UNIVERSITY OF MICHIGAN
MUSEUM OF ZOOLOGY

Miscellaneous Publications No. 17

The Structure and Growth of the Scales of Fishes in Relation to the Interpretation of their Life-History, with special Reference to the Sunfish Eupomotis gibbosus

BY

CHARLES W. CREASER

ANN ARBOR, MICHIGAN
PUBLISHED BY THE UNIVERSITY
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ALEXANDER G. RUTHVEN,
Director of the Museum of Zoology,
University of Michigan.

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THE STRUCTURE AND GROWTH OF THE SCALES OF FISHES IN RELATION TO THE INTERPRETATION OF THEIR LIFE-HISTORY, WITH SPECIAL REFERENCE TO THE SUNFISH EUPOMOTIS GIBBOSUS

By Charles W. Creaser

Introduction

The interpretation of the scale structures of fishes in terms of their life-history has made much progress since its introduction by Hoffbauer about 1898. For obvious reasons this progress has largely been concerned with those species which are of commercial importance. Only very recently have strictly fresh-water species received much attention, although the method was given its initial impetus by work on such fishes. Most of the recent efforts on the fresh-water species have been directed toward those important as food.

Only a few investigators have used the scale method to complement studies in other fields of zoology. The chief reason for the unfortunate neglect of the vital data supplied by this method is the lack of information on the subject among zoologists in general. The situation is the result of the specialized nature of the field of work (which has come to be known as "fisheries biology"), and to the scattered condition of the literature, which is mostly contained in government or society publications which are difficult to obtain or not generally read; and also to the general failure of the fisheries investigators to give due consideration to the nature of the development of the structural features of the scales on which the interpretations of the life history marks must rest. In general each species investigated has been considered as a special case and unified interpretation of the subject has usually been avoided.

Scale studies may be used to supply data essential to the interpretation of many zoological problems. By such studies the age of the fish may be determined and most of its growth history quite accurately calculated. Up to the present time this source of data has been used almost exclusively by students of the life-history of fishes. That it can supply incidental but vital facts for many studies involving fishes is, however, quite evident. Hubbs has presented several good examples of the use of scale data in connection with other problems in fishes. Some of the incidental but important uses of the data supplied by scale studies are found in these several connections.

Variation: In the study of the variation of the segmental features of fishes Hubbs (1922–1925) has compared the variation in various year classes, as determined by scale data, with the temperature of the seasons of their hatching.

Parasitology: The age of infection in fishes and the scale mark record of some parasites may prove important in studies of parasitology (Plate I C).

Pollution: The effect of pollution upon fishes is well recorded on their scales. A change in growth rate, in average size, or the absence of a year class, may indicate the effect of pollution.

Ecology: Fishes constantly change their ecological relationships with age. A study of such phenomena is rendered much more definite by actual age determinations. Any complete study of the ecology of fishes should include data on the age of the fishes under observation (see Hubbs, 1921).

Other important studies, such as sexual differences and various other items in the physiology of growth, invite the use of scale interpretation for an analysis of the true nature of the situation.

Scales have been used extensively for taxonomic purposes, and many of the data on the influence of various events in life-history on scale characters have a bearing on systematic ichthyology. Little attempt has been made here, however, to treat this taxonomic aspect in any detail.

Since nearly all types of fresh-water fishes, at least of the temperate regions, have been found to reveal much of their life-history in their scale structure, very important facts may be obtained by the utilization of tested scale data. Because of their abundance at all sizes, easily interpreted scales and the fairly satisfactory state of our knowledge of their relationships, the Centrarchidae offer particularly excellent material for a presentation of the scale method. As they are fair aquarium fishes, a study of the formation of scale marks under controlled experimental conditions can be made.

Recently Taylor (1916) and Huntsman (1919) have presented general accounts of the scale method of life-history study. Taylor (1916) and Jacot (1920) have presented evidence which leads them to question some of the most fundamental principles of the method. For this reason care will be taken to present the evidence in regard to most of these fundamental points.

A most excellent critique of the present status of this field of work has been prepared by Rosa M. Lee (1920). Her presentation has cleared many of the points formerly in much confusion, but it is to be regretted that she did not use the studies of American zoologists, and that the difficult and aberrant nature of the scales used did not permit the presentation of the problem in terms most useful in the general application of the method to zoological problems.

HISTORICAL OUTLINE

In presenting the history of the present subject, it seems advisable to take up the detailed contributions as they become necessary in the development of the point under consideration in each of the sections of the paper. Only a brief outline, therefore, is given below.

Several reviews of the literature have been presented: Baudelot (1873), Thomson (1904) and Taylor (1916) may be consulted for the historical aspect of many of the conflicting ideas in regard to our knowledge of the scales of fishes. It is sufficient for the purpose of this study to mention the historical aspects only of those ideas which have been supported by recent and critical evidence.

Scale structures have always been of interest to the observant. It is, therefore, difficult to trace the early beginnings of their study. Even before the early Greek naturalist we find that classifications of fishes as to their edibility were based on the scaled condition of their bodies. The biblical distinction between scaled and non-scaled fishes is of this nature, as it early led to an important selection in food fishes. ''Whatsoever hath no fins or scales in the waters'' was regarded as unclean. This is important since the position of the eel in this classification later led to investigations which greatly increased the knowledge of scale structures.

Immediately after the discovery of lenses, scale structures began to receive much consideration, chiefly as interesting optical objects. As early as 1566 Petrus Borellus described the essential relief features of the scale. Robert Hooke (1667) examined a large series of scales and reported upon their structure in some detail. Antony van Leeuvenhoek is to be considered the forerunner of some of the more recent aspects of scale study. In 1685, stimulated by the discrimination against this fish following biblical decree, he published his discovery of the scale of the eel and gave a very satisfactory figure of it. Clear and concise statements are contained in his work, which prove that he interpreted certain scale markings as indicative of age, and from our present knowledge of this scale, no doubt correctly (although in the case of the eel three years of larval life would have to be added to his calculations). But curiously enough, he later discarded this interpretation, and the idea dropped completely from view for more than two centuries.

In the eighteenth century there were but few references to scales as related to life-history. But as all accounts of the structure of scales must involve description of structures involved in life-history changes as well, many of the fundamentals necessary for the later interpretations are set forth in these early papers. In 1834 L. Agassiz published his famous ''Recherches sur les Poissons Fossiles'' and the development of scale anatomy as the basis for a classification of fishes was greatly accelerated. His work naturally resulted in Mandl's studies (1839–1840), in which a more detailed account of the scale structures is presented. Williamson (1849–1851) brought forth important general views on the fine structure of scales from studies of cross-sections. In 1873 Baudelot presented a paper on the structure of scales. He gave an excellent review of the literature, made exact observations on the structure of scales and presented many satisfactory explanations of their formation. Klaatsch (1890–1894) presented important papers on the histology of the scale which were followed by a study of the same subject by Ussow (1897), who summarized the knowledge of scale structures.

But scale information correlated with the events of the life-history has been largely developed in the last twenty-five years. The work has taken its progress along several lines which only recently have been brought into accord. Hoffbauer (1898, 1901) may be truly considered as the initiator of this latest interest in scale structures in relation to the life-history of the fish. Recently numerous investigators have contributed a long list of papers on this subject. These studies will receive attention under the consideration of those points upon which they chiefly bear.

STATEMENT OF THE PROBLEM

The main object of the present work has been an attempt to coordinate the widely scattered contributions which have been made in this field of zoology, exemplifying, and where possible extending, each point by original data from the centrarchid fishes.

The specific problems which an attempt has been made to solve in this paper comprise the determination of the following points:

1. The extent to which the growth and structure of the scales are modified by events in the life history of the fish, rather than by heredity.
2. The nature of the changes with age in the shape of the scales, and in the relative position of the focus and the relative size of the different fields.
3. The bearing of changes in the direction and the approximation of the ridges on the outer surface of the scale on the interpretation of age and events in the life history.
4. The bearing of changes in the points of origin of the radii and in the width of individual radii, on the interpretation of life history events.
5. The significance of the differential development of the ctenii (or spines) on the scale, and of the differential wear which these structures exhibit, in relation to the interpretation of the nature of the growth of fishes.
6. The determining characteristics of growth cessation marks on the scale.
7. The time of formation of the year marks.
8. The evidence of growth cessation in winter.
9. The characteristics of marks produced on the scale by a cessation of growth during the growing season.
10. The record of regeneration in scale structure.

11. The relation between the growth of scale and growth of fish.
12. The methods of computation of the growth of fishes by means of measurements of the scale.

MEANS AND METHODS OF STUDY

There is little that is standard in the methods that have been used in scale study. Nearly all investigators have developed methods that were intended only for use in the problem under consideration. Even these are so very seldom explained in any detail that it may prove helpful to outline the complete procedure as worked out in the present instance. The methods which are given here have proved very satisfactory both from the standpoint of labor involved and the results obtained. Although some alterations may be necessary in applying them to special conditions, in general the procedure outlined will be found very workable and practical both in the field and the laboratory.

THE MATERIAL

The material for the present study has included the sunfishes and basses of the collection of fishes in the Museum of Zoology, University of Michigan, much of which was collected by the author with aid from the Michigan State Department of Conservation and the United States Bureau of Fisheries. The entire collection has been used for the determination of comparative points.

Ample material with complete data should be obtained for life-history studies, since in the end the nature of the material used determines the real value of the results. Too much stress can not be laid upon this point even if it seems obvious.

The European investigators have used thousands of specimens in their best studies, and the work on the salmon and the white-fishes in this country has involved very large series. For any statistical results, it is an axiom that the number of cases considered must be sufficient. For the use of the life-history data in connection with other problems this is not, however, always necessary since often only the age of a single specimen is desired.

A very representative sample of the material must be obtained, which should include all sizes of the fishes. This often makes possible the construction of length-frequency groups which may be of great help in the age and growth determination. It also permits in many cases the establishment of the relation of the scale length to the fish length, as will be explained later. The large sizes are important in determining the approximate end point of growth and of age.

If the material can all be obtained at about the same time it will be of more value, since the length frequency groups will be better defined, and the average figures free from a disturbing time factor.

The racial nature of the material should be known. All the material that is used in the construction of any one curve should be a unit as to race. If material from widely separated regions is lumped together valuable data are lost, and the results are of unknown value. In the case of fresh-water fishes even a small lake may contain a distinct race, and in certain cases even remote parts of the same lake may be inhabited by different races of the same species. As an example, Mr. Hubbs and the writer have found that the perch (*Perca flavescens*) of Douglas Lake, Michigan, is quite distinct from the perch of Burt Lake or of Lancaster Lake, although the three lakes are connected by short streams.

In general, it may be said that all of the ordinary cautions which have been found necessary in the selection of material for statistical studies must be taken into consideration. Care must be used to avoid working with a selected group, or one which is for any reason not representative of the entire life-history. For this reason gill-nets, being particularly selective in their collecting, should be employed in a wide variety of sizes of mesh. Other types of nets, less selective in character, should if possible be operated in an attempt to obtain a representative sample of all ages. Where selection from a large collection is possible, or necessary, care should be taken to get a random sample. This is usually a necessary precaution in case material from the commercial fisheries is being used.

Fishes which are to be used in age determination may be preserved in the ordinary way (that is, by the use of a dilute solution of commercial formaldehyde), but they should be removed from this as soon as convenient after hardening or shipment from the field. The continued action of formaldehyde partially destroys the upper surface of the scale, which is composed of a well calcified substance. This action renders more difficult the mounting of the scales and the determination of the life-history marks on their surface. If the fishes are placed in a 70 per cent. solution of alcohol, they will be well preserved and the scales will not be injured.

Very often it is possible to obtain material of value from fishes which, for a variety of reasons, can not be taken into the laboratory. This is especially true of fishes caught by commercial or sport fishermen, from which it is much easier to obtain scales with essential data than to secure the fishes themselves. Often the taking of the scales makes possible the securing of a much larger quantity of material than would otherwise be possible, this being especially true in the case of the larger fishes.

It is very desirable, however, to have in the laboratory a well graded series of specimens, so that one may refer back to the specimen for more scales, if needed, or for data not taken with the scales. Questions which can not be settled from a study of the scales and the brief data taken with them may be answered often through a study of a series of specimens.

Such a study may yield factors or graphs which will make it possible to interpret the measurements taken in terms of other units. Often the data thus secured, as for instance that bearing on the relation of length to weight, or of standard length to the length with the caudal fin, may make it possible to bring the entire series of determinations to bear on problems which may arise in the course of the investigation. For this purpose the following procedure will be found adequate. Scales are removed first from the middle of the side. These are to be used for general purposes and for the study of the dimensions of the scales in relation to fish growth. If care is taken to remove these side scales from a specified area where they are very uniform in size and arrangement, they may be used as special scales in studying the relation of the size of the scale to the length of the fishes. A careful preliminary working over of several fishes of the species under consideration will determine those scales best fitted for specific purposes. Afterward scales from the cheek, opercle and shoulder may be included, since they often are of great use in age determination. These scales are placed in envelopes or folded in papers (in some species, as the salmon, the scales may be placed while moist on the page of a notebook, to which they will adhere). If envelopes or folded papers (or both) are used, the data may be written on the envelope or paper, or there indicated by a number, corresponding to the number in a notebook. The life-history data from much of the sunfish material was entered in tabular form under several headings, with a single number to indicate each fish. The scales and the data were later brought together on the slides.

The important data that should be recorded, if scales alone are taken, are: weight before preservation, the length both with and without the caudal fin, the sex, locality, and date. Habitat data may also prove significant. Several scales should be taken.

Scales, particularly those that are large and thick, after being folded into papers should be allowed to dry by leaving the papers free to the air for several days. In very humid regions artificial heat may be required. The samples may then be kept in closed cans or jars.

This scale material is then mounted on slides for the determination of the age and for measurements. The details of the mounting process vary with the condition of the scales.

Dried scales are removed from the papers and allowed to soak in water for several minutes. It will be found convenient to use several watch glasses, or a container with several depressions, so that the scales, taken in rotation, will have had time to become well softened. From a given set, three or four of the best scales from the side of the fish, and a few of the cheek, shoulder or other scales that have been selected especially for age determination, are cleaned for mounting. This is best accomplished by the use of a small brush, to be used with a varying amount of care according to the thickness of the scales. The scales, if from sunfishes and basses, are simply held by forceps against a plate of glass and cleaned with an ordinary tooth-brush, but more care is necessary with more delicate scales. The scales are then mounted with the rounded or exposed field toward the top of the slide and with the outer side up. The outer side may be determined by dragging the tip of the forceps over the surface of the scale, the outer side being rough, while the inner side is smooth. By following such a procedure the scale may be thoroughly oriented on the side.

For a mounting medium the best material found is glycerine-water-glass, as prepared for this purpose according to a formula given by Creaser and Clench (1923). The solution is prepared in the following manner. To an ordinary water solution of water-glass (sodium silicate), as commercially sold for the preservation of eggs, some slightly diluted glycerine is added in the rough proportion of about one part of glycerine to twelve parts of the water-glass solution. If this does not dissolve readily a little water is added until the solution is completed. This solution is kept in a bottle or ordinary balsam jar; it is spread on the slide by the use of a solid glass rod or by being carefully poured from the bottle.

The scales are removed from water, a thin solution of water-glass, or weak glycerine, and set in position on the slide; the glycerine-water-glass solution is then added, and the cover-glass inserted. These mounts set very quickly and by the next day they may be placed upright in the measuring machine. The slides are permanent, and will stand very hard usage. The excess water-glass may be removed with a little water. Discarded slides may be cleaned easily after being soaked a few hours in water. Many other media have been used for the purpose. Important among these are glycerine jelly, Farant's medium, egg-albumen and other related media in general use for total mounts; none of these, however, are in any way to be preferred to the glycerine-water-glass solution, which is not only the most easily handled but also superior in optical properties. The method of mounting scales dry yields very unsatisfactory results, as the surface markings are not clearly revealed.

METHODS OF MEASURING SCALES

There are numerous methods of measuring scales. Those in most common use are the camera lucida, ocular micrometer, mechanical stage, and various types of projection apparatus of the ordinary laboratory equipment.

At the University of Michigan much use has been made of the photomicrographic apparatus in which the image is projected on the ground glass. Van Oosten (1923) has described an instrument for use in scale study based on this principle. A machine of the same general type, described below, has been constructed and used in the study of sunfish scales.

Most of the parts may be derived from the standard equipment of a biological laboratory or built by any woodworker. It is possible to construct a machine that will serve for the study of scales of various types. Since it is of much economy in construction, it is available at all times for this specific purpose.

This machine is an adaptation of the photo-camera and has for its essential parts a microscope of the ordinary type fitted with three objectives and a 6x ocular, a stereoptican incandescent light, and a photographic ground glass.

The base of the machine is constructed of a solid piece of wood which is 5½ feet long and 18 inches wide. On the forward end of this board a wooden box, 14½ inches square and 30 inches long, is constructed, the base of the machine serving as the bottom of the box. A frame is fitted into the end of the box in which a piece of good photographic ground glass, 12 inches square, is mounted in such a way that it may be replaced with a clear glass for photographic purposes.

At the opposite end of the box a square sleeve is constructed of such size that it will just slide within the box. This sleeve is 12 inches long, and is built on a second base which rests on the main base of the machine, sliding on rollers or casters. It is constructed of paper board with wooden corners. By this arrangement the interior sleeve may be shoved forward into the outer box, which is headed with the ground glass.

An ordinary microscope is attached in a horizontal position to the extended base of this sleeve, and is secured by a winged nut on a bar which extends across the foot. The tube of the microscope slides in a light proof metal collar fitted in the closed end of the inner sleeve. Back of the microscope, and also on the movable base, there is fitted a stand on which the incandescent light, fitted with an aspherical condenser, is so adjusted that the rays pass through the microscope and the box onto the ground glass at the front of the machine.

The microscope is fitted with three control rods. The milled head of the coarse adjustment is removed and a cog wheel is put on to the shaft. A worm-gear is then fitted on the end of a long rod which is held at the microscope by a U-shaped iron angle, between the sides of which the worm-gear comes in contact with the cog fitted to the coarse adjustment. The free end of the rod extends forward through the sleeves, and out on the left side of the frame which holds the ground glass in front. It extends forward through the frame far enough to accommodate the total distance when the box is entirely extended. The microscope is fitted with a mechanical stage, the two milled heads of which are controlled by the use of long rods held to these heads by universal joints constructed of sheet metal. The rods extend through the sleeves and pass out the frame in front on the right side, one above the other, so that they may be operated by the right hand without change of position.

Each of the control rods is fitted with a wheel, so that they may be easily turned. With these control rods it is possible to bring the mounted scale into the field and its image into focus on the ground glass.

The light used is equipped with a 108-watt, 6-volt stereopticon projection lamp, which is operated on the 110-volt circuit by the use of a small resistance coil. The current switch for the light is brought forward so that it may be operated from the front with the other controls.

This machine is ordinarily used for all kinds of scale study. The seasonal marks are very well shown and all measuring and counting may be done here. It is also possible to make good photographs, and at such a moderate expense that they may be used in the ordinary routine of scale comparison. To do this the ground glass is removed from the front and a clear photographic glass fitted into its place. A second piece of glass is fitted to this by means of a hinge fastened through holes bored in the top. The image of the scale is put into focus by the use of a piece of thin paper located at the outer surface of the inner glass: the best focus for photography is just beyond the best visual focus, at a point where the valleys between the ridges show up as bright streaks. A piece of photographic print contrast paper (Azo Glossy F. No. 4 will serve) is then inserted in place of the paper, exposed and developed. The resultant paper negative is an excellent object to study and measure and may be used for half-tone reproduction without any further changes (see Plate I, A to H). As no films are used the method is very simple and inexpensive; photographs which show all ordinary and special features that one may wish to retain for later comparison may be made without special equipment while the work is in progress.

SCALE STRUCTURES IN RELATION TO LIFE-HISTORY

The development of scale structures is modified by the influence of environmental factors and by the growth of the fish in such a manner that important events in life-history are recorded on the scale. It is necessary for the understanding of these points to consider in some detail the structure of the teleost scale, especially of its characteristic relief markings, as well as the life-history of the fish.

It has also been shown that the size of the scale bears a definite relation to the size of the fish. The dimensions of the scale, then, at its present limits, or at any other limits that may be established, such as a winter mark, may be used to calculate the size of the fish at important stages in the history of its growth.

The chief contributions of such scale studies to the life-history of fishes follow from the determination of age and of the size of fish at the various ages. These contributions comprise the age at maturity, age at size of economic importance, length of life, year of hatching, the age of an abundant year class, which for years in succession may dominate the whole population of the species, and those items involving the size of fishes as computed from age determinations and scale measurements, such as rate of growth, size at maturity, and the effect of changes in ecological relations on all of these points.

SCALE STRUCTURE

Two opposed ideas as to the nature of the normal growth of the teleost scale sprang up at the very beginning of the study of scale structures. That the scales did increase in size rather than number to cover the ever increasing length of the fish seems to have been taken for granted by the earlier authors. Steinstrup (1861) seems to have been the first to state definitely that all scales except placoid scales grow throughout life and increase in size as the fish increases. Very early A. van Leeuvenhoek, in his conclusions as to the nature of growth of fish scales, did not question that they increased in size rather than in number. He believed that the increase was by additions at the edge of the scale. Later, after much discussion, he gave up this view and considered how the scale might increase in size by the addition of another layer of scale material which was slightly larger than the old scale, and which was developed from beneath while the old layer remained attached to the upper surface of the new scale. Thus the two ideas of the nature of scale growth arose very early. Before the use of scales in life-history studies both theories had been extensively considered, and much conjecture was in progress as to which was correct. The view that scales grow by the addition of increasingly larger plates held for a long time, and was at first accepted by L. Agassiz: he later rejected this theory, and adopted the views of Mandl (1839), who found that neither of these ideas alone was correct, but that a combination of the two processes was involved in the development of the scale. In addition to Mandl, Williamson (1851), Baudelot (1873), Hofer (1889), Klaatsch (1890), Ussow (1900), and Hase (1907) are responsible for most of our knowledge of the histogenesis of scale structures. Thomson (1904) has presented an excellent review of the complicated history of this subject. The main outline of scale development is presented here in order that the nature of the life-history marks may be more clearly understood.

DEVELOPMENT OF SCALE LAYERS

The teleostean scale is almost entirely of mesodermic origin. The first stages in the development of a scale are indicated by a fairly distinct and prominent aggregation of mesoderm elements, known as scleroblasts, in the upper half of the dermis just below the epidermis. These aggregations form papillae which gradually grow out in a horizontal direction, in so doing pushing the epidermis upward. As this stage is reached the cells of the papillae arrange themselves in two layers, superior and inferior, between which there soon appears a thin strip of a refractive substance, the beginning of the first layer of the future scale.

The cells of the overlying scleroblasts, the superior layer, form the first layer of the scale more rapidly than those of the underlying (inferior) scleroblasts, and consequently work around the edges and apparently enclose the cells of this inferior layer.

The superior layer of the scale is then apparently produced by the scleroblasts through the gradual change of a membranous intracellular tissue into a dentine-like substance (hyalodentine).

The position of the scale in the dermis begins to change as it increases in size. The posterior end pushes against the epidermis, which it elevates, while the anterior end sinks into the deeper layers of the dermis. Thus the scale pocket is formed, and the scale changes from a horizontal to an oblique position.

Between the plates of scale substances there exist some free portions of the dermis containing small aggregations of ordinary connective tissue cells. The number and size of these cells increase until their connective-tissue fibrils are formed. The posterior end of the scale pushes into the epidermis and pockets itself in it. Thus connective tissue is located between each two scales and surrounds each scale on all of its lower portions. Eventually this tissue forms the lower layer of the scale.

The outer layer consists of homogeneous bony tissue. Its chemical composition consists of amorphous calcium phosphate and calcium carbonate. The formative cells of this layer are situated chiefly on the upper surface. The scleroblasts of this layer form the superficial relief features of the scale, these being built up at some distance from the extreme margin of the layer. A narrow clear margin may thus be seen around each scale.

The lower layer consists of the connective tissue fibers united into bundles, all running parallel within each bundle. The bundles of one layer lie almost parallel with each other, but cross those of higher or lower planes at acute angles.

The upper layer exists for some time alone and later the other part of the scale appears. A sharp separation between the two layers is not always possible, and at the margin of the scale the layers cohere intimately with one another.

Calcareous concretions appear in the older parts of the lower layers just below the upper layer in such a number as to give the appearance of a third layer.

In brief, the history of the development of the scale may be summarized as follows. Mesoderm cells are aggregated below the basement membrane, forming papillae, which, while at first horizontal, later take up an oblique position and project into the epidermis. As the scale spreads out it becomes divided into two layers by the development of a thin stratum of skeletal substance through its center. This stratum increases in size and thickness by the addition of new strata. The top layer is formed first and becomes altered into hyalodentine. The scale continues to grow, the anterior edge inward and the posterior edge outward.

THE SHAPE OF THE SCALE

As has been suggested by Huntsman (1918), "the simple variation in the rate of growth of the parts of the scale are responsible for the differences in shape and pattern of scales from different regions" of the same fish. This central idea may be extended in considering the history of the individual scale of various species. The changes in sculpturing are closely dependent upon the changes in the shape of the scale at various periods in its history. The changes in shape are due to changes in the growth rate of the different fields of the scale, which in turn are partly dependent upon the interference of the growth of one scale with that of another (Baudelot, 1873).

This changing shape of the scale and the differences in the speed at which its various fields are laid down influence the deposition of ridges on the surface, especially in regard to whether they are parallel or at an angle to the margin, and leads to important changes in the relief features. The characteristics of the seasonal marks are also influenced by these changes since, as will be presented in detail later, many of the characteristics of the year mark are dependent upon the incomplete development always present on the margin of the scale; the expected nature of any seasonal mark, for any individual scale, at any age in its development, may be predicted only when the shape and general history of the normal development is understood.

The distances between the ridges, their direction, and the condition of their incompleteness are all influenced by the speed and character of the development of this superficial layer, regardless of whether it be the result of interference and changing scale shape or of increase in area due to the change in the size of the fish. Both may cause the same effect, so that to understand and interpret the life-history influences on the scale, the action of mechanical and life-history factors must be understood.

When the scales remain imbedded, that is, do not push their way up into the epidermis, but retain their original horizontal position in the skin, and are not imbricated, they are rounded in outline. In the adult sunfishes this condition holds only for the more or less isolated scales on the opercles and the cheeks. Here many scales of an almost circular shape are developed, and they are non-imbricate. These scales (see Plate I) are quite similar to all of the scales of very young sunfishes, or to the scales found throughout life on the body of certain fishes in which the scales for one reason or another do not come in mutual contact. Isolated body scales also tend toward this circular shape; for instance, the isolated scales of the mirror carp tend to assume a circular shape, as contrasted with the squarish scales developed in the same region on scaled carp.

Since all scales have their origin as separated imbedded plates, in the juvenile stage scales are circular in shape and may be termed regular cycloid scales.[1] The scales of Salvelinus and some other fishes do not develop beyond the juvenile imbedded condition (this probably represents a degenerate rather than a primitive condition), remaining small and comparatively simple in structure and sculpture throughout life.

As the scale increases in size it remains circular only as long as the scale growth is equal in all directions. This growth is at first regulated by the amount of available space between the scales in different directions, and later by the degree of their imbrication; an unequal growth along one axis, caused by the fact that the distance between the scales in that direction is greater than their distance apart in the opposite direction, produces a change from the circular form to an ellipse (as in the eel). The ridges on such scales remain regularly elliptical as long as the growth of the scale on the opposite sides of the focus continues equal (Plate I, A).

In imbricated scales the focus or center of origin usually remains uncovered by the scale in front, lying just behind the junction between the exposed and the concealed area of the scale, and midway between the two lateral margins. The isolated cycloid plate of the young fish quickly reaches this condition of overlap by growing with particular rapidity on the posterior margin until it overlaps the next scale behind to the focus. The growth of this field during this period is out of proportion to the growth of the fish at the same time, a situation which will be considered later in a discussion

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[1] Scales of different origin, as those of *Amia calva,* which seem to present merely a convergent development towards the teleost scale, are probably independently derived from the ganoid scale, and do not follow this sequence.

of the relation of the growth of the scale to that of the fish. The anterior margin of the scale is apparently limited less definitely by the spreading scale than by the density of the lower layers of the dermis into which it penetrates. It grows forward only as more area is made available for it by the increase in the length of the fish. Laterally there is a similar limitation of scale growth, the two adjacent scales of a given vertical row impinging on the strip of connective tissue which binds down the midline of the overlying scale pocket.

While the focus remains at the midpoint of the scale, equal growth in all directions produces a regular cycloid scale in which the ridges parallel the scale margin. But in those fishes in which the scales widely overlap, an unequal rate of growth of the anterior and posterior fields produces a shift in the relative position of the focus. This shift causes many of the ridges to end at the margin of the scale, striking it at a slight angle. Such ridges grow only at their ends, and the continuation and completion of the ridges is determined by the increase in size of the scale. This fact has an important influence on the characteristics of the winter marks.

Scales which are imbricated and whose anterior and posterior margins come into close relation with the scales in front and on either side of them, have these margins straightened. The anterior edge of the scale is restricted along a straight line and the scale grows to this line along the entire front. A similar condition exists in the lateral field.

Scales which overlap those parts which are not covered by the other scales and thus restricted are likewise circular in form. The exposed portion of most scales is rounded, in general the greater the proportion exposed the more generally rounded is the entire shape of the scale. This tendency is carried to an extreme condition in the mirror carp, a mutant form of *Cyprinus carpio* in which the scales are few in number and more or less isolated. Such isolated scales grow to a relatively immense size and have rounded margins. Where they come into contact with other scales, however, their growth is restricted, as in the scaled carp. A like example may be taken from the labrid and scarid fishes, in which the last scales along the caudal base are considerably enlarged.

RIDGES

Since the sequence and order of development of the relief features of the superior layer of the scale determines the nature of the marks on the scale produced by those events in the life-history which involve an extensive change in the rate of growth of the fish (and proportionally of the scale), the factors influencing the formation of such marks on the scale should be definitely determined, in order that their significance may be clearly understood. The importance of such a study is due to the fact that these marks are used in determining their time of formation and hence in calculating the growth of the fish.

The most important of the relief elements of the outer surface of the scale are the ridges. These are composed of a highly calcified hyalodentine developed on the surface of the original superior layer of the scale at some distance within the periphery. In many of the fresh-water fishes the ridges are very uniform, both in composition and in the method of their development, but they often form very different types of sculpturing on the surface of the scale. (This sculpturing is often very characteristic of the species or of the genus, as Cockerell and others have repeatedly shown; a study of the ridges is therefore of much value in taxonomy, provided allowance is made for differences due to age of the fish or to environmental factors.)

A variety of names have been given to the ridges. The first description of them seems to be that of P. Borello (1565), who mentions them in his Latin text as "lineis orbicularibus." Of the other names subsequently applied and still in use none are free from serious objection. The term *circulus* (usually used in the plural form—circuli) was originated by Cockerell (1911), who made his observations on scales in which the ridges are approximately circular. In many fishes, however, the ridges do not even approach a circular form; for instance, the fresh-water dogfish (*Amia calva*), in which they are longitudinal, and the herring (*Clupea harengus*), in which they are transverse. The shape of the ridges is often dependent on the shape of the scale at the time they are being formed, as will be indicated later.

The term *annulus,* as used originally by Miss Esdaile (1912), was synonymous with circulus; it referred also to the circular form which they often show. This term is open to further objection, for it has been used by Taylor and other investigators to designate the year marks. The term *sclerite* (Winge, 1915), which originated in the conception that the ridges were the upturned edges of the series of scalelets built one below the other during the formation of the larger scale, is in rather general use in England. It is based on a false conception of scale development and is, therefore, also open to objection.

All of these names, as well as the many descriptive terms which have been used, such as striae, fibrillae, concentric rings and growth rings, seem to be so much at variance with the structural facts, or otherwise confused with terms given to other structures of the scale, that they should all be avoided. Throughout the present paper these structures are referred to simply as ridges.

The exact structure of these ridges, their chemical composition, and the mode of their deposition have been much studied by anatomists, but for the purposes of this paper only a description of the superficial aspects of their formation need be given, as this alone has an obvious bearing on the formation of life-history records on the scale.

The idea that the ridges were the ends of laminae was held first, and being accepted by L. Agassiz (1834), it carried much weight. However, Mandl (1840), Peters (1841), Williamson (1851) and Salbey (1868) all brought forth evidence showing that the ridges did not agree with the laminae of the inferior layer of the scale and were not "growth lines." But this idea persisted: as late as 1906 Tims described ridges of the cod scale as the ends of superimposed scalelets, the peripheral rims of which are turned up, and as recently as 1923 Snyder wrote, "The growth of the scales proceeds from a nuclear center outwards, in concentric rings forming a succession of minute ridges, each of which for a short time is the edge or contour of the scale." But even in the salmon the ridges are not always parallel to the margin of the scale, and in many fishes the ridges form an angle with the margin of the scale.

As stated before, in defining them, the ridges are produced on the first formed stratum of the superior layer of the scale, and are composed of a transparent homogeneous hyalodentine. Baudelot recognized them as external calcifications of the upper layer, and described their formation by the deposition of calcareous material in the membranous zone near the periphery of the scale. That the ridges are being deposited near the periphery of the scale can be demonstrated by observations on a growing fish. New ridges are being started and some of the old ones are being continued at the margin, without relation to the structural layers of the entire scale. It is evident that the ridges are not laid down in any relation to the laminae of the lower layer from the fact that several of them, or even all, may end at the edge of a lamina, a condition which would be impossible if they were parts of the lamina. When a scale is divided along one of these lower laminae several ridges rather than a single one are broken off. Hoffbauer (1898) showed definitely that in sections of carp scales the number of ridges is not the same as the number of lamellae.

A further important consideration, from the standpoint of life-history, is that a ridge is not built up simultaneously in all its parts. Various detached portions of its length may be under construction at the same time. These parts are eventually united to form a continuous ridge by the joining of their ends. In those scales or parts of scales which have no radii, and in which the ridges are arranged in circular form about a central focus, the ridges are built up from various centers of growth (Plate I, A). Each ridge starts at several points of origin, the detached fragments increasing in length until they merge with one another. This simple condition is not often found except in the very young stages of scale formation in most fishes, but the ridges at the margin of the scale are at all times incomplete (see Pl. I, A–H). Frequently the union of the detached portions of ridges is inhibited by the cessation of growth in winter, and the interrupted ridges remain on the scale just within the complete ridges formed in the spring.

The introduction of radii in the anterior field involves breaks in the ridges. In the case of the sunfish, each portion of a ridge between two radii is developed from one or two symmetrically placed centers of origin. These *anlagen* of the radii are laid down just within the scale margin near the apex of the rounded outgrowths between the ends of the ridges, whose growth therefore can be continued only as the scale margin grows forward. Since these are always formed near the margin, the growing ends of the ridges are carried forward with the growth of the scale, so that the portions of the ridges between radii are curved towards the focus (see figures).

Changes in shape from the approximately circular form, more or less characteristic of all young teleost scales, involve such a change in the formation of the ridges as to alter the nature of the sculpturing being produced on the surface of the scale. There is, however, a tendency for the ridges to remain concentric. While the focus remains at the midpoint of the scale it is possible for the ridges to be complete and to coincide with its margin. This condition persists in the sunfish until about five or six ridges have been developed. But in the sunfish, as in other fishes in which the scales widely overlap, an unequal rate of growth of the anterior field, and especially in the anterolateral region in relation to the posterior field, causes the focus to become excentric. The tendency of the ridges to remain concentric causes many of them to end at the posterolateral scale margin (Plate I, A). This tendency is especially prominent in the fall of the year, but is not very evident in the spring when the growth of the scale is resumed. On the resumption of the growth in the spring, the first ridges tend to parallel the entire scale margin, and thus to cut obliquely across the unfinished ends of the outcurved fall ridges.

In the sunfishes, as well as in other groups of fishes in which the ridges become obsolescent with age on the exposed field, a reinvasion of this field by the ridges of the lateral field may take place during the earliest spring growth of the scale (Plate I, F). An examination of Gilbert's figures of the scales of Pacific salmon shows that a similar tendency obtains in these fishes. In the related Coregonidae, however, this renewed ridge formation in the exposed area seems to occur in midsummer, during the period of most vigorous growth (see figures of Van Oosten, 1923). In the sunfish the revival of ridge formation in the posterior field is more usual and more complete in the later years of the life of the fish, but the published plates of scales of the Pacific salmon (Gilbert, 1913, etc.) indicate that in these fishes the phenomenon is more characteristic of the earlier years of life.

The relative approximation of the ridges has not only a significant bearing on the character of the final relief features of the scale, but has also been interpreted in terms of the rate of growth of the fish, bands of closely spaced ridges being regarded as indicating slow growth, widely spaced ridges, rapid growth. Bands of closely approximated ridges have thus been referred to as winter bands, and bands of widely spaced ridges as summer bands.

Hoffbauer (1898), in his pioneer work in the life-history of fishes, based his age-determinations of carp of known age and history upon the relative approximation of these ridges. For these fishes he showed that the approximation of ridges was correlated with the rate of growth of the fish. Ridges that were widely spaced were formed when the greatest growth was being made during the summer, and the areas of more compact ridges in the later unfavorable period of growth. He also advanced evidence to show that over a given period of time an equal number of ridges was produced on comparable scales, and that year marks could be established on the basis of the number of ridges. In a second paper (1901) he extended his observations to *Carassius carassius, Aplites salmoides* and *Sander lucioperca,* and obtained confirmatory results. Thomson (1902) found the same condition of the approximation of ridges to hold in the Gadidae. By contrasting the areas of compact ridges formed late in each season with the areas of more widely spaced ridges laid down earlier in the growing season, he was able to calculate the age of the fish. He further stated that "It appears that in this scale [pollack] the number of lines formed during the second summer exactly agrees with the number formed during the first summer." Two years later Thomson (1904), after studying a series of scales from the same position on fishes of different age from the same locality, showed that for the Gadidae there is a steady increase in the total number of ridges on the scale as the season advances and the fish increases in age, and he used the number of ridges to indicate the age of the fish. In confirmation, Winge (1915) has shown that in the cod there is such close correlation between the number of ridges and the age of the fish, that curves constructed on a basis of successive zones of differential approximation of the ridges yielded definite indications of the age and growth of the fish. Cutler (1918) has extended this method of study to the plaice (*Pleuronectes platessa*) and the flounder (*Flesus flesus*), and has obtained similar results. A graph constructed for a salmon scale (*Oncorhynchus tschawytscha*), based on a photograph by Gilbert, gives the same result. Well marked depressions of the curve (Fig. 1) are found at the winter marks. A similar graph for the sunfish (Fig. 2) (*Eupomotis gibbosus*) scale shows only a slight tend-

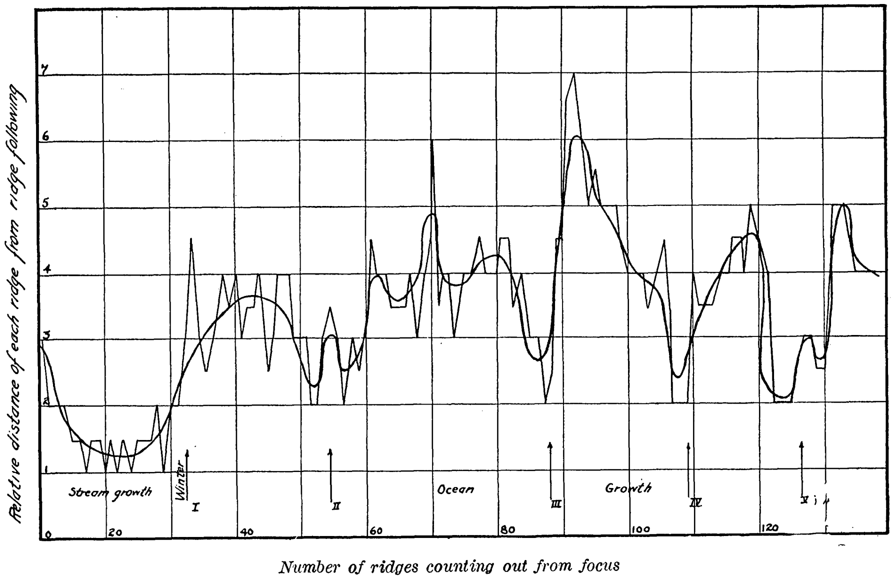

FIG. 1.—A graph showing the relative distance of each ridge from the ridge following (ordinates) compared with the number of the ridges counting out from the focus (abscissae) in the scale of the salmon *Oncorhynchus tschawytscha* from a photograph by Gilbert. Numerals indicate the position of the annuli. Marked depressions in the line at these points show that there is a noticeable approximation of the ridges before the annuli, making it possible to determine the number of annuli from the graph.

ency to form the same sort of curve. Slight depressions occur at the winter marks but it would be impossible to determine and count these marks on the basis of the curve alone; even in the case of the salmon this would be difficult. Johnston (1905) successfully interpreted the history of the Atlantic salmon on the basis of bands of approximated ridges, as other workers have since done with many other fishes.

A special case of rapid growth of the scale known by experiment to be accompanied by a wide spacing of the ridges may be mentioned in this connection. In the case of regenerated ("latinucleate") scales the initial ridges outside the enlarged focus are spaced about 1.5 times as widely as the ridges in the same region of normal scales. The fishes (*Helioperca incisor*) used in these experiments were not growing at all, but the regenerating scales were growing very fast (Plate I, G). A similar but even clearer relation holds in the redevelopment of certain portions of the scale which have been lost by resorption during starvation, by the attack of parasites, or by mechanical injury. This redevelopment was found to be due to a very rapid growth of the new portion of the scale (Plate I, A, B, E), bringing it into line with the unbroken outline. The relief features of such a portion are often developed by a continuation of the ridges being formed farther outward on the normally growing parts of the scale. The rapidly growing portion of the scale has therefore as many ridges as the slowly growing portion. This is a clear instance of the influence of the rate of deposition of the scale base to the number of ridges per unit of length.

Other workers, however, claim to have found that there is little or no relation between the number of ridges laid down and the time of their formation, or between the approximation of the ridges and the seasons or the rate of growth of the fish. Tims (1902) showed that in the cod and other species of the same family the total number of ridges on scales from the same fish varies as much as from thirty to ninety, depending largely on the region of the body from which the scales were taken. Miss Esdaile (1912) has shown that there is much variation in the number of ridges within those portions of the scales produced during the different years of growth, even if the scales be taken from the same position. Even those portions of scales produced in the same year and having the same width showed variations in the number of ridges. The number of ridges formed in a year was found to differ widely on different parts of the same fish, even though the number found was, within limits, proportionate to the width of the scale.

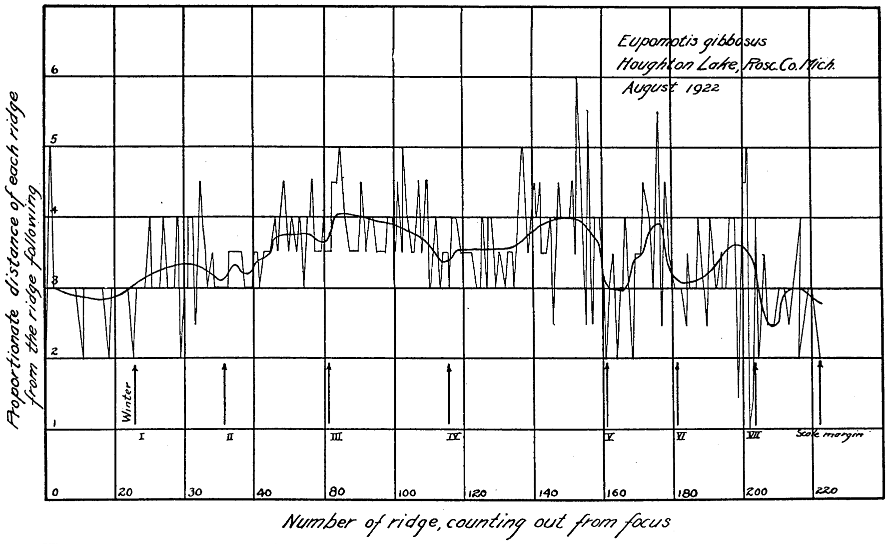

FIG. 2.—A graph showing the relative distance of each ridge from the ridge following (ordinates) compared with the number of the ridges counting out from the focus (abscissae) in scales of *Eupomotis gibbosus*. Roman numerals indicate the position of the annuli. While slight depressions are to be noticed at the annuli, which indicate a slight approximatum of ridges, it would be impossible to determine the position of the annuli from the graph.

Taylor (1916) claimed that this approximation of the ridges was not a conspicuous character of the scales of *Cynoscion regalis* and *Orthopristis chrysopterus,* having found that the ridges are almost equidistant from the focus to the scale margin. ''Their separation does not vary in the vicinity of the annuli (winter marks), nor does their separation vary with different distances from the periphery.'' He was unable to harmonize these conclusions with the results of previous investigations, and stated that ''The conclusion of previous investigators that annuli are approximations of circuli and are caused by retarded growth is rendered questionable.'' He also contended that since the ridges were equidistant they were not a measure of time, that bands representing equal lengths of time do not exhibit at least approximately an equal number of ridges. But this condition need not be the case when consideration is given to the fact that the ridges are built up to about a given height during the variation of several factors instead of one. The rate of production of new base and the rate of the deposition of the ridges vary even in one scale to produce differences in approximation in different fields, as will be considered later. The scale would have to be producing ridges and scale base at the same speed for the production of the same number of ridges per unit of base.

Jacot (1920) has inferred since he did not find this approximation of ridges in the mullets (*Mugil cephalus* and *Mugil curema*), that these fishes fed undiminishingly throughout the winter. The line (''linea'') which he misinterpreted as a ''migration annulus'' and around which he found no approximation of the ridges, is the winter mark on the scale (as will be indicated later). The facts, however, seem to indicate practically undiminished growth until there intervenes a sharp cessation of feeding and of growth in late fall, neither of which is resumed until the next spring.

The approximation of the ridges in the sunfish is influenced by inherent differences in the rate of formation of the ridges on the different fields of the scales, as well as by seasonal variations in the rate of growth of the fish. Ridges are produced much less rapidly, and hence are more widely spaced, and are fewer per unit of space on the exposed portions of the sunfish scales than on the covered portions. Hence, many of the ridges on the anterior field are not continued around the lateral fields to the posterior or exposed portion of the scale, being discontinued chiefly at the anterolateral and posterolateral angles of the scale (see Table I).

This condition is in direct opposition to the usual contention that those ridges far apart are formed during the rapid growth of the fish in the summer, and those closer together during a time of slow increase in the winter. That growth of the same rate may be accompanied by differences in the spacing of the ridges is especially evident from the fact that different numbers of ridges are developed in the same distance on each side of the line

TABLE 1

Number of ridges in different fields of the scale, from the first winter mark inward over a distance of 0.2 mm. Eupomotis gibbosus: Douglas Lake, Michigan.

Field of scale	Number of ridges														
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Av.
Posterior field just behind posterolateral angle of scales		4	18	6											5.1
Lateral field just in advance of the posterolateral angle					4	20	4								8.0
Anterior field, along midline of scale									2	5	34	29	9	1	13.5

of contact between the exposed and unexposed surfaces of the scale (Plate I, A, D). Under any given condition of the environment there is produced therefore a variation in the spacing of the ridges which bears no relation to the comparative rate of growth of the scale in the different fields. That there is an approximation of the ridges during slackened growth of the scale is indeed true, as is indicated by the figures obtained when the number of ridges over an area 0.2 mm. in length of scale on either side of the winter mark are compared. For several sunfishes the average number of ridges inside the line of the first winter mark was found to be 13, while outside this winter mark it was found to be 11. These figures on the approximation of the ridges apply only to this given area of the scale over the given year of growth. An approximation may be demonstrated at each winter mark but the figures are not comparable.

Ridges are also produced less rapidly and are more widely spaced in the middle as compared with the younger portions of the same scale. In several three-year-old sunfishes the average number of ridges for 0.2 mm. of distance inside the line of the first winter mark was found to be 13, while outside this mark it was 11. Before the third winter mark there was found on the average 10 ridges and outside the winter mark 9. This is likewise shown by an initial rise in the curve of the graph showing the relative distance apart of the ridges for the sunfish and the salmon scale (figs. 1, 2). Taylor (1916) similarly concluded, from an examination of Gilbert's photographs of salmon scales, that in the older parts of the scale the ridges are more widely spaced than in comparable areas of the younger portions of the scale.

Where ridges are far apart they are much wider than those in areas where they are compact: in the sunfish the ridges, where spaced 6.5 to each 0.1 mm., are two-thirds as wide as those spaced 4.5 to 0.1 mm., and two-fifths as wide as those spaced 1.5 per 0.1 mm.

Cutler (1918) attempted to show the causative factors involved in the spacing of the ridges and the formation of the annulus by experiments on the flounder and the plaice. He brought these fishes under certain controls of temperature and food and presented data on the formation of ridges under these known conditions. These experiments, however, are of little use in determining the factors involved in the production of ridges. The fishes used only increased a few millimeters in length, the greatest increase being 25 mm., but for most of the examples growth was less than 10 mm. over the 10 months period of the experiment. For fish No. 15 of the "hot tank" 10 ridges were produced for a 4 mm. growth during the period between January to May, and 6 ridges from the period of May to October during which – 2 mm. of growth was recorded. This case is typical of the data presented, from which it is evident that the experiments have little bearing on the problem of the relative approximation of ridges as correlated with the growth of the fish. Since ridges are produced on non-growing fishes only in cases of scale regeneration it is possible that this is what Cutler is recording, in which case these experiments are interesting from a standpoint of the influence of food and temperature on scale regeneration. Thus, it could be concluded from his data that temperature, rather than food, is the important factor in the production of ridges in regenerated scales.

It is evident, therefore, that the approximation of ridges is not dependent alone upon the factor of the rate of scale growth. Other inherent factors must be considered in any interpretation of the approximation of these ridges. Over a limited area in the same field an increase in the number of ridges per unit of scale base does indicate a change in the rate of growth of the scale and of the fish. Certainly various fields of the same scale or widely separated parts of the same field can not be compared. In general, in a given area of a given scale, the increased approximation exhibited as the season progresses may be construed as evidence that the fish is growing at a much slower rate. The ridges of the sunfish formed late in the season are narrow and weak as compared with those of the early part of the season, hence it is not to be expected that an increase in the approximation of the ridges is due to an increasing rate of activity of the tissue building up the ridges. It is more likely that the ridges are brought together because less area is being produced during the interval of time when they are forming, that is, the scale base and the fish are growing at a slower rate. It is certain that a rapidly growing scale base produces widely spaced ridges but there is also a very definite limit to the approximation; hence the scale can only give at most a rough indication of the variation in its rate of growth and of the fish.

RADII

The more or less characteristically radial breaks which cut across the ridged surface of the scale have been designated *radii.* They are usually present only on the anterior embedded portion of the scale, but in some species breaks of a more or less definite nature are found in both the anterior and the posterior fields, while in others radii extend entirely around the scale. When radii are present on the posterior field of the scale, the ridges of this field are usually comparable with the ridges of the anterior field, and ctenii are not developed. Such scales are found in the suckers (Catostomidae) and in the carp and other cyprinid fishes. In the present discussion only the radii of the same general type as those found in the Centrarchidae will be referred to. Such radii as are found in the carp and various other species of cyprinid fishes are more nearly tubular in form, and present a very different appearance. They sometimes pass clear through to the very center of the scale, and may even cross the focus. Some of them appear to have been formed after the deposition of the upper layer on the scale.

The radii are constantly being continued forward as the scalloped anterior margin of the scale grows. The superficial layer of the scale grows forward only along the rounded margins of the scalloped edge, leaving only the lower layer in the streak (radius) between each two scallops. The radii therefore are streaks of the inferior layer of the scale underlying linear interruptions on the upper layer (see Plate I). Williamson (1849) recognized this structural fact, denying at the same time Mandl's hypothesis (1840) that the function of the radii was the transportation of nutrition to the center of the scale.

Radii begin on the anterior field of the body scales of the centrarchid fishes as soon as the scale plate is deposited and ridges start forming on the surface. Sometimes there are one or two unbroken ridges on the anterior field, but often even the first one is broken by the radii. Later in life, after the end of the first year, the radii of the sunfish become nearly equally spaced along the anterior margin of the scale. As the scale grows and the anterior field increases in width the same radii continue regularly spaced because they evenly diverge. The divergence, however, is often a little less than that of the anterolateral axes of the scale, so that the space between these axes and the outermost radius of each side gradually becomes wider than the intervals between radii. If this lateral space becomes about twice the interradial distance, a new radius is here inserted (Plate I, E).

Several features of the radii are significantly correlated with life-history events. Chief of these features are their points of origin and of discontinuity, and the condition of their development.

Taylor (1916) has suggested that the radii are hinges or organs of flexibility, and that the number of radii on a given scale is an index to the flexibility of the part of the fish from which the scale was taken. ''The fact that all degrees in the formation of radii, from total absence, then many folds, then a few to finally numerous radii are found and that these correspond with the mobility of the part, which varies from zero, then slight, and finally to the maximum on the peduncle, is alone sufficient evidence to support the hypothesis that radii are simply hinges.'' Further he states that, ''the number is found to increase to a certain extent as the periphery is approached, afterwards diminishing, until there are no more radii at the periphery than at the focus. This is explained by the relative activity of the fish at different seasons. If this explanation is correct we have an index of the relative activity of the fish throughout life.'' It is quite clear that radii are intimately connected with the need for flexibility in the scales. Their uncalcified structure permits the scale to bend and a continued bending along one line would prevent the formation here of the superior layer, but not of the inferior layer, which is composed of a more flexible material.

In the sunfish there is a correlation between need for radii and their presence. No radii at all, or only a few, often intermittent or only weakly developed radii, are found on the scales of the cheek, opercles and other parts of the head. Many of these scales have developed radii (likewise the absence of radii on the head regions of the squeteague is not total, as Taylor states). Scales which are nowhere deeply embedded show no radii. The number and degree of development of the radii is primarily dependent upon the degree to which the movement of a scale is restricted by overlying tissue. Whatever portion of the scale is thus held down, whether the anterior or either of the anterolateral fields (Plate I, B), develops radii. On some of the cheek scales of the sunfish, namely those which do not overlap until late in life, the development of radii is delayed for several years, appearing first when the scales become imbricated.

It is quite evident that radii in the sunfish are formed on those scales in which the stress caused by the activity of the fish must be accommodated by changes in the scale structure, and where this stress is sufficiently strong and localized to prevent the formation of the superior layer of the scale along the lines which later become the radii. Early in life the radii are ill defined and the ridges only slightly interrupted. The scale is flexible along its entire margin, hence there is no localization of stress. Those scales on parts of the body, such as the cheek, where there is only slight activity, develop only weak discontinuous radii along the concealed margin of the scale.

The degree of development of the radii may be dependent on the flexibility of the whole scale as well as on the activity of the fish. Because of variations in its elasticity, equal stresses may produce different effects on the scale. Older scales, having become thicker, more calcified, and more rigid, are forced to move as a whole. As the scale can then bend little or not at all, the superior layer often closes over the radii. The greatest stress on the scale remains at the center of the anterior field, where the radii were first formed, and where they persist even late in life. The zone of least stress is toward the lateral edges of the anterior field, where for a time new radii may be added, but later discontinued in the inverse order of formation, that is from the lateral margin toward the center.

In conclusion, it may be stated that the production of radii is dependent on the structure and thickness of the scale, on the degree of activity of the portion of the body where the scale is located, and on the degree of overlap of the scales.

Several of the characteristics of the radii of various fishes have been correlated with life-history events. Baudelot (1873) noted that "the number of radii of an individual is capable of varying with age, and if the number increases with age it may also be reduced." Hoffbauer (1899) showed that in the carp several of the radii of the old area of the scale often end or new radii of the new area may begin at the contact of these two areas. Taylor (1916) showed for the squeteague (*Cynoscion regalis*) that radii were serviceable in determining the position of the year mark.

Not only may the actual discontinuance or origin of the radii be found helpful in determining the position of the winter mark but also the change in the form of the radii which are continuances may have a like bearing. Often, especially in the later years of the life of the fish, the radii on the scales of the sunfish are nearly or entirely bridged over by one or rarely several of the ridges first formed after the winter cessation of growth. In such cases probably the radii are not formed, because the thickening and calcification of the scale over winter has rendered the margin too inflexible.

A more constant modification of the form of the radius of the sunfish at the winter mark involves an expansion of the radius at the end of the year's growth, hence just within the restriction of the radius just mentioned as formed at the resumption of growth in the spring. This mark usually presents a bell-shaped appearance under the microscope. Somewhat similar marks, but usually more rounded in outline, are found during the growing season, probably in response to temporary changes in the activity of the fish or in the flexibility of the scale. In fact the width of a radius is never wholly constant, narrowing and widened more or less throughout its length (Plate I, E).

Ctenii

Scales have been classified as cycloid and ctenoid according to the absence or presence of spines on the posterior field of the scale. A given fish may have either type of scale on different parts of the body. In the common sunfish, *Eupomotis gibbosus* (and in fact in all fishes having ctenoid scales), the scales are at first of the cycloid type. In most of the scales of the body below the lateral line this condition persists only for a short time, but occasional scales are found which pass almost an entire year without the addition of ctenii (Pl. I, D). On the body above the lateral line most of the scales do not become ctenoid until after their first year, while on the head, cheek and opercle some scales do not develop ctenii until late in life, or may never become ctenoid. In the green sunfish, *Apomotis cyanellus,* ctenii are only developed late in life, and only on the scales of the lower sides.

Duncker (1896) has shown for the plaice that ctenoid scales are developed from cycloid scales only when the posterior edge of the cycloid scale is raised out of the enclosing epithelium so that a layer of substance bearing ctenii may be laid down over the surface of the scale. This condition is probably universal. In the case of the sunfish it appears that only those scales which extend posteriorly into the epidermis as they become imbricated develop ctenii. When the scale is first formed it is an embedded cycloid plate, but as soon as it grows into the epidermis by the rapid extension of its posterior margin in the oblique direction taken by overlapping scales, ctenii begin to be formed on the surface. At first, on these small scales only one or two ctenii are formed, and these are located on the most advanced part of the margin of the posterior field (Plate I, A). In scales that become ctenoid later and are of larger size many ctenii may be formed at the start, as the broad posterior margin pushes into the epidermis (Plate I, B, D). The number of ctenii formed at first is therefore usually dependent on the width of the area that composes the advanced portion of the posterior margin of the scale. Examples may be found in the figures of the scales of the squeteague and pigfish published by Taylor (1916) and of the mullets published by Jacot (1920).

In the sunfish the area covered by ctenii increases in width as the scale grows larger, but only the most advanced portion of the posterior field which is exposed and which overlaps the scale back of it ever bears ctenii (evidence for a possible homology between shark denticles and ctenii). The ctenoid area is consequently of a triangular form.

Modifications in the detailed shape and general relief of this area are often significant in life history studies. The V-shaped ctenoid area of the sunfish scale, as already noted, is often invaded and occasionally completely crossed by ridges during the earliest spring growth of the scale (Plate I, F). Differential wear, as indicated by the relative bluntness of the ctenii, gives a rough measure of the time of their formation. They usually show a succession of stages of bluntness, each stage coinciding with a year's increment of growth. The first ctenii laid down in the spring are abruptly longer than those which were formed during the growth of the previous year, and which have been subject to wear during the long cessation in the growth of the scales over the winter (Plate I, E).

The fact that long and sharp ctenii, obviously freshly formed, are always to be found on the posterior margin of the scales of even the oldest sunfishes taken during the growing season is strong evidence that these fishes never cease growing.

LIFE-HISTORY SCALE MARKS

Upon the scale there is being produced at all times during the growth of the fish a certain sculpturing which varies with the position of the scale on the body and with its stage of development, and which is also affected by changes in environmental factors. It is these environmental changes that have given rise to the interpretations of scale structure in terms of life events. The environmental changes are resultant upon two chief causes: a change in the rate of growth of the scale, and in the relative degree of mineralization or fixation of the pattern.

The chief environmental marks which have been described are winter marks, marks indicating a check in growth but not caused by winter conditions and marks produced by spawning or other conditions indicative of unfavorable conditions for growth. It will be best to classify these into three types, (1) those of the cessation of scale growth, (2) those of variation in the rate of scale growth, and (3) those of regeneration.

GROWTH CESSATION MARKS

When the fish stops growing the scales reach a point where they can no longer continue to grow until increase in length is resumed. Certain changes then take place in the normal deposition of the relief elements. These changes form characteristic marks in the sculpturing at that point, which can be identified later as the point on the scale where such growth cessation occurred. These growth cessation lines, when periodic in occurrence, have been interpreted as year marks or annuli.

It will be necessary at this point to consider the characterizations of the annulus as it has been understood and defined throughout scale study. A. van Leeuwenhoek observed marks on scales which he considered as year marks, referring to these as "rings of growth" as in trees, and thus the association of the ridges with the year marks was made. Hoffbauer described year marks from the scales of carp and later from *Carassius carassius, Aplites salmoides,* and *Sander lucioperca,* and in each instance pointed out the character of the ridges in relation to the observable marks. He likewise pointed out that there were other characters of the annulus.

The divergence of the ridges in the lateral posterior region of the scale and the character of the radii were also included in his description of the mark.

Thomson (1902) next applied the method to the Gadidae, and described the annulus in these words: "The formation of these annual rings results from the fact that the lines of growth on the scale surface are comparatively widely separated from one another in that portion of the scale formed during the warmer season of the year; but much less widely separated in that part built up during the colder season. Thus by following the arrangement of the lines of growth on scales it is a simple matter to observe the starting place of any year's growth by the comparatively wide separation of the growth-lines at that portion of the scale and in this way the surfaces of scales appear mapped out by annual rings." He also used the number of ridges as an index of time, supposing that an equal number of ridges were deposited over an equal period of time.

The scale method was later used in work on the salmon by Johnston (1905–6–7–9), who found that the approximation of ridges was the best character for age determination. The winter area of ridges was referred to as the "winter band," and no analysis of the nature of the annulus or other characteristics of it were described. This characterization of winter bands has continued until the present time in the work on the Pacific salmon (Gilbert 1922; Snyder 1923) although other important characters of the true annulus were pointed out by Masterman (1913a).

Taylor (1916) insisted that annuli were not approximated ridges because this feature of the salmon annulus did not appear on the scales of the fishes with which he was dealing. The possibility suggested by Taylor that the marks produced on the squeteague and pigfish scales might have been produced in the summer rather than in the winter will be considered under a treatment of the time of formation of the annulus. He defined the annuli of *Cynoscion regalis* as "narrow areas parallel with the contour of the scale, in which the regularity of the circuli is interrupted, manifested as branches, breaks, or terminations." "They are edges of laminae, and are not composed of circuli occurring closer together; they do not represent periods of retarded growth; they probably represent differences in degree of calcification."

Many of the later workers on scale study have realized that the year mark is, in fact, a growth cessation mark, that it is a line rather than a band and that it is a developmental mark and not a special structure. The work of Huntsman (1918), Jacot (1920), Lee (1920), Hubbs (1921), Van Oosten (1923) and Creaser (1926) all reflect this view, and these writers have considered fishes having wide ranges in character of scale pattern.

A winter mark or annulus may be defined as the change in sculpturing produced when the normal scale pattern of the fall is discontinued by the cessation of growth, and the unfinished edge of the scale is circumscribed by the resumption of the normal spring growth, the elements of which are developed without reference to the unfinished parts of the fall edge. The year mark affects all the relief feature elements on the scale, and the mark may therefore be traced entirely around the scale (Plate I, C). Since growth cessation occurs over all of the body, all of the scales bear a mark for each cessation they have been through. Unless each mark is present on all the scales there is some question that it is a year mark.

It follows that the characters of any complete growth cessation mark will vary with the nature of the unfinished edge of the growing scale. With this general principle of annulus formation in mind, it is possible by observing the characteristics of the unfinished scale edge at different seasons to predict and to understand the character of the annulus on that particular scale, and to determine whether given marks on the scale are or are not complete stoppage marks.

Scales of sunfish taken in the early spring, before the growing season has started, show the same sort of margins as do those from fishes taken late in the fall. This condition, as shown by experiment, remains until the fish starts to grow (Plate I, F, H). When the fish starts to grow after the winter period of growth cessation, the new elements are laid down without reference to the uncompleted relief features of the fall. The figures of bluegill scales (Plate I, F, H) taken in February show this uncompleted fall condition, of which the chief character is the incompleteness of the ridges around the lateral posterior angle of the scale, several of the ridges terminating at the scale margin. These ridges could only have been continued around the scale to completion by the continuation of scale growth in the lateral posterior field. Since the ridges in this posterolateral field in fall diverge more widely posteriorly than in other seasons, these last ridges show, then, an especially sharp change in direction, their posterior ends turning so as to meet the margin at a greater angle than at other seasons. During the winter, furthermore, short sections of ridges may remain uncompleted between the radii (Plate I, A).

This discontinuity of the ridges at the margin of the scale involves more ridges in those scales in which the focus is not at the center; the greater the excentricity in the focus, the better defined is the condition. In scales from the cheek of sunfishes where the focus is central, as also in many salmon scales, very little of this discontinuity is evident. However, many of the salmon scales do show ridges which end at the margin, rather than being parallel to it (see photographs in papers by Gilbert, 1913–1922).

During the cessation of growth of winter the calcification of the scale continues; this is evident from the fact that the portions of the scale produced in successive years stain differently with picro-carmine. As a result the incomplete scale pattern is fixed, so that when the growth of the scale is resumed the new sculpturing is formed without reference to the old.

The first elements are produced in the spring on the unsculptured calcified margin, rather than, as later, on the uncalcified growing scale. The first ridges are formed around the scale margin, and therefore cut across the ends of those fall ridges which, as indicated above, terminated at the scale margin near the posterolateral angle of the scale. This feature of the annulus is one of the most distinctive; when this condition is found on both sides of the scale, there can be little question that the mark is an annulus.

Along the lateral field of the scale the chief character of the annulus is the wide clear unsculptured space between the two contrasting growths.

In the anterior field the resumption of sculpturing upon the calcified margin results in the formation of straight ridges, some of which may invade or even cross the radii of the previous year (see p. 29). The chief character of the annulus in the anterior field is, therefore, the succession of the short portions of ridges left unfinished at the end of the fall growth by the straight and continuous ridges of the spring growth (Plate I).

In those salmon scales in which few of the ridges terminate at the margin of the scale, the chief character of the annulus is found in the approximation of ridges, the area of widely spaced ridges produced in the summer contrasting with the area of approximated ridges laid down just before and after winter. Often short portions of ridges are found at the edge of the fall growth, as in other fishes.

In the area of the ctenii of acanthopterygian fishes, the chief characteristics of the annulus are the bluntness of the ctenii and the lateral invasion of this area by the ridges of the adjacent fields during the spring growth (see p. 20). In scales on which ridges are formed over the entire posterior surface often the only indication of the annulus in the posterior field is found in the weaker structure or the obsolescence of these ridges.

In scales having no superficial posterior sculpturing, like those of the salmon, the continuation of the annulus around the posterior field may be marked by a streak in the lower layer of the scale. Such streaks have been used also in the location of the annuli in the herring.

THE TIME OF FORMATION OF YEAR MARKS

In order to be interpreted as year marks, it must be known that these unconformities of the scale sculpturing have been formed at definite intervals of time.

Hoffbauer (1898–1901) showed that on carp which had passed through a period of hibernation, marks having definite characteristics were formed. He was able to follow this history through the third year.

Thomson (1904) showed that his age groups determined from the scale structure of cods agreed with those established by Cunningham and Fulton on the number of modes in length-frequency curves.

Johnston (1905) was able to correlate the year marks of the Atlantic salmon with facts in the life-history of the fish determined by other means, thus indicating that they were year marks formed over the winter period.

Tims (1902–1906) raised several objections to the use of scales in age determination, as did also Brown (1904). These objections, however, were directed against the use of the number of ridges rather than the structure of the annulus in age determination.

Dahl (1909–1911) attempted to show in the salmon that "the formation of these two different series of growth-rings or zones takes place in the winter half or the summer half of the year respectively."

Masterman (1913), in his critique of the salmon work, considered that the marks laid down in early life were year marks formed in the winter, but he is doubtful of the reliability of the later marks as indicative of years. His contentions were based also on the interpretation of year marks in terms of broad and narrow bands of ridges rather than on the nature of the contrast of these bands, although he pointed out many of the characters of this contrast which had been (and still are) more or less neglected or unmentioned in the salmon studies.

Masterman summarized the evidence on the time of formation of the year marks which had been presented up to 1913 under these headings.—Morphological: critical evidence that a broad zone of ridges is formed in summer and a narrow zone in the winter has not yet been produced. Experimental: convincing evidence from fishes of a known age kept under known conditions exists for the first two years. Statistical: "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."

Since this time much evidence from several independent sources has accumulated in favor of the view that these characteristic marks of the scale are yearly marks and are formed over the winter period. Recently Taylor (1916) and Jacot (1921) have, however, presented papers bringing evidence which has led them to question whether the marks were produced in the winter: they have suggested that they might be produced in the summer (Taylor), or during migration (Jacot). Orton (1923), in a note on the growth marks of cockle shells, in the young of which several marks were found during the year, has asked the question: might not the same condition hold for the otoliths and scales of young fishes? The evidence as to the time of formation of the marks and the number formed per year is now so clear that a complete presentation of the subject is possible.

Taylor (1916) and Jacot (1920) have presented evidence which has led them to the conclusion that in certain fishes the annulus is not formed over the winter period. Taylor believed that retardation of growth had nothing to do with the formation of the annulus, a fact due largely to his failure to understand the true nature of the annulus. He has no explanation as to why they are yearly except an indefinite and inaccurate suggestion that the "fish passes through year cycles of growth and one lamina is formed each year." His evidence that annuli do not represent winters may be stated in his own words: "If the annuli represented winters, then in July and August the number of circuli between the periphery and the last annulus ought to be at least half the average number of circuli between any two adjacent annuli. But the small number of circuli formed points to May and June as the time of formation of the last annulus. In the case of the comparisons of measured and calculated lengths, if the annuli represented winters a discrepancy between the averages would be expected; for the fishes measured would be approximately an even number of years old (spawned in June and measured in July and August), while the winters represent points midway between birthdays. But the calculated and the measured lengths agree remarkably, suggesting the view that annuli are year old marks, but not winter marks." As I have pointed out, the annulus is formed when the scale resumes growth in the spring, and the date of the annulus is therefore not winter but spring. All of Taylor's photographs of scales show that considerable growth had taken place since the formation of the annulus, indicating that it was formed several months previous. As has been discussed elsewhere in this paper, the number of ridges bears no definite relation to absolute time of formation, and only roughly to season of growth, hence the development to July or August of less than half the number of ridges between the preceding annuli might not indicate that half the growth of that full year had not taken place. The agreement which Taylor found to hold between the calculated length (considering the annuli as summer bands) and the measured length made in July and August, is in part caused by an error in calculation. As will be discussed later, several investigators have shown that the calculated length, uncorrected, is always too low. For a proper comparison an addition to the calculated length should have been made; this would have indicated that the annulus was formed later in the year.

Jacot (1920) concluded, from the fact that the annulus of the mullets (Mugil) showed no approximation of the ridges, that these fishes fed undiminishingly throughout the winter, and hence that no retardation of growth took place then. He advanced the hypothesis that the line-like annulus of these fishes is produced during a spring migration because it shows no approximation of ridges. But the annulus he describes for the mullet is almost identical with those found in the sunfish, and known to have been produced by a cessation of growth during winter; little or no approximation of ridges is found in these fishes. This is an indication of growth cessation, not of undiminished feeding and growth. Likewise, as pointed out by Hubbs (1921) in regard to the hypothesis that these marks are formed during a migration time, it is possible that the disappearance of the mullet in the fall is due to their movement into deep water, from which they return in the spring. The fact that an annulus was not evident near the margin of scales of mullet taken at Beaufort in early spring indicates that the spring growth of these fishes had not yet started, and hence that the contrast characters of the annulus had not been developed, and does not indicate that they were exceptional non-migratory individuals.

That the annulus is formed by the contrasting characters of the scale growth in the fall and spring and is therefore truly a "winter mark" is a natural conclusion from the evidence of the structural features of the scale.

The increasing distance of the annulus from the margin of the scale during the course of the year demonstrates that it is formed on the scale after the period of growth cessation in the winter. 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 (Plate I, H). 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.*[2]

At Douglas Lake, Michigan, an investigation of the scales of many of the fishes showed that in June an annulus had only recently been formed. As the season progressed, the annuli were found to be farther and farther away from the scale margin, the greatest distance being in late August, when the work was discontinued. This period is about three-fourths of the growing season for that lake: killing frosts occur late in May and even into June, and in fall by early September (Seeley, 1922). During this period of growth no true annulus was formed. For many local fishes examined it has been found that the annulus is at the greatest distance from the margin of the scale during fall and winter and very near to the margin of the scales in spring. This is in effect what Dahl (1910) and Fraser (1917) found in different species of salmon and Creaser (1926) in smelt. Fraser noted that in the salmon (*Oncorhynchus tschawytscha*) no annulus was present on the

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[2] Prof. Frank Smith, University of Illinois, has kindly permitted the writer to examine scales and photographs of scales of a green sunfish (*Apomotis cyanellus*), upon which one of his students had experimented after the same procedure as given for the bluegill.

winter scales, but in the spring an annulus was produced at the margin of the scale.

Lea, as reported by Hjort (1914), found that each ring in the herring scale did represent the cessation of growth during the winter. He followed the growth of the band month by month during the year and found that as the season progressed the summer growth became wider and wider until winter came, when it ceased and the darker ring of winter was found at its margin.

Van Oosten (1923) has followed the growth of aquarium whitefish (*Coregonus clupeaformis*) throughout the year, and shows "that the annulus is a winter mark due to a *retardation* or cessation of scale growth and is completed upon the resumption of rapid scale growth in the spring of the year." His tables (II and III) show that there is a cessation of growth over winter in all the scales, a period of retardation never extending over the winter period.

The evidence that these scale features are year marks and that they are produced during the period of growth cessation over the winter may be presented under these several heads.

THE EXPERIMENTAL CORRELATION OF KNOWN AGE WITH COMPUTED AGE

Experiments to determine if the number of year marks on the scale agreed with the known age of the fish have been carried on in two different ways. Fishes have been reared over a period of years in ponds or aquarium tanks and the scales of these fishes of known age studied in an effort to determine the true time relation of the marks. Other workers have marked fishes which were released into their natural waters and recaptured later. The known history of the scale was compared with the history interpreted from the scale.

Hoffbauer (1898–1901) in his original work used aquarium carp (*Cyprinus carpio*) of known history, and he observed that marks were produced on them over the winter period, and that the ridges were closer together at the winter period of the scale. He worked with other fishes (*Carassius carassius, Aplites salmoides,* and *Sander lucioperca*) and confirmed these results.

Recently several investigators have studied the scales of fishes of known age over most of the period of their life and the results have in each case confirmed the correlation of scale age and fish age.

Fraser (1918) examined the scales of several salmon (*Oncorhynchus nerka*) which had been reared in a pond of a hatchery. These fishes were four years old when the scales were examined. They had spawned, as normally, in their fourth year. The figure given of one of the scales shows the four years recorded on the scales; furthermore, Fraser states that the four years of record could be quite readily made out on the scales of all the fishes studied. Three fairly distinct breaks can be observed on the scales which have the same characters as those found on the normal free living fishes.

Van Oosten (1923) has examined the scales of whitefishes kept for nine years in the New York aquarium and has found that even these nine-year-old fishes bear a record of each winter on their scales.

Several small large-mouthed basses and bluegills, which were kept in tanks for experimental purposes, have acquired over the winter period a typical year mark (Plate I, F, H).

In the early work with the salmon in Scotland and in England, marked fishes when returned the next year were found to have added one growth ring in each case. The addition of one annulus over one winter for fishes of various ages led these workers to place confidence in the interpretation of the annuli as winter marks.

Recently the results of some marking experiments on the Pacific salmon have been presented by Snyder (1921, 1922, 1923). In 1920, three marked king salmon were captured. They had been liberated in the Sacramento River in 1918, having been hatched in 1917 and held in ponds until 1918. All showed the expected three winter marks. In 1919, 250,000 marked king salmon were released from the Fall Creek Hatchery. Twenty-three king salmon bearing the mutilation mark were recaptured in 1921 when they were returning up the Klamath River to spawn. The scales of all showed a history of two winters and their return in the year expected is evidence that the history, as worked out for these fishes from their scales, is identical with the true history, and that computed age agrees with the real age. Another fish from an earlier marking is included in the study. A king salmon obtained in 1919, showed by its marks that it belonged to the marking experiment of 1916; both its history and its scales showed it to be five years old in 1919. This extends the period of correlation with known life up to the five-year period. In 1923, Snyder examined the scales of more fishes of the 1919 experiment mentioned first, and found that all returned agreed with known history, and were now four years old. No salmon of the 1919 year mark had other than four-year-old scales.

THE CONFIRMATION OF SCALE INTERPRETATIONS

The work of Lea and others has also produced evidence of a slightly different nature which tends to confirm the correlation of actual and computed age. The clearest evidence of this relation comes from the history of the 1904 group of herring. Lea discovered that the most abundant fishes in the herring catch were the 1904 group, and from a knowledge of the growth of the herring he could predict the influence of this 1904 group on the catch. His predictions were correct, and he was able to follow for several years this abundant year group, which the scales showed always to be the 1904 group. This coincidence of age and abundance can hardly be taken to indicate anything else than a correlation of scale age and the actual age of the fish.

Gilbert (1913), in discussing the age at maturity of the Pacific salmon, concluded from scale data that the majority of the sockeye salmon spawn at four years. This conclusion coincides with the findings of previous workers, based on the return at four years of fry introduced in streams of Tomales Bay, California, and in New Zealand, not originally frequented by the species, on marking experiments, and on the quadrennial increase in the Fraser River runs to form the ''big run,'' obviously the long continued influence of a very successful hatching at one particular season many years ago.

Recently Storrow (1922), as reported in ''Nature'' (1923), has shown that the failure of the herring fisheries in the North Sea in 1921 was due to the scarcity of the 1917 year group, as determined from the scales. In the Firth of Clyde, where there was no failure of the fishes in 1921, the 1917 group was of normal abundance.

This direct evidence is supported by a rather large series of other correlations, which because of their different nature tend to give one even more confidence in the correctness of the major principles of scale study. The chief of these are the correlation of length groups with age groups determined by scale studies, and the correlation of the structural features of the annulus with the known conditions of growth over the winter.

One of the first methods used to ascertain the age of fishes was that of Peterson (1892). He found that the lengths were grouped around certain modes. He inferred that these length groups were year groups, and that each size mode represented a different hatching (fig. 3). He used *Zoarces viviparus,* in which such year groups were found to be well marked.

Thomson (1904) found that ''Corroboration of the truth of this hypothesis, that the ages of certain marine fishes may be determined by means of annual rings on the scale, is afforded by the fact that the ages ascertained by my method agree in the main with the results calculated out by other workers who have worked at the subject of the age of fish from a different standpoint. Fulton has worked out the subject in a very complete manner after Petersen's method.''

Taylor (1911) has established similar year groups for *Cynoscion regalis.*

Hubbs (1922) has found in *Notropis atherinoides* and *Helioperca incisor* that the first two year classes as indicated by length frequency graphs coincide with those in which age determination was made from the scales, and in 1921 the same author found a like correlation to hold for *Labidesthes sicculus.*

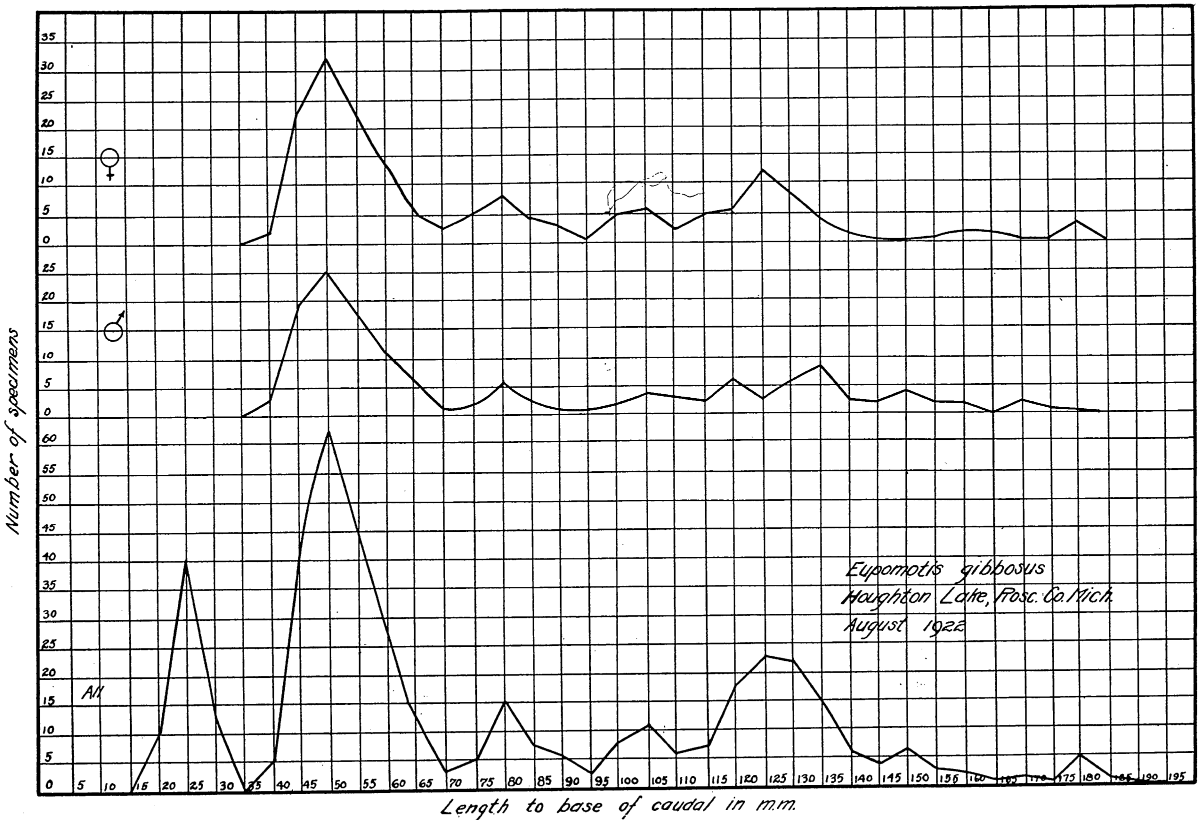

FIG. 3.—The freqnency of the various lengths of the specimens of *Eupomotis gibbosus* from Houghton Lake, Michigan, in 1922. The definite grouping of sizes indicates year classes, as is demonstrated in figure 4. There is a slight indication of differential growth of the sexes in the graph of the separate sexes. The ordinates indicate the number of specimens, the abscissae the length of the fish to the base of the caudal fin in mm.

Such length frequency graphs as worked out for the common sunfish of Houghton Lake, Michigan, show definite groups. These groups, based on the length of the fishes and supposedly representing year groups, coincide very well with the year groups established for these same fishes on a basis of scale data (fig. 4).

Similar length-frequency modes are present in most of our freshwater fishes, as indicated in the investigation of the fishes of Douglas Lake, Michigan, conducted by Mr. Hubbs and the writer. Such a correlation could hardly be explained except on the basis that the total scale marks represented total years since hatching.

CASES OF DISAGREEMENT BETWEEN AGE AND NUMBER OF ANNULI

Several cases have, however, been noted in which the age of the fish is not the same as the number of annuli. All of these are in connection with the early history of the fish.

In the European eel there are no scales in the leptocephalus and elver stages. Not until the metamorphosis takes place does the scale start its development (Ehrenbaum and Marukawa, 1913); thus for a period of years no record is found on the scales. In *Hippoglossoides platessoides,* Huntsman (1919) found that the scales do not start growth until the metamorphosis from the larval stage. This usually occurs late in fall but in some cases growth of the scales does not start until after the first winter. Such fishes, then, do not record the true number of winters in their life.

In several viviparous perches (Embiotocidae), Hubbs (1921b) has found that the embryos before birth have scales of normal characteristics, but the most recently born young have a fairly typical annulus formed at the margin of the scale during the summer just after birth. This ''metamorphic annulus'' he considers the result of a temporary retardation of growth immediately following birth, and as caused by the changes in the method of feeding and respiration forced upon the young fishes at birth. These fishes have, then, one more annulus than winters of life, and the metamorphic annulus is not to be counted in age determination.

THE EVIDENCE OF GROWTH CESSATION IN WINTER

There is considerable evidence that the Centrarchidae and some other fishes actually cease growing in winter, when the annulus is formed.

Reighard (1906) states that during the winter the small-mouthed bass (*Micropterus dolomieu*) stops feeding, and begins to hibernate. Minnows ordinarily consumed in a short time live in the hatching ponds with the basses over winter, and form their food in the spring when ice leaves the ponds and feeding is resumed.

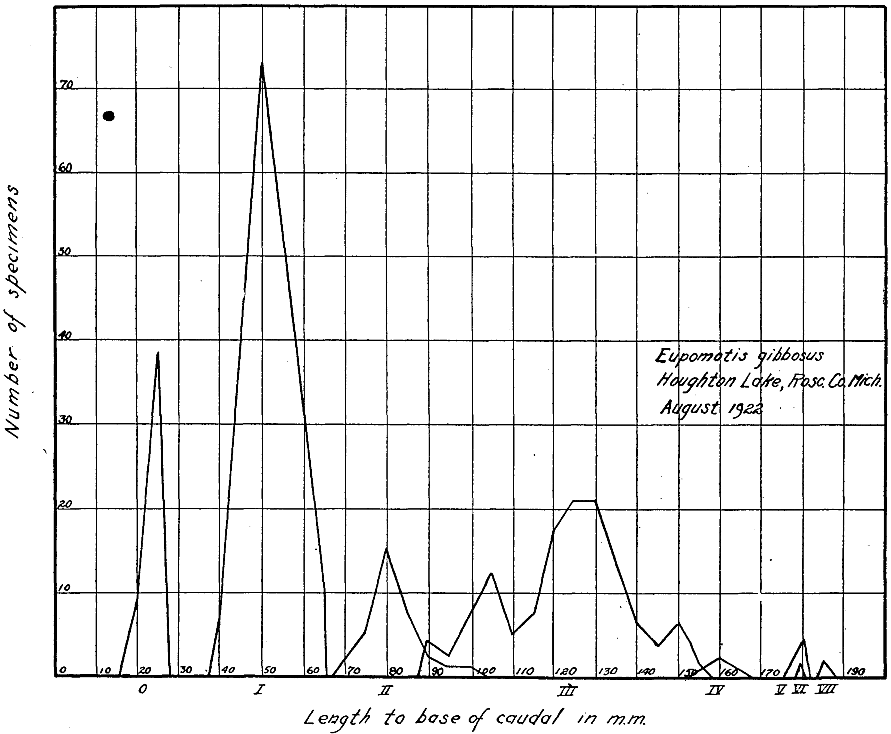

FIG. 4.—The frequency of the various lengths of each year class in *Eupomotis gibbosus*. Year groups are indicated by Roman numerals. The ordinates indicate the number of specimens while the abscissae indicate the length in mm. to the base of the caudal fin.

Pearse (1919) found that "adult crappies" (*Pomoxis sparoides*) do not appear to feed in the winter. Though fishing was carried on each week with gill nets or with hooks and lines, none were caught from October 14 to February 14. His table of the average length of young crappies from Lake Wingra, Wisconsin, at various times in the year also shows that this fish certainly does not grow after the first of November. The average length on July 31 was 30.8 mm., on August 29, 37.8 mm., on November 18, 47.7 mm., and on December 2, 47.2 mm. This shows a growth of 7 mm. for the period between July 31 and August 29. If this rate of growth continued throughout the winter, by December 2 the fishes would have attained an average size of 58 mm., rather than 47.2 mm.

Hubbs (MS.) determined that *Notropis atherinoides* and *Helioperca incisor* taken in December contained no food.

Jacot (1920) presented a table of the lengths of forty-four catches of young mullets (*Mugil cephalus* and *Mugil curema*), which shows that for most of the December, January and February period the young mullets pass the winter without growth.

Hubbs (1921c) found that in *Labidesthes sicculus* "during winter there occurs a cessation of growth," which is evident from a comparison of the size of the young late in fall and the size of adults in spring.

Van Oosten (1923) shows that for the whitefish (*Coregonus clupeaformis*) living in the New York Aquarium "the scales of the aquarium whitefish ceased growing sometime in August or September and resumed growth in April or March."

Several bluegills (*Helioperca incisor*), taken in the winter, were measured and kept in aquariums supplied with cold water. Live food was placed in the tanks but the fishes ate very little. As long as the fishes were retained in the cold water no growth of the fish or the scales took place, but when the fishes were placed in tanks of warm water they ate the food supplied and started to grow; an annulus was then formed on the margin of the scale. All fishes examined from this series taken in the winter time showed the fall condition of the scale. Only when growth started was an annulus formed (Plate I, F, H). Such annuli are therefore formed by a period of growth cessation in the winter time. The similar structure of the annuli of most of our freshwater fishes suggests the probability that the same condition holds for all.

Townsend (1923) indicates that small-mouthed basses kept in the New York Aquarium feed very little during the winter period.

The study of the rate of growth of newly hatched fishes has shown they increase at such a rapid rate over much of their growing period in the summer that if this rate of growth were continued throughout the winter the fishes would be much larger at the end of the winter than the year-old fishes actually are. This is an indication of a retardation, at least, of the growth rate during the winter.

Jacot's (1920) contention that the mullets (Mugil) feed undiminishingly throughout the winter, as indicated before, is based on an incorrect interpretation of the approximation of the ridges and the characteristics of growth cessation marks.

Taylor (1916) concluded from feeding experiments that "feeding habits have no influence upon the formation of annuli." He used fishes already growing; some of these were fed well, while others were starved. No annulus was formed, but this might have been expected, as it requires not only a period of cessation of growth, but also a resumption of growth to produce a mark on the scale. The well-fed fishes continued to grow while the starved fishes stopped growing, and died before a renewal of growth took place.

It may be concluded from all the evidence that an annulus is produced after a period of growth cessation which occurs in the winter time, and that only one true annulus is produced in a year.

GROWTH CESSATION DURING NORMAL GROWING SEASON

On many scales marks are often produced which are not indicative of yearly growth (Plate I, F). In some cases these marks are found on a few scales only, but in others the mark may be present on all scales. Such marks may readily be confused with true annuli, and thus lead to a false determination of age. In those fishes in which the approximation of the ridges is the chief character used in the determination of the annulus, much care and experience is necessary to properly interpret these accessory marks formed during the growth of the scale. In rare cases a scale may show such a confusion of marks that it is impossible to determine its history.

When the mark is found on a few scales only it may be indicative of an individual scale condition and hence not of general interpretation in terms of the growth history of the fish. But when the mark is found on most of the scales it is indicative of some event in the history of the fish which has effected the entire body.

These growth marks do not have all the characteristics of the year mark, hence their determination as marks formed during the growing season rather than as true year marks often may be made on the lack of characteristics and upon their position on the scale. They are usually at a distance from the preceding annulus, which would be abnormal for a winter mark.

Such marks are produced on a growing scale and, in contrast to annuli, which are formed by growth resumption after a period of growth cessation, they usually do not mark a discontinuity in the sculpturing of the scale. They often involve only the anterior margin of the scale, being indicated by an approximation of the ridges or by a sudden straightening of the ridges across the space between two radii. Often only one straight ridge is formed and this may involve only one part of the anterior margin. A space wider than the normal distance between two ridges may also be present along the part of the margin involved. In some cases the mark may be traced onto the lateral field or even to the posterior field on one side but usually not on both sides. If the accessory mark goes entirely around the scale, certain characters may serve to distinguish it from a true annulus, such as its position in reference to the last formed annulus and the fact that the change in direction of the ridges in the posterolateral angle is developed only late in the fall and is not, therefore, a characteristic of the marks formed during the growing season even if it involves the posterolateral field.

These marks formed during the growing season seem to be caused by a short period of growth cessation, during the normal growing period, or, if only an approximation of ridges is present, to a retardation of growth.

SCALE REGENERATION

Several of the life-history marks of the scale depend for their formation on scale regeneration. Certain irregularly centered scales present a condition of total regeneration (Plate I, D, G) while marginal regeneration is found to accompany certain life-history events (Plate I, A, B, E, F).

Very early in the study of scales it was noted that a few scales presented a very different focus and central region. The chief differences noted were in the presence of an unusually large focus followed by widely spaced ridges (Plate I, C).

Agassiz (1834) suggested that this condition of the focus was due to a wearing down of the older part of the scale. Peters (1841) and Salbey (1868) insisted that this could not be the case as the scale was covered with epidermis, which would protect the scale from any such wear. They intimated that the scale grew in size in this central portion after the ridges were produced on the surface.

Hoffbauer (1898) noticed that some scales from a given fish often showed this abnormal focus, while others on the same fish did not.

Johnson (1904) postulated that these abnormal foci marked regenerated scales. Dahl (1911) offered a similar explanation. Scott (1911) presented a paper on regenerated scales experimentally produced in *Fundulus heteroclitus*. From the photographs of these it is very clear that they are identical with those abnormal scales found on fishes with otherwise normal scales. Even up to the present time the history of these scales has remained in doubt, for Scott's paper has been overlooked in life-history investigations, and in preparing it he was apparently not aware that similar scales had been described from normal fishes and had caused confusion in the work on life-history.

The following experiments and observations made upon regenerated scales serve to make the determination of such scales certain and leave no doubt as to their characters. The general facts and explanation of the production of scales and of the sculpturing of their surface which are presented in this paper are found to hold in the case of regenerated scales, in such a way as to confirm the validity of these observations and inferences.

Several small bluegills (*Helioperca incisor*) obtained during their first winter were measured and the forward section of one side completely denuded of scales. These fishes were kept in a tank and starved. Later examination showed that clear plates representing the enlarged foci of regenerated scales were being developed on the side denuded of scales (Plate I, G). As the regenerating scales were examined from time to time it was found that ridges were being formed about the growing scale margin. When the plates attained the condition of imbrication ctenii were developed on that part of the surface which overlapped the enlarged focus of the regenerating scale next in front. During all this time the fish had not grown any in length, yet many ridges, very widely spaced but otherwise normal, were produced.

Fraser (1917) realized the value of the regenerated scales in indicating the time of the loss of the old scale and in the size of the fish at the time of the loss. The number of annuli and the position of the last one in reference to the margin of the scale give the years and parts of years since the loss of the scale. Measurements of the scale give, by calculation, the size of the fish at the time of the loss of the scale. Fraser did not correctly interpret the regenerated scale, however, and his computations are consequently incorrect. He measured to the edge of the focus and indicated that the growth from there out was made after the scale had been lost and represented proportional growth in the fish. As was indicated above some of the ridges are laid down while there is no corresponding fish growth. As soon as the scale reaches a size large enough to cover the space available for it this rapid production of ridges is replaced by normal scale growth and development. If the fish is growing at the time of regeneration no very sharp line is produced on the scale, the widely spaced ridges grading into the more closely approximated normal ones. If, however, the regenerated scale is being formed on a fish that is not growing, a sharp line is formed, the widely spaced ridges closely abutting the normal ones. It is from this line of contact, where the scale growth is limited by the growth of the fish, that computation of the regenerated scale should start, not from the edge of the large focus (Plate I, D).

The regenerating scale thus goes through the same history as the normal scale, except that the area to be covered before the length of the scales is restricted by the growth of the fish is much greater than it is in the case of the initial scales. The same clear central area, the focus, is present, though larger in accordance with the fact that the amount of area available determines the size of the focus of the scale. The same widely spaced ridges are laid down as a result of their formation on a rapidly growing base, just as in the initial juvenile scale.

Ctenii are developed after the first few ridges have been formed and the scale overlaps to the focus. Since a wide portion of the margin of the scale is pushing outward at about the same time, rather than the relatively narrow margin in the original scale, several spines are usually developed in the first row rather than the one or two which usually are formed on the original scale (Plate I, D). Gilbert and Hubbs (1920) have similarly noted that the number of spinous ridges in the scales of certain macrouroid fishes is much higher in regenerated than in normal scales.

On the anterior margin radii are produced in the same manner as in the ordinary scale, but they are usually more numerous.

Regeneration in this case recapitulates the original development, for the regenerated scale is produced by the action of the same tissues working under conditions which are similar except for differences in the area of surface involved.

MARGINAL REGENERATION

Several conditions may cause the destruction of the margin of the scale after it has been laid down. During periods of starvation the shrinking of the body often brings scales into closer contact with each other laterally so that either or both may lose part of the lateral edge of the scale (Plate I, F). Other injury, such as the entrance of a parasite (Plate I, A, C, E) or a mechanical injury, may cause a partial loss of the scale (Plate I, B). Such partial areas of destruction are rebuilt as soon as the scale can start growth. The broken contour of the ridges of the scale sculpturing is left, however, and may be readily identified later.

An important case of marginal regeneration is found in the spawning mark of the scale of the Atlantic salmon. This mark was first described by Johnson (1905). He explained it as the result of absorption at the periphery of the scale at the time that the fish went into fresh water to spawn. He attributed the destruction of the margin to the mechanical vicissitudes of river life and the act of spawning. Creaser (1926) has studied a similar case in the smelt. Masterman (1913) has shown, however, that the spawning mark is often produced before the fish enters the river, and in some cases long prior to spawning. He suggests that the scales are absorbed in the same manner as other tissues during the development of the gonads. Whatever the cause of the absorption may be, it is certain that the characteristics of the mark are caused by the destruction of the marginal sculpturing and the later rebuilding of the destroyed parts of the scale.

In cases of extreme starvation, such as may occur in overcrowded aquariums or ponds, the scales, as mentioned above, may lose a portion of their lateral margins (Plate I, F). Not all scales are involved in this loss but those of the side are especially effected. If later, under more favorable conditions, the scale begins to grow by increase around this broken margin a characteristic mark is left. Such marks were experimentally produced in a small-mouthed bass. The extent of the absorption indicates the degree of starvation, and by computations from the scale some estimate of the amount of loss in size and in weight may be determined.

Frequently, at the edge of the exposed field of the scale in its ventral or dorsal margin, a triangularly shaped indentation is found. This is apparently the point of invasion of a parasite, for cysts of parasites are occasionally found in these openings (Plate I, C), which occur in a few scales only. The indentations are later filled in by the growing edge of the scale (Plate I, A, E), ridges being extended into the opening along with the reforming base of the scale. Since these rebuilt sections are so characteristic it is possible to determine if there has been an invasion of the scale by a parasite, the time of the year in which this occurred and the size and age of the fish when the parasite entered.

The chief characteristics of any partial regeneration are the broken margin of the scale about which new ridges are formed and the wide spacing of the ridges in the quickly reformed area. Partial regeneration is usually found on the dorsal and ventral borders of the scale, frequently on the posterior border and only very rarely on the anterior margin of the scale.

THE SIZE OF THE SCALE IN RELATION TO THE SIZE OF THE FISH

One of the earliest observations in regard to the nature of the growth of fish scales was the fact that they increased in size rather than in number to cover the growing fish. All the early scale anatomists realized this fact, and it was clearly stated by Steenstrup (1861) that scales, except placoid denticles, increase in size as the fish increases. The value of this fact in relation to life-history studies was first appreciated by Johnston (1904). He devised from it the method of calculating the length of the fish for each year of its life by a comparison of the proportional width of the yearly areas of the scale. Since this time the study of the relation of the scale increase to fish increase has been taken up in order to establish the true mathematical relation of this proportion.

That scales do increase in size rather than in number is concluded from the following evidence. The average number of scales in a given species from a given locality is about the same for small fishes as for larger fishes. For example, the one-year sunfishes from Douglas Lake, Michigan, have an average of 35 scales, while several larger fishes on which scales were counted showed an average of 36. Both sizes stay within the limits of individual variation. Factors of race and temperature (Hubbs, 1922) may alter the number. The variation within a given race is often so slight as not to interfere with the collection of valuable data on the relation of fish growth and scale growth, but in some fishes there is so much individual variation in the number and consequent size that satisfactory demonstration of the relation of fish growth and scale growth can be made only by selecting fishes with the same number of scales.

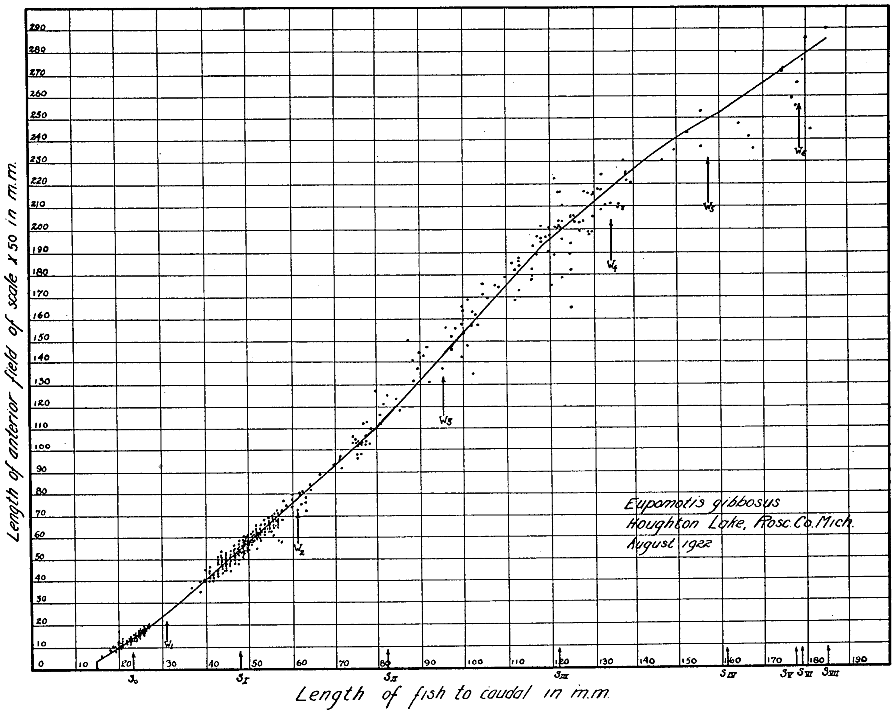

FIG. 5.—The length of the anterior field of the special scale in mm. × 50 (ordinates) as compared to the length of the fish to the base of the caudal fin mm. (abscissae). The dots indicate the position of each reading for all the specimens from Houghton Lake. The arrows indicate the position of the summer and winter lengths as determined from the average.

Scales have been shown to increase in size with the growth of the fish. This fact is very well shown by the relation of the size of the scale to the size of the fish in a wide ranging series of sunfishes (*Eupomotis gibbosus*) from Houghton Lake, Michigan. Here such a definite relation is found between the fish length and the scale length that it is possible to compute the length of a fish from the size of the special scale that was used in the study (Fig. 5).

Individuals of the bluegill (*Helioperca incisor*) and the large-mouthed bass (*Aplites salmoides*), from which scales had been removed, were later examined after the fishes had increased in length, and the scales were found to be much larger. In other fishes of the same species, the point on the scale before growth started was known (for the winter mark was at the scale margin); when examined later after an increase in length of the fish all scales were found to have grown beyond this point (Plate I, F, H).

If scales were formed later in life they would not show the same age and record of growth as scales formed early in the life of the fish. Almost all scales do show the same history and those few which do not are known by their special features to be regenerated scales. These regenerated scales have been produced in several fishes experimentally and their character is known so they can always be recognized. Furthermore, they just replace the missing scale.

Johnston's observation may be stated in mathematical terms as $L:S::L':S'$ where $L=$ length of fish, $S=$ length of scale, $L'=$ the unknown length of fish at the time the scale was at any point S'; therefore, $L'=\frac{L\times S'}{S}$. From this formula it is possible to determine the approximate length of the fish at any previous margin of the scale, as at an annulus or other life-history mark. This method was much extended by Dahl (1911). He found that there was a differential rate of growth of the unscaled parts included in the length, but showed that for the Atlantic salmon this error was negligible (Figs. 9, 10).

In 1910, E. Lea attempted to determine if this equation actually held. His investigation of the comparative rate of growth of scales and body were made on the herring (*Clupea harengus*). His method was to compare the size of a certain scale for a series of fishes of different lengths. A peculiar scale just behind the gill-cover was selected for measurement, its length being compared with the fish length of ages from one to twelve years. He measured the long diameter or dorsoventral diameter of the scale and found that the ratio of the total length of the fish to the length of the scale decreased slightly with age, but the ratio of the scale-covered length of the fish to the length of the scale was practically constant.

Miss R. M. Lee (1912) noticed that there were variations in the calculated lengths for various ages of fishes. Her tables of length calculations show that in general the older the fish the smaller is the average calculated length for any winter period. She suggested that a contraction of the scale would cause such a result.

Milne (1913) tested out the method of calculation from scales by measurements taken of some marked Pacific salmon. He found in one case only one-half an inch error for the kelt measurements between the actual and the calculated length as determined from the scales of a 27-inch salmon. In another case an error of three-quarters of an inch between the actual and the calculated length was found. In another fish, however, he found an error of 6 inches for a 26¼-inch fish. From this he concluded "either that the scale is abnormal, or that Dahl's system of measurement is not applicable to a fish that has spawned." He also found some lack of agreement in measurements of different scales from the same fish.

E. Lea (1913) found that the calculated yearly increments in length of herrings, determined from different ages, showed a similar variation. The computations of the first three annual increments decrease with the increasing age of the scale from which they are determined. For the next three annual increments (4–7) they increase as the age increases, while for later increments (8–11) they apparently remain constant. His explanation is (p. 35): "These differences are not due to methodical errors occuring in the material used. On the contrary they represent important features in the biology of the fish, *viz.*, sexual development correlated to the growth, separation of the individuals of a year group in components of different sexual development and intermingling of these components in the course of time."

Winge (1915) determined for four specimens of codfish the relation of scale growth to fish growth. His determinations were based on fishes which were measured, marked, and later recaptured after a varying growth. These four grew from 31 centimeters to 43; 40 centimeters to 45 centimeters; 40 centimeters to 51 centimeters; and from 43 to 66 centimeters. For this relatively short period of growth he found that in general there is a close correlation between fish and scale growth.

Huntsman (1919) analyzed the results arrived at by Winge, showing that for the smallest cod the scales on the average grew proportionally more than did the whole fish. In the three larger cods the scales grew proportionally less than the fish. Huntsman concluded that "these results indicate a definite change in the growth of the scale relative to the growth of the fish, namely an early more rapid and a later less rapid growth."

Meek (1916) has concluded from the discrepancies between the calculated and actual values of the average lengths of herring of a certain year that "it is evident therefore that the scale does not grow exactly at the same rate as the fish."

In 1915, Fraser introduced a constant into the scale equation which relieved much of the discrepancies of the notably low computed value obtained for the sizes of young fishes. Since the fish did not have scales until of some size, he subtracted this unscaled size from the length of the fish.

With the introduction of this constant the scale formula takes the form of $L' = C + \frac{S'}{S}(L - C)$, C being the constant of the size of the fish at the time the scales are formed.

Huntsman (1919) studied the relation of scale length to fish length for several species of fishes. He extended the method of Lea and measured selected dimensions of scales from the same position on the body of fishes of each size. For *Clupea harengus* he found that there was a decrease in the value of fish length divided by the total scale length which at first was very rapid but later extremely slow. These lengths, when compared by plotting one against the other, indicated that the scales appear when the herring is approximately 45 mm. long, which agrees with the actual observations. For the forward measurements of the scales taken from the sides of the fish, he found that after the scale begins to grow there is a very rapid fall in the body-scale ratio, which becomes more gradual as the larger size is reached. In the much later stages of growth the scale grows proportionally less than the body, so that the ratio again rises.

Using such data the changes in the calculated values are: ''The length of the first winter period decreases rapidly at first, 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 remaining periods the length increases from the first, but more at the beginning than later.''

He likewise found in fishes belonging to such diverse groups as the Clupeidae (*Clupea harengus*), the Labridae (*Tautogolabrus adspersus*) and the Pleuronectidae (*Pseudopleuronectes americanus*), there ''is a lack of correspondence in the rates of growth of the scales and of the body as judged by their anteroposterior diameters. The scale begins its growth later, grows relatively more rapidly than the body during the first half of life and more slowly than the body during the second half.

''In the Alewife (*Pomolobus pseudoharengus*) scales from different regions show differences in time appearance and in rate of growth. The anterior and posterior fields of the scale do not appear at the same time nor grow at the same rate. The posterior field appears first, grows very rapidly for a short period and then at approximately the same rate as the entire fish. The anterior field does not grow uniformly, there being a lack of correspondence in the increase not only of the two chief diameters (transverse and longitudinal) but also of the several longitudinal diameters (median and lateral).''

Miss Lee (1920) has shown that ''there is a tendency for the youngest fish at any size to have smaller scales than the older fish, *i.e.,* the scales in rapidly growing fish have not developed in the same degree as in slow growing fish. It is shown that as the differences are very small and as ratios only of the scale length are used, these facts have no significant effect on the average results.''

Van Oosten (1923) worked out the correlation between growth in length of body and scales for the whitefish (*Coregonus clupeaformis*) by a comparison of the actual average size of a series of fishes of the same age with the size calculated from the scales. He found that the calculation from the anterior scale length gave an average value somewhat lower than the average of actual measurements over the third year where there were numbers sufficient for reliable data. The posterior field gave values much higher, while the total diameter of the scale gave a figure very close to the actual average. He concludes from his data that "the diameter increases in length in simple proportion to the increase in the length of the body during the fourth year and increases at a slightly slower rate relative to the body in the fifth and seventh years and presumably also in the sixth for which no value can be given." "The anterior radius of the scale grows faster relatively than the body with age whereas the posterior radius grows more slowly with age. None of the measured scale dimensions therefore grow strictly proportionate to the body."

Data on the actual increase in length of a scale during a known increase in length of fish has been obtained for the bluegill (*Helioperca incisor*). Fishes captured during the winter with the scales at the first winter mark were fed until an increment of about 10 mm. had been made. The increase of fish and scales from various parts of the body is shown in the table for one fish which grew 10 mm. This fish growth when compared with the scale increase shows that for many scales there is little deviation from the direct proportion during the short scale increment of about 0.2 mm. It is possible, then, to calculate the size of the fish to a point attained soon before capture, in the case of the yearling fishes. One can then accurately determine the winter size of such fishes from the known size of the fish during the following summer and the measurement of a scale. The size of such fishes taken at any time throughout the growing season, therefore, may be directly compared by calculating back to the winter mark at the end of the last full season of growth.

For the establishment of the relation of scale increase to fish increase in the common sunfish, a definite scale from an area where the scales are quite uniform in size was measured and compared with the length of the fish. This scale (on the eighth series behind the gill opening at the lower edge of the opercular flap, and on the fourth row below the lateral line) could usually be quite definitely located and since all the scales in this region were quite uniform in size and shape a fairly close comparison could be made.

Except for certain errors this method quite closely reveals the growth of the scale. The chief source of error is in the individual variation in the number of scales which throws out of agreement scales that may have had about the same proportional growth. The loss of scales may tend to allow surrounding scales to grow at an increased rate. But where the individual variation is low and no absorption of the scale margin has taken place, and a large number of a series of sizes are measured, the relation of scale growth to fish growth can be determined very accurately.

TABLE 2

Growth of fish and of scale in the bluegill (Helioperca incisor)

Size of the fish at the year mark 57 mm. to base of caudal
Size of fish at death 67 mm.
Growth increment, 10 mm.

Region of Body	Length of scale x50		Calculated lengths	
	To annulus	To margin	Increment	Length at annulus
Scales just posterior to opercular flap	65	76	10	57
	57	66	9	58
	65	76	10	57
	60	71	10	57
Scales from opercle	50	60	11	56
	30	34	8	59
	40	45	7	60
	20	22	6	61
Scales from lower side of fish between pelvic and anal fin	56	67	11	56
	60	69	9	58
	60	70	10	57
	60	70	10	57
Scales from midpoint between anal and origin of soft dorsal	70	80	8	59
	71	82	9	58
	72	82	8	59
	75	82	8	59
Scales from caudal peduncle	70	81	9	58
	65	75	10	57
	65	75	10	57
	65	75	10	57
Just below spinous dorsal	40	47	10	57
	40	48	11	56

When these scale measurements are plotted against the fish length, a regression line is formed (fig. 5). If the proportion between scale length and fish length were a simple direct one, a straight line originating at the zero-zero point would result. The equation would then be $L' = \frac{L \times S'}{S}$, the original scale equation. This is not, however, the form of the actual curve, which does not originate at the zero-zero point but at some distance from it at that length attained when the fish first develops scales. This correction may be made in the ordinary way by the introduction of this value as a constant in the equation, subtracting it from the length before the cal-

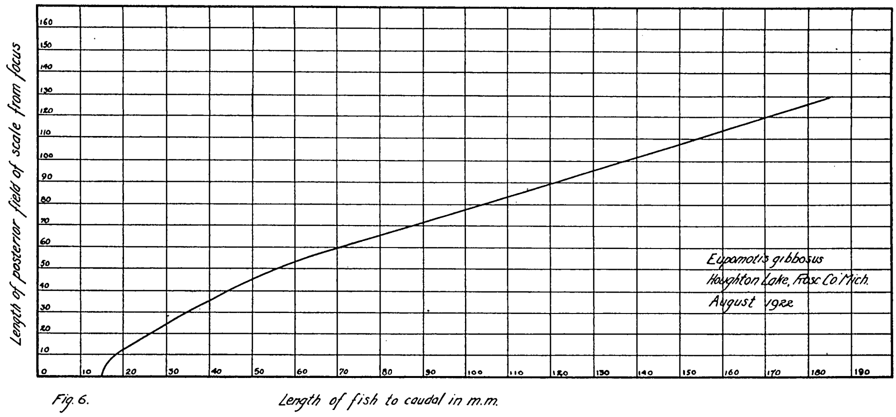

Fig. 6.

FIG. 6.—A graph formed after the method used for figure 5, but from which the dots have been omitted, showing the relation between the posterior field of the scale in mm. x 50 (ordinates) as compared with the length of the fish to the base of the caudal fin in mm. (abscissae). The data for this graph are contained in Appendix II.

culation is made. The formula as already stated, then, takes the form $L' = C + \frac{S'(L - C)}{S}$, but this will hold only in general since the line is not a straight one from this correction point. In many cases the above formula gives results which are not at all in accordance with the facts.

For the sunfish (*Eupomotis gibbosus*) an analysis was made of the relation of the posterior, anterior, and total length of the scale to the length of the fish. In each case the actual length of the area of the particular scale was plotted against the corresponding fish length. The relation in each case was found not to be direct, for the regression line took the form of a curve originating at some distance from the zero-zero point (figs. 5, 6, 7).

The posterior field of the scale grows very rapidly at first and recovers the loss occasioned by the late formation of the scale. The measurements for the posterior field were taken from the center of the focus, all of which is formed at approximately the same time; therefore, the curve rises straight for about 3 mm. or one-half the size of the focus. The posterior field then continues to grow proportionately faster than the fish until the fish is about 60 mm. long, at which time a direct relation is established between the rate of scale growth and fish growth, indicated on the graph by a straight line. This does not mean that one can properly make growth computations in the fishes larger than 60 mm. by means of the ordinary formula. For example, fishes 150 mm. long have the posterior field of the scale 2.2 mm. long on the average, while those 85 mm. in length have this field averaging 1.4 mm. long, not 1.25 mm. as would be the case if a direct proportion held throughout life. It does, however, show that in the older fishes this posterior area grows in a constant proportion to the growth of the fish. Only points in line with each other and the zero-zero point (or the correction point if the equation involving Frazer's correction is used) agree with the formula. No simple formula can be given for this curve. The later part of it (after 60) might be written easily to hold for calculations back to 60 mm., but there would be an ever changing relation for the remainder of the curve. For calculations from the posterior field, it is better to refer past scale margins directly to the curve, which will indicate the size of the fish on the average for that scale length. In the sunfishes, since it is difficult to determine definitely the annuli on the posterior field, no calculations were made from measurements of this field.

The proportionate length of the anterior field of the scale and the length of the fish also shows an interesting relation when plotted as a regression line (fig. 5). The line starts at 15 mm. from the zero-zero point and quickly rises to 3 mm., due to the inclusion of one-half of the focus in the measurements. At first the scale gradually grows more rapidly in proportion than the fish length and the curve bends upward. This continues and is increased more at a fish length of about 80 mm. As the fish reaches about 120 mm. in length, the scale grows proportionately 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. The form of the curve has important relations to the form of the growth curve for this fish, as will be taken up later in this paper.

From the shape of the curve, it is at once evident that no simple formula can be derived to calculate accurately the length of fishes at past scale margins or annuli. The calculation of an average length of fish for an average size of scale at a given annulus may be readily and accurately determined by reference to the curve. This process is at once more accurate and simple than that of averaging calculations made by any corrected formula. In the case of individual scales, however, it is not safe to avoid the use of calculations. Scales which are small for one reason or another, on the average doubtless grow in much the same general relation to the growth of the fish as does the average scale from a selected point. For the calculation from these 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 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

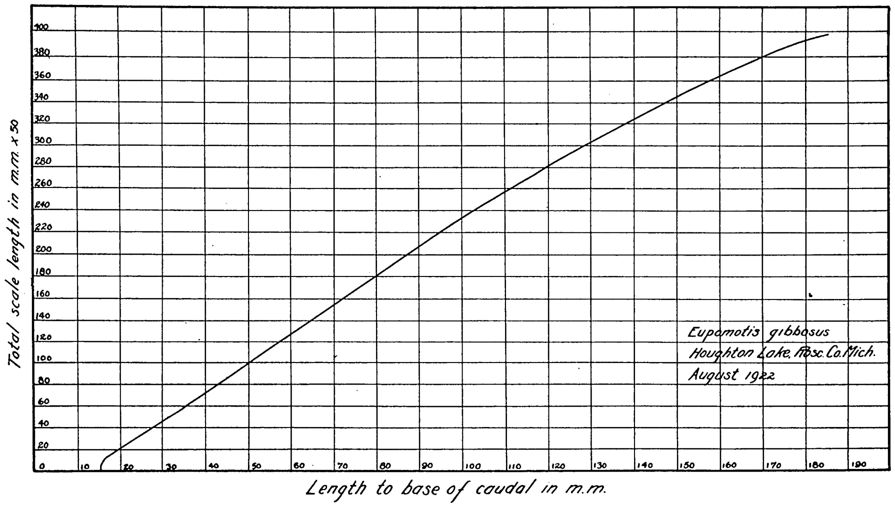

FIG. 7.—A graph formed after the method used for figure 5 from which the dots have been omitted, showing the relation between the total scale length in mm. x 50 (ordinates) and the length of the fish to the base of the caudal fin in mm. (abscissae). The data for this graph are in Appendix II.

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.

For the sunfish, using the average size of the scale at the annuli for the various year groups at Houghton Lake, Michigan, the following corrections to the computation formula were found necessary.

From fishes in second summer to fishes at first winter, add 1 mm.
From fishes in second summer to fishes at second winter, add 1 mm.
From fishes in third summer to fishes at first winter, add 2 mm.
From fishes in third summer to fishes at second winter, add 5 mm.
From fishes in third summer to fishes at third winter, add 3 mm.
From fishes in fourth summer to fishes at first winter, add 1 mm.
From fishes in fourth summer to fishes at second winter, add 2 mm.
From fishes in fourth summer to fishes at third winter, subtract 1 mm.
From fishes in fourth summer to fishes at fourth winter, subtract 5 mm.
From fishes in sixth or seventh summer to fishes at first winter, subtract 0 mm.
From fishes in seventh summer to fishes at second winter, subtract 0 mm.
From fishes in seventh summer to fishes at third winter, subtract 5 mm.
From fishes in seventh summer to fishes at fourth winter, subtract 12 mm.
From fishes in seventh summer to fishes at fifth winter, subtract 3 mm.

When these two curves are combined, that is, the total scale length is plotted against the length of the fish, a very different regression line results. Originating at the point corresponding to the formation of the scales, it rises in a straight line to a point corresponding to a length of about 120 mm., after which the whole scale grows proportionately less than the fish and the curve bends downward (fig. 7).

By the use of this total length of the scale, the simple formula involving Fraser's correction will give accurate results up to the 120 mm. size. For larger sizes the formula will give results much too low, especially in the older year groups. The use of the total length of the scale in the sunfish involves the errors and difficulties encountered in the measurements of the posterior field, and hence is impractical.

Van Oosten (1923) has determined by a different method, explained before, that for the whitefish (*Coregonus clupeaformis*) the total length used in the formula without Fraser's correction yields the most satisfactory results. This is likewise true of much of the later growth of the sunfish scale, as shown on the curve. Van Oosten's tests are based on material of the older year groups and there is reason to believe that computations so derived will be far too low for the first winter.

To a slight degree, the divergence from a direct ratio taken by the growth of the scale and of the fish is the result of the differential growth of the head and trunk. That this factor will not account for all the divergence is evident from the amount of this retarded increase in the total length due to the decreasing proportionate size of the head (fig. 9). A curve showing the relation of the anterior length of the special scale to the length of the scaled

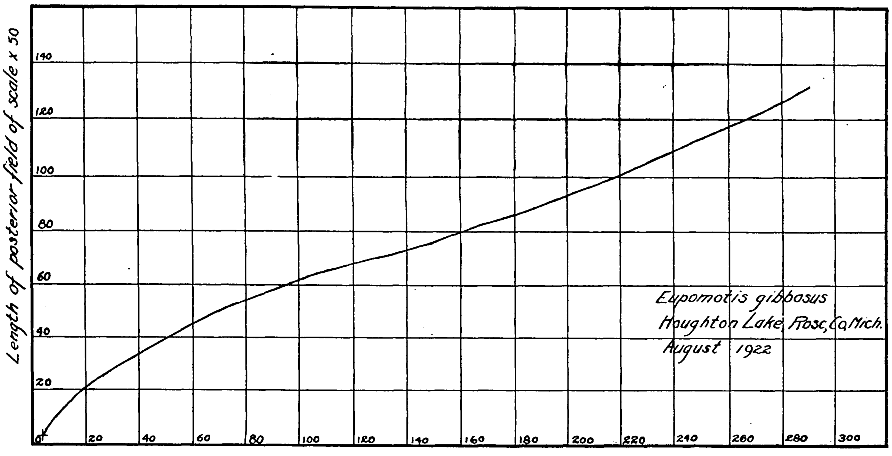

FIG. 8.—A graph showing the relation of the length of the posterior field of the scale in mm. x 50 (ordinates) as compared with the length of the anterior field of the scale in mm. x 50 (abscissae). Drawn after the method used for figure 5. Data for this graph are in Appendix II.

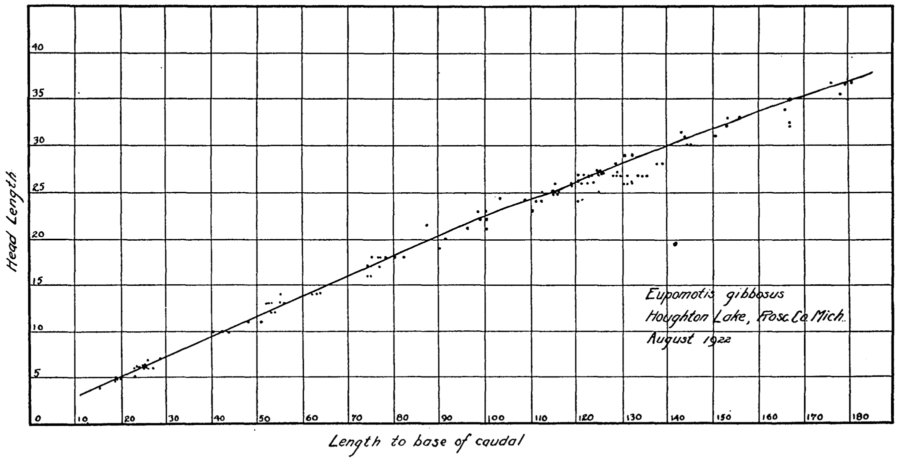

FIG. 9.—A comparison of the length of the head (ordinates) with the length of the fish to the base of the caudal fin (abscissae). In later years the head grows more slowly than the rest of the body. This differential growth introduces an error into the length determination used in the scale formula.

body to the base of the caudal fin clearly shows that the curve, as thus corrected, is of about the same form as the uncorrected curves. For computations, therefore, a complex correction would still be needed, so that in routine practice it will not be advisable to consider the point.

GROWTH CURVES

Growth curves may be based on the average size of the year classes at a given season. Such curves represent the growth quite accurately if the collection is all made within a short period of time, particularly when growth is greatly retarded or has entirely ceased, and of course if the material is sufficient. By the use of scale data, however, much more satisfactory curves may be constructed, both for the individual and for the group. If the size of the particular scale at the first annulus is measured for all ages and sizes of fishes, the average of these measurements may then, by reference to the curve showing the average relation of scale length to fish length, indicate the size of the fish at the first winter. These lengths would be winter lengths, and represent the average length of the fish at the end of the first growing season for several year groups. The length of the scale to the second annulus is then measured and in like manner the average size of the fish at the second winter is computed, and so on throughout the series. The resultant average lengths at the various winters or periods of growth cessation involves the entire series over as many years as the fishes are old, and thus gives averages that include several seasons. The growth curves obtainable by this method (one is indicated in fig. 11) are much more readily determined and are of a higher degree of accuracy than curves obtained by average computations involved in applying the ordinary formulae.

By the use of these scale curves the history of a given fish or of a given year group may be accurately determined. For the series of sunfishes at Houghton Lake, Michigan, the history of each group is presented in figure 12. The size of the fish at the annulus is determined from the average size of the identical scale at each annulus, and referring to the scale curve for corresponding average fish length.

There is an interesting relation between the form of the growth curve and the curve showing the relation between scale growth in the anterior field and fish growth. The growth curve (fig. 11) shows that there is an initial rapid growth of the fish. During this period the curve of scale-length relation shows that the anterior field of the scale is growing proportionately faster in reference to the growth of the fish. As the growth increment curve rises even more rapidly in later periods of immaturity, the anterior field of the scale grows even faster in proportion, its divergence from the direct proportion being much sharper. At about 120 mm., the curve of length increment starts on a decline throughout the period of maturity. This decline in somatic growth at maturity probably results from a shifting of mitotic activity to the germ plasm. The curve showing the relation of the

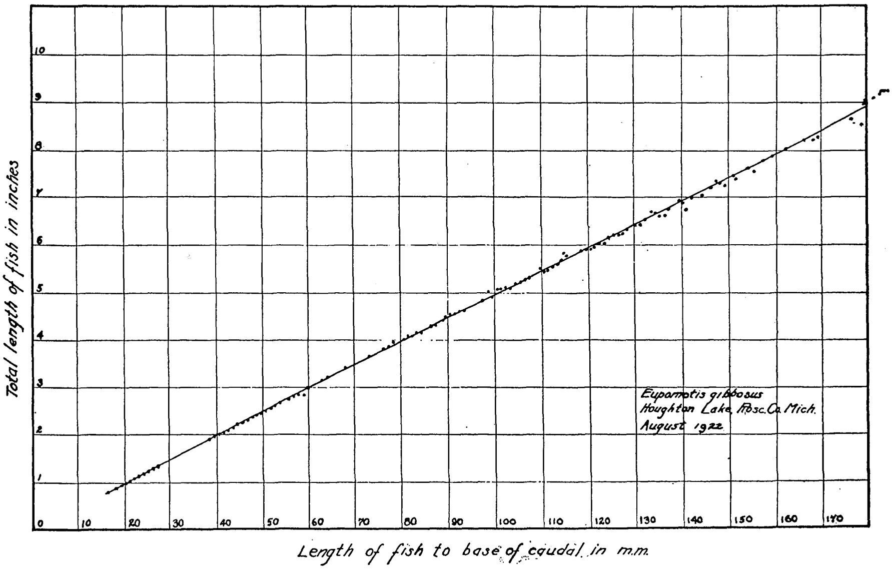

FIG. 10.—The length of the fish, including the tail (ordinates), compared with the length of the fish without the tail (abscissae), indicating that the caudal fin increases in length at about the same rate as the rest of the fish.

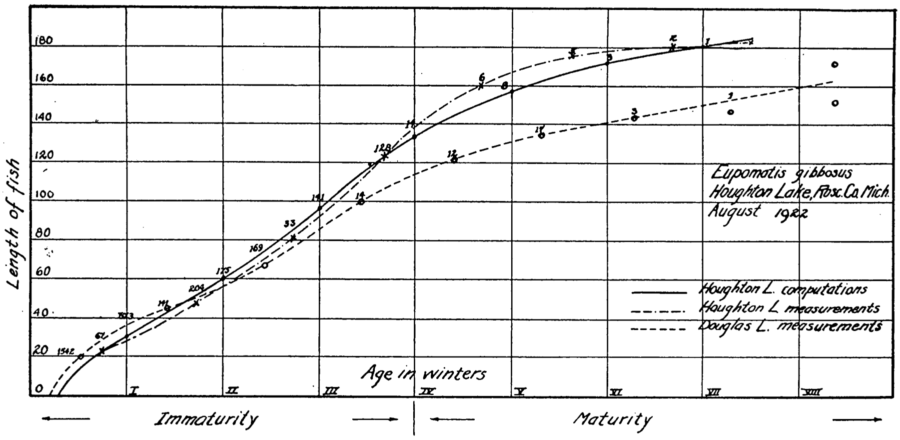

FIG. 11.—The growth increment curve of *Eupomotis gibbosus* of Houghton Lake, Michigan, as determined from the average size of the specimens of the various year groups, all collected in 1922, and from those collected from Douglas Lake in 1921. The numbers indicate the number of specimens. The ordinates indicate the length in mm. to the base of the caudal fin and the abscissae the time in years.

anterior length of the scale to the length of the fish also shows a proportionately increasing lower relation throughout this period; the curve turns downward, indicating that the scale is growing much slower than would be necessary to maintain a direct proportion. It is evident from this that the anterior field of the scale seldom, if ever, grows in direct proportion to the growth in length of the fish. When the growth of the fish is rapid the growth of the anterior portion of the scale is even greater than is necessary to maintain a direct proportion, and when the growth of the fish is retarded after maturity the growth of the anterior field of the scale is even more reduced proportionately.

CONCLUSIONS AND ACKNOWLEDGMENTS

An attempt has been made in the present paper to summarize critically and extend the major principles involved in the study of the scales of fishes in relation to the interpretation of their life-history. These principles are stated in the conclusions.

1. Tested scale data may be used effectively in the study of the life-history of fishes. The sequence of events in the life-history of the fish has important correlations with the nature and characteristics of the structure of the scale. The order and manner of development of the relief features of the superior layer of the scale determines the nature of the marks on the scale which are produced by those events in the life of the fish which involve an extensive change in the rate of growth of the fish and proportionally of the scale.

2. The shape of the scale is an important condition in the determination of the character of the life-history marks. In the juvenile stage of the sunfish scales, the shape is circular, but later an unequal growth of the anterior margin produces the characteristic shape found in adult scales. A change in the relative position of the focus accompanies this change in scale shape. In the sunfish, the focus is at first central, next anterior, and then posterior. Since the fields of the scale are measured from the focus, the change in shape and in the relative position of the focus determines their relative size.

3. The ridges on the sunfish scale are denticulated crests formed of transparent homogeneous hyalodentine deposited at the periphery of the scale. They are not necessarily parallel to the periphery of the scale but are often found to be at an angle to it. This may be correlated with change in shape of scale.

In the sunfish, as in many other fishes, the approximation of the ridges is not dependent alone upon the factor of the rate of growth of the scale. Inherent factors markedly affect the degree of approximation of the ridges in the different areas of the body and in the different fields of the scale. An approximation of the ridges in the sunfish scale may be demonstrated at each winter mark, but the figures are not comparable throughout

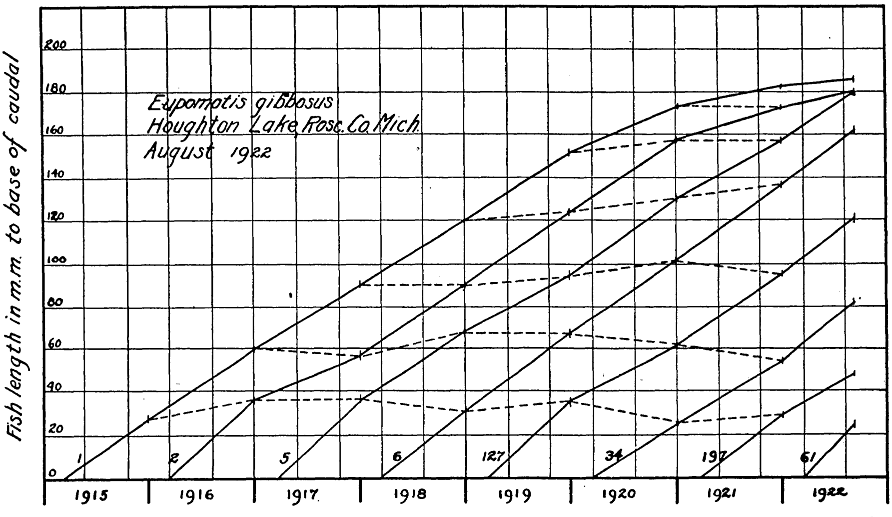

FIG. 12.—Growth increment curves of each of the year groups of *Eupomotis gibbosus* as computed from their scales, using the curve shown in figure 5. The corresponding positions of the annuli have been connected with dotted lines to indicate the corresponding growth of the various year classes. The number of specimens is indicated by numerals on the growth lines. The ordinates indicate the length of the fish to the base of the caudal fin in mm., the abscissae the year of growth.

the history of any one scale. Other special conditions of approximation are demonstrated, but in general in a given area of a given scale the increased approximation of ridges on the scale as the season progresses may be construed as evidence that the fish is growing at a much slower rate in late fall.

4. The radii are streaks of the inferior layer of the scale underlying linear interruptions on the upper layer. They seem to be regions specialized for the accommodation of flexibility and are formed on those sunfish scales in which the stress caused by the activity of the fish must be accommodated by the scale, and where the stress is of sufficient strength and is localized to prevent the formation of the superior layer of the scale along the lines which later become the radii.

The production of radii is seemingly dependent on the structure and thickness of the scale, on the degree of activity of the portion of the body where the scale is located, and on the degree of overlap of the scale.

5. Sunfish scales are at first cycloid; later they may become ctenoid by the addition of spines. These spines or ctenii are formed on the posterior surface of the scale, as soon as it grows into the epidermis, by the rapid extension of the posterior margin of the scale in the normal oblique direction.

A differential development of the ctenii (or spines) is present on the sunfish scale. These areas of differential development coincide with the year marks. The long, sharp, obviously freshly formed ctenii are always found in the posterior margin of the scale, even of the oldest sunfish. This is taken as evidence that even these oldest fishes had not ceased growing.

6. Scale marks are formed by a cessation or change in the rate of growth of the scales and by a change in the degree of mineralization or fixation of the pattern. Three types of marks are described, (1) those of the cessation of scale growth, (2) those of variation in the rate of scale growth, and (3) those of regeneration.

7. A winter mark or annulus may be defined as the point of change in sculpturing produced when the normal scale pattern of the fall is discontinued during the cessation of growth, and is circumscribed by the resumption of the normal spring growth, the elements of which are developed without reference to the unfinished sculpturing of the fall edge. In some species an approximation of the ridges during the fall, contrasted with the wide-spaced ridges of spring, serves to mark the annulus. It is not, however, a universal character.

8. That the annulus of northern fishes is produced during a period of growth cessation in winter is evident from the observed time of formation, the correlation of known age with computed age, the nature of the formation, and the confirmation of the predictions based on scale data.

9. Marks are produced on some scales which resemble year marks, but are not indicative of yearly growth. They often involve only the anterior margin of the scale and have other characteristic features. These marks formed during the growing season seem to be caused by a short period of growth cessation or a retardation of growth.

10. Lost scales are replaced by scales characterized by an unusually large focus followed by widely spread ridges. If a portion of the scale is lost it is also regenerated. The spawning mark of the Atlantic salmon is caused by such regeneration. Extreme starvation, invasion of parasites, and mechanical injury leave characteristic marks of regeneration.

11. The relation of the increase in size of the scale to the increase in the length of the fish is found to be a complicated one. In the sunfish the relation of the posterior, anterior, and total length of the scale to the length of the fish was established by the measurement of these fields on a special scale throughout a wide series of sizes from Houghton Lake, Michigan. From the shape of the regression lines obtained from these measurements, it is evident that no simple formula can be stated for the calculation of the length of fishes at past scale margins or annuli. The calculation of an average length of fish for an average size of scale may be readily and accurately determined from the regression lines. For the calculation of individual scales, it is best to use the ordinary scale formula with the addition of a correction, obtained from the regression line, for the various year groups, by projecting a line from the average size of the year groups in question as explained in the text.

12. By the use of scale data at least two types of growth curves may be constructed. The average size of a given age group forms the data for one type, while the average size at all ages of all material based on proportionate length of scales and fishes forms the data for the other. The two types agree very well in the sunfish. The growth history of any one year group may be worked out from such data. Since these figures are based on a known relation of scale length to fish length, very accurate results are obtained in contrast to the unknown accuracy of the results obtained from the ordinary scale formulae.

This study has been carried on under the immediate direction of Carl L. Hubbs, whose remarkable knowledge of fishes has always been at the writer's command, and whose assistance has made the study possible. Professor Alexander G. Ruthven has contributed important aid in obtaining material and throughout the work has held its best interest always in mind. The Michigan State Department of Conservation, The United States Bureau of Fisheries, and Professor Frank Smith have aided in obtaining material. To all of these the writer is delighted to acknowledge valuable assistance.

ADDENDA

After this paper was first prepared, a number of pertinent contributions have come to hand. Several of these need to be referred to here.

Henry W. Beeman (Habits and propagation of the small-mouthed bass. Trans. Amer. Fish. Soc., Vol. 54, 1924 (1925), pp. 92–107) has confirmed earlier workers in showing that the small-mouth black bass is inactive over the winter. A. G. Huntsman (Growth of the young herring (so-called sardines) of the Bay of Fundy. Can. Fish. Exped., 1914–1915 (1919), pp. 165–172) has indicated that young herring cease to grow over the winter. Frances N. Clark (The life-history of *Leuresthes tenuis,* an atherine fish with tide-controlled spawning habits. Fish Bull., Calif. Fish & Game Comm., No. 10, 1925, pp. 1–58) has shown that an annulus is formed on the scales of this fish when it ceases to grow during its prolonged summer spawning, but is rarely formed over the winter, when growth is ordinarily continued.

A. H. Leim (The life-history of the shad (*Alosa sapidissima* (Wilson)) with special reference to factors limiting its abundance. Contr. Can. Biol., N. S., Vol. 2, 1924, pp. 161–284), following Huntsman's methods, referred to in this paper, has made a study of the relative growth of scale and fish in the shad. In another study of the same species, N. Borodin (Age of shad (*Alosa sapidissima* Wilson) as determined by the scales. Trans. Amer. Fish. Soc., Vol. 54, 1924 (1925), pp. 178–184. Also in: A report on investigations concerning the shad in the rivers of Connecticut; Hartford, 1925, pp. 46–51) has introduced a new method of age-determination, in which he has counted the number of transverse radii. The validity of this method has been confirmed, through a study of the otoliths, by R. L. Barney (A confirmation of Borodin's scale method of age-determination of Connecticut River shad. Trans. Amer. Fish. Soc., Vol. 54, 1924 (1925), pp. 168–177. Also in: A report on investigations concerning the shad in the rivers of Connecticut; Hartford, 1925, pp. 52–60).

The first detailed account of the life-history of a centrarchid fish has been published by R. L. Barney and B. J. Anson (Life-history and ecology of the orange-spotted sunfish *Lepomis humilis.* App. 15, Rep. U. S. Comm. Fish., 1922 (1923), pp. 1–16). These authors used the scale method for the determination of age and growth, and their figures show annuli of the same type as those discussed in the present paper.

Einar Lea (Report on "Age and growth of the herring in Canadian waters." Can. Fish. Exped., 1914–1915 (1919), pp. 75–164) has presented the results of his careful study of the life-history of Canadian herring. In the section (III) on the "Structure of herring scales," he shows in conclusive fashion that summer bands and winter lines in their entirety are structures of the distinct superficial layer of the scale; that this external covering does not thicken with age; that the lower section, however, does increase in thickness; that this lower part is composed of overlapping fiber-sheets, and that the lamellae of the lower layer are wide in the spring and thin in the fall, and therefore that the lower as well as the upper layer of the scale builds up a record of the seasons through which the fish has passed.

Frank W. Weymouth (The life-history and growth of the Pismo clam. Fish Bull., Calif. Fish & Game Comm., No. 7, 1923, pp. 1–120) and F. W. Weymouth, H. C. McMillan and H. B. Holmes (Growth and age at maturity of the Pacific razor clam, *Siliqua patula* (Dixon). Bull. U. S. Bur. Fish., Vol. 41, 1921, pp. 201–236) have successfully read the life-history of certain clams from the year lines on the shells, produced by the cessation of growth in the winter, and have given a good general discussion of growth and life-history problems.

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APPENDIX I

LENGTH OF ANTERIOR FIELD OF SCALES OF EUPOMOTIS GIBBOSUS

The first value in each line represents the number of the annulus out to which the measurement was made. The second figure is this measurement in mm. Following this is given the number of individuals (in parenthesis) for each specified year of hatching.

I 0.24: 1920(2), 1921(4), total(6).
I 0.26: 1918(1), 1920(4), 1921(5), total(10).
I 0.28: 1920(2), 1921(3), total(5).
I 0.30: 1920(4), 1921(11), total(15).
I 0.32: 1920(5), 1921(8), total(13).
I 0.34: 1920(4), 1921(10), total(14).
I 0.36: 1920(3), 1921(13), total(16).
I 0.38: 1920(3), 1921(9), total(12).
I 0.40: 1915(1), 1918(2), 1919(6), 1920(1), 1921(24), total(34).
I 0.42: 1917(1), 1919(1), 1920(2), 1921(13), total(17).
I 0.44: 1917(1), 1919(10), 1920(1), 1921(14), total(26).
I 0.46: 1918(1), 1919(5), 1920(2), 1921(9), total(17).
I 0.48: 1919(4), 1921(8), total(12).
I 0.50: 1916(1), 1919(6), 1920(1), 1921(14), total(22).
I 0.52: 1919(4), 1921(6), total(10).

I 0.54: 1919(8), 1921(2), total(10).
I 0.56: 1919(4), 1921(6), total(10).
I 0.58: 1919(2), 1921(4), total(6).
I 0.60: 1917(1), 1919(5), 1921(11), total(17).
I 0.62: 1919(1), 1921(5), total(6).
I 0.64: 1919(2), 1921(4), total(6).
I 0.66: 1919(4), 1921(1), total(5).
I 0.68: 1919(7), total(7).
I 0.70: 1918(1), 1919(8), 1921(8), total(17).
I 0.72: 1919(6), total(6).
I 0.74: 1919(7), 1921(1), total(8).
I 0.76: 1919(5), total(5).
I 0.78: 1919(7), 1921(1), total(8).
I 0.80: 1917(1), 1918(1), 1919(9), 1921(2), total(13).
I 0.82: 1919(4), total(4).
I 0.84: 1919(1), 1921(1), total(2).
I 0.86: 1919(1), total(1).
I 0.88: 1919(2), total(2).
I 0.90: 1916(1), 1919(2), total(3).
I 0.92: 1919(1), total(1).
I 0.94: 1919(1), total(1).
I 0.96: 1917(1), 1919(1), total(2).
I 0.98: 1919(2), total(2).
I 1.00: 1919(1), total(1).

Averages for measurements to first annulus for each year of hatching (number of cases in parenthesis): *1915,* 0.40(1); *1916,* 0.70(2); *1917,* 0.64(5); *1918,* 0.50(6); *1919,* 0.65(127); *1920,* 0.34(34); *1921,* 0.45(197; average for all years, 0.50(373 cases).

II 0.98: 1919(1), total(1).
II 1.00: 1919(2), total(2).
II 1.02: 1920(1), total(1).
II 1.04: 1919(1), 1920(1), total(2).
II 1.08: 1919(1), total(1).
II 1.10: 1919(6), 1920(4), total(10).
II 1.12: 1920(1), total(1).
II 1.14: 1919(3), 1920(1), total(4).
II 1.16: 1920(1), total(1).
II 1.20: 1916(1), 1917(1), 1919(7), 1920(3), total(12).
II 1.22: 1919(4), 1920(1), total(5).
II 1.24: 1919(3), 1920(2), total(5).
II 1.26: 1918(1), 1919(3), total(4).
II 1.28: 1919(3), total(3).
II 1.30: 1917(1), 1920(4), total(5).
II 1.32: 1919(1), total(1).
II 1.34: 1919(3), 1920(2), total(5).
II 1.36: 1919(5), 1920(3), total(8).
II 1.40: 1917(1), 1919(4), 1920(3), total(8).

II 1.44: 1919(1), 1920(1), total(2).
II 1.46: 1919(1), 1920(1), total(2).
II 1.48: 1919(3), 1920(2), total(5).
II 1.50: 1915(1), 1918(1), 1919(10), 1920(2), total(14).
II 1.52: 1919(2), total(2).
II 1.54: 1919(6), total(6).
II 1.56: 1919(4), total(4).
II 1.58: 1919(1), total(1).
II 1.60: 1916(1), 1918(1), 1919(4), total(6).
II 1.62: 1919(1), total(1).
II 1.64: 1919(1), total(1).
II 1.66: 1919(2), total(2).
II 1.68: 1919(2), total(2).
II 1.70: 1919(6), total(6).
II 1.72: 1919(2), total(2).
II 1.74: 1919(4), total(4).
II 1.76: 1919(1), total(1).
II 1.78: 1919(1), total(1).
II 1.80: 1919(9), total(9).
II 1.82: 1919(1), total(1).
II 1.84: 1918(1), total(1).
II 1.86: 1919(1), total(1).
II 1.88: 1919(1), total(1).
II 1.90: 1917(1), 1919(3), 1920(1), total(5).
II 1.92: 1919(1), total(1).
II 1.98: 1919(2), total(2).
II 2.00: 1918(1), 1919(4), total(5).
II 2.10: 1918(1), 1919(3), total(4).
II 2.12: 1919(1), total(1).
II 2.16: 1919(1), total(1).
II 2.26: 1919(1), total(1).
II 2.40: 1917(1), total(1).

Average for measurements to second annulus for each year of hatching (number of cases in parentheses): *1915*, 1.50(1); *1916*, 1.40(2); *1917*, 1.62(5); *1918*, 1.72(6); *1919*, 1.54(127); *1920*, 1.30(34); average for all years, 1.49(175 cases).

III 1.80: 1919(2), total(2).
III 1.96: 1919(1), total(1).
III 2.00: 1919(7), total(7).
III 2.04: 1919(1), total(1).
III 2.06: 1919(1), total(1).
III 2.12: 1919(1), total(1).
III 2.14: 1919(1), total(1).
III 2.20: 1919(4), total(4).
III 2.22: 1919(2), total(2).
III 2.30: 1919(2), total(2),
III 2.40: 1918(1), 1919(5), total(6).

III 2.42: 1919(1), total(1).
III 2.44: 1919(1), total(1).
III 2.46: 1919(1), total(1).
III 2.48: 1917(1), total(1).
III 2.50: 1919(1), total(1).
III 2.52: 1917(1), 1919(1), total(2).
III 2.58: 1919(3), total(3).
III 2.60: 1916(1), 1917(1), 1919(1), total(3).
III 2.64: 1919(3), total(3).
III 2.66: 1919(2), total(2).
III 2.68: 1919(1), total(1).
III 2.70: 1916(1), 1919(6), total(7).
III 2.74: 1919(2), total(2).
III 2.76: 1915(1), 1918(1), total(2).
III 2.80: 1919(7), total(7).
III 2.84: 1919(1), total(1).
III 2.86: 1919(1), total(1).
III 2.88: 1919(3), total(3).
III 2.90: 1919(2), total(2).
III 2.92: 1919(2), total(2).
III 2.94: 1919(2), total(2).
III 3.00: 1919(9), total(9).
III 3.04: 1919(1), total(1).
III 3.06: 1917(1), total(1).
III 3.10: 1918(1), 1919(7), total(8).
III 3.14: 1919(1), total(1).
III 3.16: 1919(2), total(2).
III 3.18: 1919(2), total(2).
III 3.20: 1919(5), total(5).
III 3.22: 1919(1), total(1).
III 3.24: 1918(1), 1919(2), total(3).
III 3.26: 1919(2), total(2).
III 3.28: 1919(1), total(1).
III 3.30: 1919(1), total(1).
III 3.32: 1919(2), total(2).
III 3.34: 1917(1), 1919(2), total(3).
III 3.36: 1919(1), total(1).
III 3.38: 1919(1), total(1).
III 3.40: 1919(4), total(4).
III 3.42: 1919(1), total(1).
III 3.44: 1919(1), total(1).
III 3.46: 1919(1), total(1).
III 3.50: 1919(2), total(2).
III 3.52: 1919(1), total(1).
III 3.54: 1918(1), total(1).
III 3.56: 1919(1), total(1).
III 3.60: 1918(1), 1919(2), total(3).
III 3.72: 1919(1), total(1).
III 3.78: 1919(1), total(1).
III 3.80: 1919(1), total(1).

III 3.82: 1919(1), total(1).
III 3.86: 1919(1), total(1).
III 3.90: 1919(1), total(1).

Averages for measurements to third annulus for each year of hatching (number of cases in parentheses): *1915,* 2.76(1); *1916,* 2.65(2); *1917,* 2.80(5); *1918,* 3.10(6); *1919,* 2.84 (127); average for all years 2.84(141 cases).

IV 3.80: 1916(1), total(1).
IV 3.94: 1917(1), total(1).
IV 4.00: 1915(1), total(1).
IV 4.08: 1917(1), total(1).
IV 4.12: 1917(1), total(1).
IV 4.18: 1918(1), total(1).
IV 4.20: 1918(1), total(1).
IV 4.32: 1916(1), total(1).
IV 4.44: 1917(1), total(1).
IV 4.60: 1917(1), 1918(1), total(2).
IV 4.64: 1918(2), total(2).
IV 4.70: 1918(1), total(1).

Average for measurements to fourth annulus for each year of hatching (number of cases in parentheses): *1915,* 4.00(1); *1916,* 4.06(2); *1917,* 4.24(5); *1918,* 4.49(6); average for all years 4.30(14).

V 4.60: 1917(1), total(1).
V 4.80: 1915(1), 1916(1), total(2).
V 4.92: 1917(1), total(1).
V 5.00: 1916(1), 1917(1), total(2).
V 5.04: 1917(1), total(1).
V 5.30: 1917(1), total(1).

Averages for measurements to fifth annulus for each year of hatching (number of cases in parentheses): *1915,* 4.80(1); *1916,* 4.90(2); *1917,* 4.97(5); average for all years, 4.93(8).

VI 5.10: 1916(1), total(1).
VI 5.40: 1915(1), 1916(1), total(2).

Averages for measurements to sixth annulus for each year of hatching (number of cases in parentheses): *1915,* 5.40(1); *1916,* 5.25(2); average for all years, 5.30(3).

VII 5.70: 1915(1), total(1).

APPENDIX II

The measurements of the scale of *Eupomotis gibbosus* from Houghton Lake, Michigan, listed with the length of the fish and the age.

The first value in each represents the number of annuli on the scale. The second value is the length of the fish to the base of the caudal fin in mm. The third value is the total length in inches and fractions. The fourth is the length × 50 in mm. of the anterior field of the special scale. The fifth is the length × 50 in mm. of the posterior field of the same special scale.

0:16; 13/16:5; 7
0:18; 14/16:8; 10
0:19; 15/16:7; 10
0:19; 15/16:10; 11
0:19; 15/16:10; 12
0:20; 1:9; 12
0:20; 1:12; 13
0:20; 1:12; 15
0:20; 1:12; 15
0:21; 1:9; 10
0:21; 1 1/16:10; 11
0:21; 1 1/16:10; 11
0:21; 1 1/16:12; 15
0:21; 1 1/16:11; 14
0:21; 1:10; 14
0:21; 1 1/16:13; 15
0:22; 1 2/16:11; 14
0:22; 1 2/16:12; 15
0:23; 1 2/16:12; 14
0:23; 1 2/16:12; 13
0:23; 1 2/16:14; 17
0:23; 1 2/16:14; 14
0:23; 1 2/16:13; 16
0:23; 1 2/16:13; 14
0:23; 1 2/16:13; 14
0:23; 1 2/16:13; 15
0:24; 1 3/16:16; 20
0:24; 1 3/16:14; 12
0:24; 1 3/16:14; 15
0:24; 1 3/16:14; 15
0:24; 1 3/16:12; 12
0:24; 1 3/16:13; 15
0:24; 1 2/16:16; 16
0:24; 1 2/16:15; 18
0:24; 1 2/16:13; 17
0:24; 1 4/16:16; 16
0:25; 1 4/16:16; 20
0:25; 1 3/16:16; 19

I:48; 2 6/16:54; 40
I:48; 2 5/16:56; 41
I:48; 2 4/16:54; 40
I:48; 2 6/16:59; 44
I:48; 2 7/16:52; 40
I:48; 2 7/16:57; 37
I:48; 2 3/16:55; 41
I:48; 2 6/16:53; 42
I:48; 2 6/16:52; 45
I:48; 2 6/16:50; 41
I:48; 2 6/16:53; 45
I:49; 2 7/16:55; 45
I:49; 2 7/16:55; 45
I:49; 2 7/16:57; 45
I:49; 2 7/16:54; 45
I:49; 2 7/16:56; 42
I:49; 2 7/16:54; 47
I:49; 2 6/16:52; 42
I:49; 2 7/16:55; 43
I:49; 2 6/16:50; 42
I:49; 2 6/16:58; 40
I:49; 2 9/16:52; 42
I:49; 2 5/16:58; 45
I:49; 2 6/16:53; 42
I:49; 2 7/16:54; 41
I:49; 2 7/16:59; 41
I:49; 2 7/16:61; 49
I:49; 2 7/16:59; 45
I:50; 2 8/16:59; 48
I:50; 2 8/16:59; 42
I:50; 2 8/16:60; 46
I:50; 2 8/16:56; 46
I:50; 2 7/16:63; 45
I:50; 2 8/16:60; 47
I:50; 2 8/16:59; 62
I:50; 2 8/16:55; 41
I:50; 2 8/16:54; 40
I:50; 2 8/16:54; 38

0:25; 1 4/16:17; 20
0:25; 1 3/16:15; 19
0:25; 1 3/16:15; 14
0:25; 1 4/16:15; 15
0:25; 1 4/16:17; 18
0:25; 1 4/16:17; 17
0:25; 1 4/16:14; 14
0:25; 1 4/16:18; 21
0:25; 1 4/16:16; 17
0:25; 1 4/16:17; 17
0:26; 1 5/16:18; 19
0:26; 1 5/16:18; 20
0:26; 1 4/16:18; 21
0:26; 1 4/16:16; 18
0:26; 1 4/16:15; 19
0:26; 1 5/16:18; 20
0:26; 1 5/16:15; 17
0:26; 1 4/16:18; 16
0:26; 1 5/16:19; 19
0:27; 1 6/16:19; 21
0:27; 1 5/16:19; 19
0:27; 1 6/16:20; 17
0:27; 1 5/16:20; 17

I:38; 1 11/16:37; 31
I:39; 1 15/16:40; 35
I:39; 1 15/16:35; 30
I:40; 2.40; 34
I:40; 1 15/16:46; 37
I:40; 2:40; 36
I:41; 2 1/16:42; 38
I:41; 2:45; 38
I:41; 2 1/16:47; 40
I:41; 2:40; 35
I:41; 2:45; 38
I:42; 2:43; 37
I:42; 2 2/16:41; 35
I:42; 2:42; 38
I:42; 2 1/16:43; 34
I:42; 2 2/16:52; 34
I:43; 2:43; 34
I:43; 2 3/16:50; 43
I:43; 2 2/16:49; 40
I:43; 2 2/16:44; 38
I:43; 2 2/16:50; 36
I:43; 2 3/16:48; 38
I:43; 2 3/16:51; 41
I:43; 2 1/16:45:32
I:44; 2 3/16:47; 34

I:50; 2 8/16:58; 47
I:50; 2 9/16:57; —
I:50; 2 7/16:60; 46
I:50; 2 7/16:57; 45
I:50; 2 8/16:50; 45
I:51; 2 8/16:58; 44
I:51; 2 9/16:61; 43
I:51; 2 9/16:58; 41
I:51; 2 8/16:61; 47
I:51; 2 8/16:58; 48
I:51; 2 8/16:63; 46
I:51; 2 9/16:57; 50
I:51; 2 8/16:59; 44
I:51; 2 8/16:58; 43
I:51; 2 7/16:59; 44
I:51; 2 8/16:57; 45
I:52; 2 9/16:64; 66
I:52; 2 9/16:61; 48
I:52; 2 10/16:60; 40
I:52; 2 9/16:63; 41
I:52; 2 10/16:66; 47
I:52; 2 11/16:60; 47
I:52; 2 9/16:55; 43
I:52; 2 9/16:61; 45
I:52; 2 10/16:61; 43
I:52; 2 8/16:63; 44
I:53; 2 10/16:65; 49
I:53; 2 10/16:64; 50
I:53; 2 10/16:66; 48
I:53; 2 10/16:60; 48
I:53; 2 11/16:56; 48
I:53; 2 11/16:59; 51
I:53; 2 10/16:62; 50
I:53; 2 10/16:63; 46
I:54; 2 11/16:57; 44
I:54; 2 11/16:63; 42
I:54; 2 10/16:62; 45
I:54; 2 11/16:68; 48
I:54; 2 11/16:66; 49
I:54; 2 11/16:64; 49
1:54; 2 11/16:68; 50
1:54; 2 12/16:63; 46
1:55; 2 11/16:64; 50
I:55; 2 11/16:63; 47
1:55; 2 11/16:68; 66
I:55; 2 10/16:65; 64
I:55; 2 12/16:66; 50
I:55; 2 12/16:69; 67
I:55; 2 11/16:65; 40

I:44; 2 4/16:49; 40
I:44; 2 3/16:50; 39
I:44; 2 3/16:54; 40
I:44; 2 3/16:47; 37
I:44; 2 4/16:44; 43
I:44; 2 3/16:46; 34
I:44; 2 3/16:51; 38
I:44; 2 2/16:47; 37
I:44; 2 3/16:49; 38
I:45; 2 4/16:53; 35
I:45; 2 2/16:49; 36
I:45; 2 2/16:48; 38
I:45; 2 5/16:57; 40
I:45; 2 3/16:46; 37
I:45; 2 4/16:46; 40
I:45; 2 4/16:46; 37
I:45; 2 5/16:50; 40
I:45; 2 4/16:51; 37
I:45; 2 3/16:50; 36
I:45; 2 4/16:52; 42
I:45; 2 4/16:50; 43
I:45; 2 3/16:49; 36
I:46; 2 5/16:48; 42
I:42; 2 5/16:49; 43
I:46; 2 5/16:54; 38
I:46; 2 4/16:48; 38
I:46; 2 4/16:52; 41
I:46; 2 5/16:51; 40
I:46; 2 4/16:50; 39
I:46; 2 4/16:49; 37
I:46; 2 4/16:45; 40
I:47; 2 6/16:51; 44
I:47; 2 6/16:52; 38
I:47; 2 5/16:55; 40
I:47; 2 5/16:57; 40
I:47; 2 6/16:53; 42
I:47; 2 6/16:51; 43
I:47; 2 4/16:50; 40
I:47; 2 5/16:48; 42
I:47; 2 6/16:51; 37
I:47; 2 4/16:54; 40
I:47; 2 5/16:55; 38
I:48; 2 6/16:55; 40
II:67; 3 6/16:89; 58
II:70; 3 9/16:92; 49
II:72; 3 9/16:97; 63
II:72; 3 10/16:92; 64
II:72; 3 10/16:96; 66
II:75; 3 11/16:104; 53

I:55; 2 11/16:64; 45
I:56; 2 11/16:61; 46
I:56; 2 13/16:66; 50
I:56; 2 13/16:65; 53
I:56; 2 12/16:70; 51
I:56; 2 12/16:60; 47
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PLATE I

Fig. A. A typical scale of the common sunfish (*Eupomotis gibbosus*) from Houghton Lake, Michigan, August, 1922. The normal characteristics of the relief elements in relation to the shape of the scale and to the year marks formed are shown. The fish is in its second summer.

Fig. B. Scale from sunfish (*E. gibbosus*); Houghton Lake, Michigan; August, 1922. The scale has been twisted in the pocket early in the second summer. It shows how radii are formed only along the anterior field; how a rapidly growing scale base is accompanied by wide spacing of the ridges; new ctenii are being formed along the new exposed border which is now coming into contact with the epidermis.

Fig. C. Scale of sunfish showing a parasite embedded in the lateral margin of the scale. This scale has passed one year without the addition of ctenii.

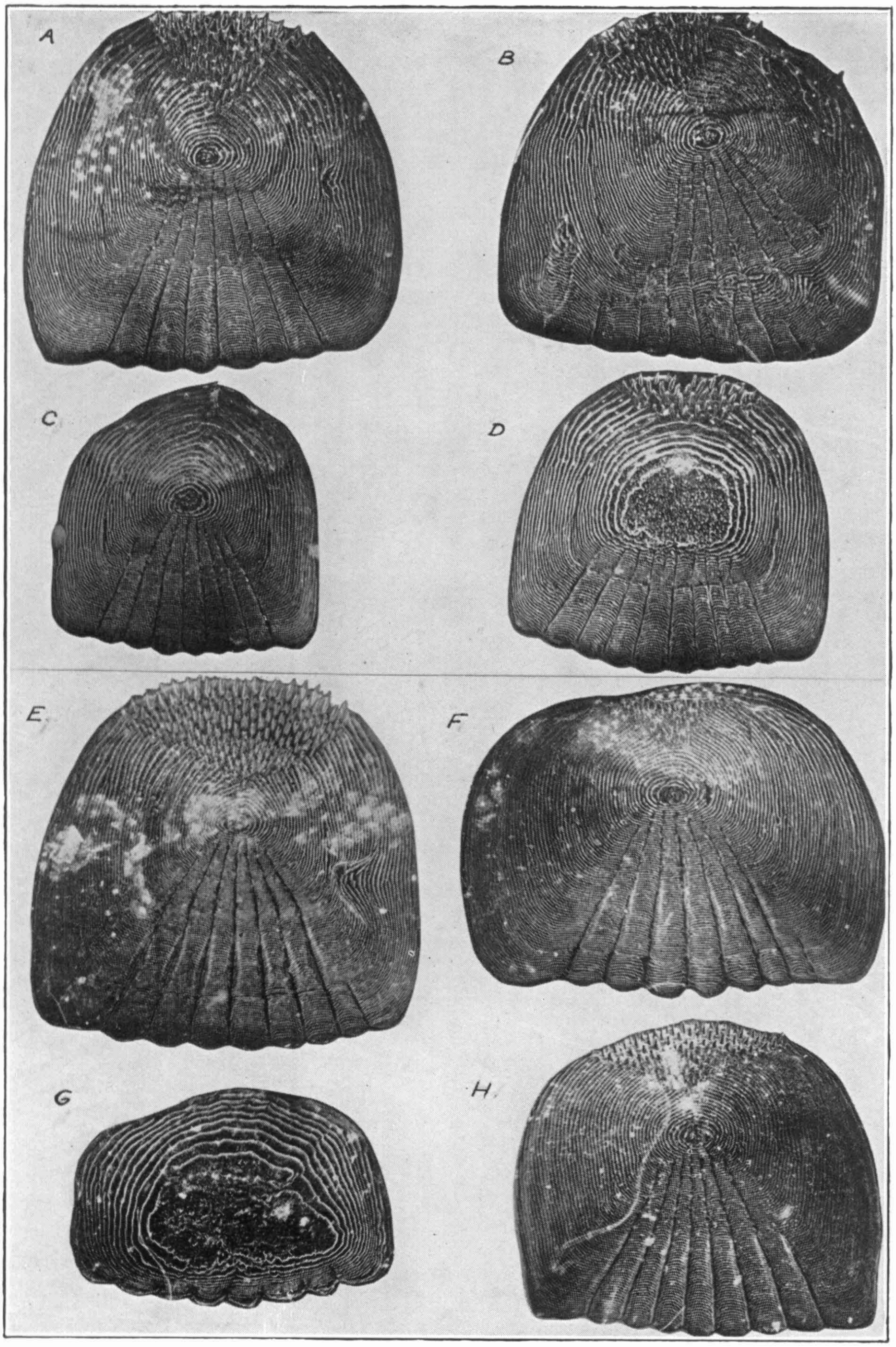
Fig. D. A completely regenerated scale found on a sunfish from Houghton Lake, Michigan, in 1922. A scale was lost before the first winter.

Fig. E. A scale from a common sunfish, in its third summer, from Houghton Lake, Michigan; August, 1922. A case of partial regeneration is indicated.

Fig. F. A scale taken from the same fish as that of Fig. H, after the fish had started its growth. A normal annulus is present. The peculiar contour of the posterior margin was caused by early starvation in the tank before growth started. There is a seasonal mark about half way toward the focus.

Fig. G. Scale regenerated on the side of a bluegill (*Helioperca incisor*), from which all the scales on the side had previously been removed.

Fig. H. A scale of a bluegill (*Helioperca incisor*) from the Huron River, Ann Arbor, Michigan, taken in winter (February, 1924). When the fish started to grow an annulus was formed as shown in Fig. F.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