*e*) that in the period 1919 to 1922, inclusive, fish in their first year of life, in general, grew more rapidly each successive year (during this period there was progressive increase of growth rate in 1-year fish, although in 1922 the increase was very slight—1 millimeter); (*f*) that during the period 1919 to 1923, inclusive, the growth rate of the second and third year fish did not increase in successive years but remained virtually constant at the increased rate attained in 1919; (g) that the growth rate for the fourth and later years likewise tended to remain constant in the years 1919 to 1924, inclusive; (*h*) that all fish 3 years of age and younger in general reached progressively greater lengths each successive year after 1918, while the 4-year fish did likewise after 1919; and (*i*) that fish older than 4 years, hatched after 1917 attained greater average lengths at the same age than those hatched before or in 1917, the fifth age group of year class 1918 excepted.

51. The low growth rates that prevailed among the herring of Saginaw Bay during the period 1915 (1916) to 1918 were abnormal; in general, higher rates prevailed before 1915 (1916) and were resumed in 1919.

52. The low growth rates of the Saginaw Bay herring during 1915 (1916) to 1918 were due to some unfavorable local conditions of growth in Saginaw Bay.

53. The growth alteration of the Saginaw Bay herring during the period 1915 to 1922 is explained best as due to the temporary chemical pollution in 1915 to 1917 by the Dow Chemical Co., of Midland, Mich., by wastes containing dichlorobenzol. Temperature, light, and fishing intensity as factors of growth do not explain all the data satisfactorily and therefore do not appear to have been the controlling factors in the growth of these fish.

54. Rough computations based on growth data and herring statistics show that the indirect economic losses, due to retardation in growth, in the herring fisheries for the years 1917 to 1923, inclusive, totaled 4,450,224 pounds, with a value to the fishermen of $135,753. These indirect losses are believed to have been occasioned principally by the chemical pollution of 1915 to 1917.

CONCLUSIONS

This study shows that the structural characters of the scales of the coregonoid fishes of Lake Huron are so clearly recognizable as to permit their use by the scale method. It shows, further, that the fundamental assumptions underlying the scale method are warranted in so far as they apply to the lake herring (*Leucichthys artedi* Le Sueur). The scale method is therefore valid when applied in a study of the life history of the lake herring. The life history of the lake herring that occur in Lake Huron is described in detail in this paper for the first time.

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