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The Life History of Leuresthes Tenuis, an Atherine Fish with Tide Controlled Spawning Habits

By
FRANCES N. CLARK

TABLE OF CONTENTS.

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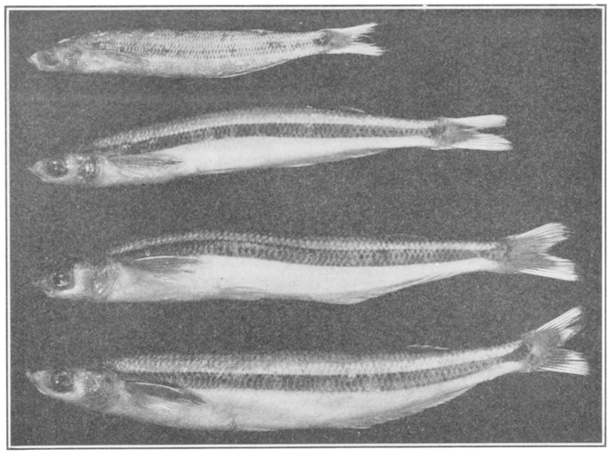
CONTENTS—Continued.



Leuresthes tenuis. Females taken November 11, 1923, representative of the O, I, II and III groups of that date. Body length, 96, 132, 149 and 158 mm.

1. I. INTRODUCTION

1.1. 1. Spawning habits

The highly specialized spawning habits of the atherine fish Leuresthes tenuis render its life history unique among those of the fishes of this family, in fact of all fishes so far recorded. In southern California, where the species is best known, the periodic spawning runs of the "grunion" are watched for with much interest by those who frequent the long, sandy beaches. The details of this peculiar method of spawning have been accurately worked out by Thompson (1919*b*). The results of his work may be summarized briefly as follows:

These fishes deposit their eggs during high tides in the sand of the beach. In accomplishing this, the fish is carried by the wash of the waves up onto the moist sand, where the female digs in, tail foremost, and there deposits her eggs, which the male simultaneously fertilizes while lying arched around her.

According to popular belief, these runs of grunion occur on the high tides of the second, third and fourth nights after the full moon. Thompson made his first observations in April, 1919. The moon was full on the fifteenth; the first fish were taken on the sixteenth, and the last on the eighteenth. Again, in May, the moon was full on the fourteenth, and the first fish observed on the sixteenth. In both cases, the run lasted three days, the sixteenth, seventeenth and eighteenth of the month. The conclusion drawn was that "the spawning run comes shortly *after* the full of the moon, in other words, *after the highest tide of the series,* which is really the significant fact."1

The advantage accrued by the grunion by spawning on these high tides immediately following the full of the moon seems clear. It was demonstrated by Thompson that the females deposited their eggs at the upper edge of the area of sand eroded by that series of tides, and that successively lower tides on the following days actually buried the egg pods more deeply in the sand than the female had been able to deposit them. Here they lie relatively unmolested2 until two weeks later when, during the next series of high tides, the waves, by renewed erosion, actually dig the eggs out of the sand.

Egg pods were collected immediately after a spawning run and taken into the laboratory where the development was watched. It was found that the eggs were ready to hatch in ten days after spawning, but that the fish were not actually liberated until the eggs were agitated and thus freed from the sand.

Throughout the summer months of 1919, March to July, the tides associated with the dark phase of the moon were one to two feet higher than those accompanying the full of the moon. With this phenomenon in mind the author concluded that the spawning of L. tenuis on the tides immediately following the full of the moon served to practically assure the liberation of the larvae by the tides accompanying the dark of the moon two weeks later.

This opportunity is taken to acknowledge the help received from many sources. Thanks are due especially to Dr. Peter Okkelberg for suggestions in connection with the cytological work; to Dr. A. G. Ruthven for many courtesies; to Mr. Carl L. Hubbs under whose immediate supervision the work was carried out, and who gave constant advice and criticism; to the California Fish and Game Commission which, through its Fisheries Laboratory, collected the material and bore much of the expense of the work; and finally, to Mr. Will F. Thompson who suggested the problem, supervised the collection of material and followed the work critically from its inception to its completion.

The possibility of the spawning runs occurring also on the dark of the moon tides was discussed. Eggs spawned at this time might remain in the sand for a period of four weeks, unless the runs occurred on tides late in the series which would be approximately no higher than those of the next full moon series. On June first and second, three days after the dark of the moon, fishes were in fact found spawning on tides of 5.7 feet and 5.0 feet, respectively. The predicted height of the next full moon tide was, on June thirteenth, 6.0 feet, thus high enough to liberate the larvae. Since the fish observed running on these two dates were very few, "the conclusion that the main run *does* occur during the full of the moon seems therefore entirely probable."3 The data presented in this paper, however, are not in accordance with this conclusion; this problem will be discussed further under the section dealing with frequency of spawning.

The spawning season was considered as beginning in March, and later Thompson (1919*a*) recorded a small run on July 15 and 16 and August 14. The spawning may thus be said to extend from March to August.

1.2. 2. The problem

This knowledge of how and when L. tenuis spawns opens up several questions concerning the life history of this fish. First, does each fish spawn but once in a season, or does it spawn on each series of favorable tides? Second, what is the age at first maturity, and do the fish spawn more than one season? Third, what is the rate of growth for the species, and does the peculiar spawning habit have any unusual influence on its growth?

An attempt has been made to answer the first of these questions by a detailed study of the history of the ova. Their growth has been traced carefully from its onset in January until after the close of the spawning season in August. The second and third problems have been attacked by means of scale studies and of length-frequency data.

2. II. METHODS

2.1. 1. Collection of material

With the exception of one collection, all of the material used in these studies was obtained by a commercial fisherman at the instigation of Will F. Thompson, in charge of the California State Fisheries Laboratory. The collections were made at stated intervals from March, 1923, to August, 1924, either within San Pedro Harbor, just outside the San Pedro breakwater or off Long Beach, California. A small series was taken near by, in Anaheim Bay, by Carl L. Hubbs on October 7, 1922.

2.2. 2. Studies of the ova

The history of the ova has been interpreted from measurements of the rate of growth and by cytological examinations. To trace their growth, measurements of the diameter of the ova were made by means of an eye-piece micrometer in a compound microscope, at a magnification which gave a value of 0.039 mm. for each micrometer unit. The diameter was determined by placing the micrometer in a horizontal position across the field of the microscope and then reading the diameter of the egg along whichever axis lay parallel with the micrometer. As the ova, due to unequal pressure and to distortion in preservation, are almost never spherical in shape, this method resulted in measurements of all axes between the shortest and the longest diameter of the egg.

In an effort to determine the statistical dependability of this method, measurements were made of the longest and shortest diameter of about two thousand ova, and the average of the two determinations taken as the true diameter for each ovum. The eggs used in these test series were from the anterior and posterior regions of the gonads of two different fish. There resulted four series of measurements of approximately five hundred eggs each. Each series was plotted as a frequency curve and compared with a similar curve based on measurements in which the diameter was determined by chance. In all cases comparison was made between curves containing an equal number of measurements of ova from the same fish. Two curves thus compared differed no more than did any two curves obtained by the same method of measurements. Therefore, it was considered safe to continue the measurement along only one axis of an ovum, this axis to be determined by the chance relation of the position of the ovum to the eye-piece micrometer. All egg measurements used in this paper were made in this manner.

For each series a very small portion of an ovary was teased out on a slide and measurements made of all ova in the field of the microscope. This process was continued until the desired number of ova from any one fish had been examined. The material was preserved in formaldehyde and the eggs to be measured were teased out in this medium.

The material for the cytological studies was sectioned in paraffine. Ordinary methods of technic were employed with the exception that cedar oil instead of xylol was used as a clearing agent. The usual difficulties in sectioning eggs were experienced, and it was found that cedar oil was more satisfactory, as the xylol tended to harden the eggs. The material was placed in xylol for only five minutes before putting into the paraffine bath. Sections were cut 10[u]. in thickness; stained in iron haematoxylin, and counter-stained with eosin.

2.3. 3. Length and weight determinations

In determining the length of each fish, two measurements were used; one from the tip of the snout to the base of the caudal fin, and the second from the tip of the snout to the posterior extremity of the midray of the tail. The first measurement, termed the body length, has been used exclusively in this paper. The second measurement was employed only as a check on the former. Measurements were made with a pair of dividers, and read on a millimeter rule to the nearest millimeter.

Weights were determined on a calibrated spring balance scale graduated to grams and read to the nearest gram. The weight, as well as the length determinations, were based on material preserved in formaldehyde. The fishes were removed from the liquid and left until the excess moisture had drained off, but they were not dried out in any manner.

2.4. 4. Statistical treatment of data

For the length-weight ralationship, the fish were grouped to the nearest half centimeter, and the average of all weights falling at each such length class was ascertained. The calculated length-weight curve was based on the formula $W=KL^3$, in which W is the weight; L, the length; and K, a constant factor which in L. tenuis was found to be 0.0089.

Other formulas used in the statistical treatment of the data are as follows:

$$\sigma = \sqrt{\frac{\Sigma f(d^1)^2}{n} - \left(\frac{\Sigma f d^1}{n}\right)^2}$$

$$\text{PE Mean} = \pm 0.67449 \frac{\sigma}{\sqrt{n}}$$

[q] represents the standard deviation; f, the frequency; d^1, the deviations from an assumed mean; n, the number of individuals; and PE, the probable error.

The probable error of the difference between the average weights for the fall and winter fish has been calculated by extracting the square root of the sum of the squares of the probable errors of the two results.

2.5. 5. Studies of scales

Scales were examined in a preliminary study from various parts of the fish, and it was found that those most favorable for study were taken either just above or just below the silvery lateral band, between the verticals from the origin of the first dorsal and the posterior margin of the second dorsal. Scales from this region were, therefore, exclusively used. Three scales were taken from each fish, cleaned in water and mounted in the sodium silicate-glycerin mixture described by Creaser and Clench (1923). Consequently all scale readings are based on at least three scales from each fish, and on a greater number in doubtful cases. To help assure an unbiased age determination, readings were made without reference to size or sex data.

Measurements were made from the center of the scale to the margin, along the anterolateral angle (see Fig. 9), by means of an eye-piece micrometer, the units of which had a value of 0.05 mm.

3. III. HISTORY OF THE MATURING OVA

3.1. 1. Growth of ova during January and February

Throughout this paper interest in the growth of the ova has been centered around those eggs whose size exceeds 0.23 mm. in diameter. It was found in collections made after the spawning season that all adult females had eggs of very uniform size limit. Any series of measurements made of ova from adult fish taken from August to December, resulted in a characteristic frequency polygon with a mode at 0.08 mm. and with an upper limit never exceeding 0.27 mm. This group of eggs has been termed the immature class and is illustrated by the uppermost polygon of Graph I. This polygon represents a combination of measurements made of 200 *ova from each of five fish* taken on November 14, 1923.4

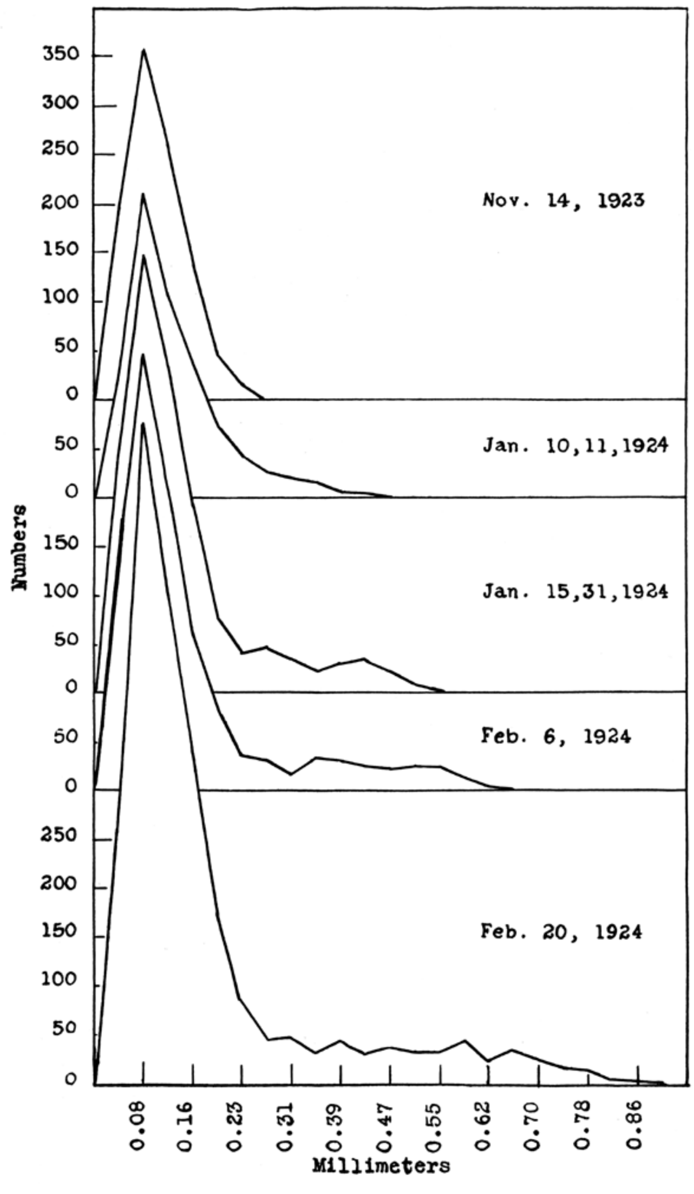
Since this class of eggs is present in every adult female during all seasons of the year, any increase in size beyond this point has been considered an indication of the beginning of growth toward maturity for the next spawning period, and the history of the maturing ova has been traced from this point.

The onset of such growth was first observed in fish collected in January. Measurements were made of ova from seven fish taken January 10 and 11, 1924. All but one of these seven fish contained ova with diameters exceeding 0.27 mm. and one showed ova 0.47 mm. in diameter. This growth continued throughout January and February. On January 31, ova were found 0.585 mm. in diameter; on February 6, 0.62 mm.; and on February 20, 0.86 mm.

Graph I illustrates this growth. Measurements of ova from five fish have been combined in each of these frequency polygons. The second polygon contains measurements of 200 ova from each of four fishes taken on January 10 and from one fish taken on January 11; the third represents 300 measurements from one specimen taken January 15 and from each of four taken January 31; the fourth, 300 measurements from each of five individuals taken February 6; and the last, 500 measurements from each of five taken February 20. For each polygon, measurements from the five fish which contained the largest ova on the date or dates concerned were combined. For example, on January 10 and 11, ova were measured from seven fish but only the measurements taken from the five with the largest ova were used in the polygon. In the two fishes omitted, the largest ovum was 0.27 mm. and 0.31 mm., respectively. Similarly, on February 20, measurements were made from fifteen fish, but again only the five containing the largest eggs were used. Among the ten omitted all stages of growth were represented from fish with ova no greater than 0.35 mm. to fish with ova of the size shown in the polygon for that date.

It is recognized that this method of combining data lends itself to criticism from a statistical viewpoint, especially since ova were not measured from an equal number of fish on each date. The selection of five fish out of seven on January 10 and 11 might not yield as great a dispersion and as high a size limit of ova as if five fish had been selected out of fifteen measured, as was done for February 20. The error thus introduced is probably slight, however, since an examination of the gonads of more than 500 females taken on these two dates in January, showed that none contained ova conspicuously advanced in size beyond the immature stage, nor approaching the upper limits of the intermediate class.

The reason for combining measurements from fish with the largest eggs only was to indicate with greater clarity the growth of the ova during January and February. Had all the data been included the upper limits of growth on any date would have been obscured by the presence of many fish in which the ova were no farther advanced than



GRAPH I. Frequency polygons of the diameters of ova measured from fish taken in November, January and February.

GRAPH I. Frequency polygons of the diameters of ova measured from fish taken in November, January and February on the previous dates. Graph I shows, therefore, the growth of the ova of the fishes which mature earliest in the season.

From Graph I, it will be seen that the immature group, as represented in the polygon for November 14, maintains its identity throughout all the polygons, but that by January growth has started beyond this point. As a result, succeeding polygons take on a multimodal character. This new group of eggs, now evident, has been termed the intermediate class for reasons which will be apparent when the later history of the maturing ova is discussed.

As the intermediate group increased in dispersion and in numbers, apparent modes became manifest and the possibility was considered, that each of these modes might represent a group of eggs which had originated simultaneously from the immature class and which would be spawned at one time, but further study seemed to discount this view. These modes could not be traced from one frequency polygon to the next with any certainty, and it appears probable that they are the result of natural or artificial irregularities.

An effort was made to determine whether the growth from the immature to the intermediate class was a constant one or whether it occurred periodically. For this purpose the data from the fish taken in January and February were combined in two ways, on the basis of the average of the cubes of deviations from zero and on the basis of the upper limits of the intermediate class. However, no definite conclusions concerning the nature of the movement from the immature to the intermediate class could be drawn from the polygons obtained by such combinations.

As already stated, all the fish collected on any one date during January and February were not in the same condition in respect to the size of their ova. The fish taken in February which had ova no larger than those in January would undoubtedly begin to spawn later in the season than those which contained eggs with diameters falling well toward the upper limit of the intermediate class.

In tracing the growth of the ova during this prespawning period the significant facts are as follows: During the first half of January no ova occur much beyond the limit of the immature class, a fact indicated not only by the measurements of 200 ova from each of seven fishes, but also by an examination of the ovaries of 537 additional females. On each succeeding data ova were found of constantly greater diameter until the latter part of February, when the upper size limit of the intermediate class (approximately 0.78 mm.) has been reached.

When the eggs have attained a diameter approximating 0.78 mm. a change in color marks the beginning of the last stage in the history of the maturing ova. The intermediate and immature eggs are of a creamy-white color, while those which are about to grow beyond the limits of the intermediate class, take on an orange hue characteristic of the mature eggs of most fishes. Ova from a few fish collected February 20 showed this change in color, and, as spawning begins in March, it is possible that these fish might have spawned on the first favorable tides on that month, March 6 to 8.

3.2. 2. Conditions during the breeding season

Growth of ova between two spawning periods.—As collections were not made after February in 1924, it is necessary to consider data obtained during April and May of 1923, in order to trace the history of the ova beyond the intermediate class. Collections were made at two or three-day intervals from April 8 to May 9. This period covered two series of high tides, one accompanying the dark of the moon, April 16, and one associated with the full of the moon, April 30. The bearings of these collections on the frequency of spawning will be discussed under that heading.

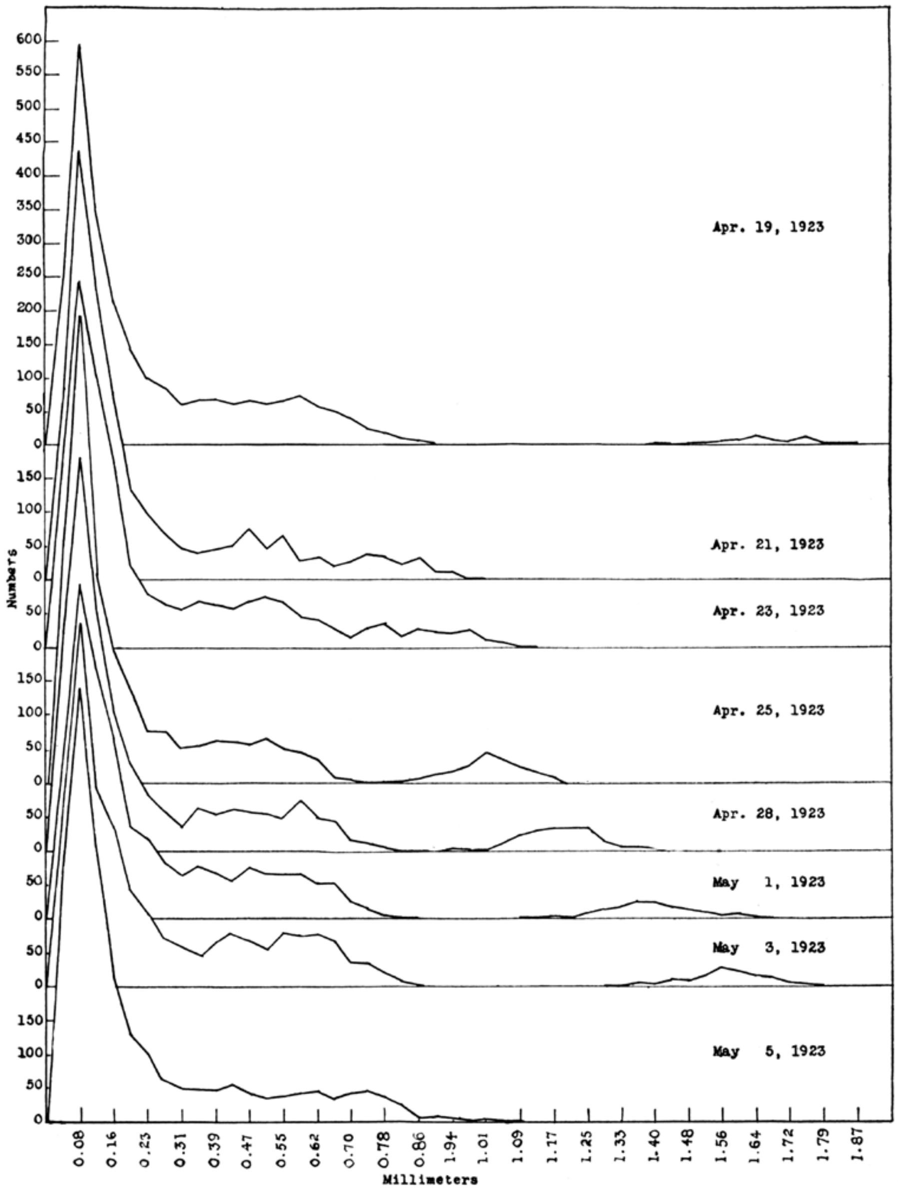
On April 8, two-thirds of the 94 females contained orange-colored ova. Measurements of eggs from fish collected on this date showed that such ova formed a distinct group somewhat larger than the upper limit of the intermediate class. In five fish, the eggs of the intermediate class did not exceed 0.78 mm. in diameter, while this new group showed a dispersion from 0.74 mm. to 1.29 mm., with the mode at 1.05. Since this new group continued to grow as a unit until actual maturity was reached, it has been termed the maturing class.

In collections of succeeding days, this maturing class showed a rapid increase in size until April 19, when it had disappeared in 18 of the 25 specimens examined. On April 21, only one fish, 4 per cent of the collection for that date, contained the maturing group, while the remainder had no eggs larger than those in the intermediate class. That the disappearance of these mature eggs was due to spawning seems unquestionable, as the first tides favorable for spawning occurred on April 17. The fish undoubtedly began to spawn on the seventeenth or eighteenth and continued on three or four days following.

Data for April 19 and following days are given in Graph II, which shows frequency polygons for eight successive dates from April 19 to May 5. Each polygon was obtained by a combination of measurements of 500 ova from each of five fish. The polygon for April 19 is made up of measurements from one fish containing mature ova and from four with immature and intermediate ova only. On April 21 and 23 the fish were selected from the collections at random, but on the following dates a maturing group was discernible and fish which contained this group were selected. On May 5, there was again no maturing group evident and the fish were consequently chosen at random.

The polygon for April 19 shows a small group of mature ova (1.40–1.91 mm.), representing the one fish in the combination which had not yet spawned, and an immature and intermediate class very similar to those two classes in the polygon for specimens taken February 20, 1924, before the beginning of the spawning season (Graph I. On April 21, growth of ova at the upper limit of the intermediate class had taken place, and the future maturing group is discernible in the mode which falls at 0.74 mm. On April 23, this group is still more clearly defined, on April 25 it barely overlaps the intermediate class, and on April 28 it has become entirely differentiated. Growth continued until May 3, when eggs of this group, now mature, averaged 1.57 mm. Tides favorable for spawning occurred on May 2, 3 and 4, and undoubtedly the fish spawned on these nights, for in the collection of May 5, no fish were found with mature eggs, and the polygon for this date shows only the intermediate and immature classes of ova.

It is apparent from the polygons of Graph II that during the time that the maturing group makes its rapid growth from the intermediate class to maturity, little change takes place in the intermediate group. Again, as in Graph I, modes are suggested in this class, but they are indefinite in location and inconsistent in number; their significance, if there is any, can not be determined from the data. However, on May 3, when one class is mature, the origin of the next maturing class



GRAPH II. Frequency polygons of the diameters of ova measured from fish taken during the spawning season.

GRAPH II. Frequency polygons of the diameters of ova measured from fish taken during the spawning season

can be detected in the increase of the measurements from 0.74 to 0.82 mm.; on May 5, this future maturing class has become clearly evident, while the mature group has been spawned out. Thus, as one group of ova matures and is spawned, it is immediately replaced by a movement of a new class outward from the intermediate group.

On May 1 and 3, the increase of the number of ova 0.16 and 0.195 mm. in diameter might indicate that at this time (the maturing class is just reaching maturity) there may have been a movement from the immature to the intermediate class. A similar condition, although less marked, was noted in the data of April 17, at a corresponding stage in the development of the maturing group. It was possible that the combining of the data according to date had obscured the true evidence concerning this suggested periodic movement from the immature to the intermediate class; especially so, since Leuresthes spawns over a period of three or four days and individual fish showed a considerable variation in the number of ova with diameters from 0.16 to 0.195 mm. To eliminate this possibility, the average size of the maturing class of ova was calculated for each fish, and combinations made on this basis. Data from three fish with maturing groups practically identical in size were used in each combination. Fifteen frequency polygons, covering a period from April 8 to May 9, were thus obtained, but they gave no clearer evidence, either positive or negative, of such a periodic movement.

Although no growth from the immature to the intermediate class could be demonstrated during the spawning season, it is fairly certain that a movement of some sort outward from the immature group takes place during this time. If all ova which were to be spawned during one season, had grown to the intermediate class by the beginning of the season, as each successive group of maturing ova moved out, the numbers of the intermediate class should be correspondingly reduced. In all frequency polygons obtained, however, the numerical ratio of the three classes remained relatively constant, thus indicating that the loss resulting from a movement from the intermediate to the maturing class was nearly equated by a similar movement from the immature to the intermediate class.

An actual count of the number of ova in the intermediate class could not be made, but the ratio of the number of intermediate ova to the number of those maturing was estimated from counts made from a small portion of an ovary. A section 1.5 mm. in thickness was cut from an ovary and all the eggs above 0.23 mm. in diameter counted. Counts were confined to dates in which there was no overlapping in the dispersion of the intermediate and the mature class, and these two groups were separated on the basis of color.

TABLE 1.—Ratio of Maturing to Intermediate Ova as Ascertained by Actual Counts from a Section of the Ovary.

Date	Length of fish in mm.	Number of maturing ova	Number of intermediate ova	Ratio, maturing to intermediate
March 13, 1923	157	50	244	1 : 4.9
March 13, 1923	144	34	164	1 : 4.8
April 5, 1924	122	51	257	1 : 5.0
April 25, 1923	131	37	129	1 : 3.5
April 25, 1923	133	56	184	1 : 3.3
May 1, 1923	130	43	187	1 : 4.3
May 1, 1923	149	64	238	1 : 3.7
July 24, 1923	147	42	72	1 : 1.7
July 24, 1923	157	60	124	1 : 2.1

TABLE 1.—Ratio of Maturing to Intermediate Ova as Ascertained by Actual Counts from a Section of the Ovary

Table 1 shows the results of such counts. In March, at the beginning of the spawning season there were approximately five times as many intermediate as maturing eggs. In the latter part of April and the first of May this ratio had been reduced to a little less than four to one. In July, the intermediate ova were about twice as numerous as the maturing. If, as Thompson (1919*b*) found, the grunion spawn every four weeks, by July 27, four maturing groups should have arisen from the intermediate class, while if it be assumed that the fish spawn every two weeks, a probability discussed under frequency of spawning, approximately eight maturing groups should have arisen by this time. Since there were not more than five times as many intermediate as maturing eggs at the beginning of the season and in July twice as many still remained, it seems probable that, during the spawning season, there is a movement from the immature to the intermediate class. This growth may be a slow continuous one or it may be periodic, taking place at the time that the movement from the intermediate to the maturing class occurs. The fate of this remnant of the intermediate class found after the spawning season, will be discussed later.

While a periodic origin of a maturing class of ova from an intermediate group, described above, may be unique for Leuresthes, the presence of three classes of ova in the gonad during the spawning season has been demonstrated in many fishes. Calderwood (1892) found "minute," "small" and "great" ova in fishes in general. However, he considered that the "great" ova would be spawned at the present season, the "small" ones a year later, and the "minute" in succeeding years.

Fulton (1899) having investigated fishes of several groups, concluded, for species with demersal eggs, that the large, yolked opaque eggs found in the ovaries before spawning were markedly larger in size than the small, transparent eggs which would be spawned in following years. In the case of species in which the ripe eggs are extruded all together, as the lumpsucker (Cyclopterus lumpus), or at brief intervals, as the herring, only the large and small groups of ova were found. In others, as the sticklebacks (Gasterosteus), the pipe-fishes (Syngnathus) and Liparis, three series of eggs, each marked off from the other by a difference in size, were found in the ovary during the spawning season. This latter condition was met with in small fishes which deposit few eggs at one time, and which shed their eggs in more than one batch during each season. In species which produced pelagic eggs, a sharp demarcation between the large, yolked eggs and the small, transparent ones was not always found. Large fish, as the cod, ling, plaice, tusk and turbot, had few intermediate eggs, while in the haddock, whiting and gurnard intermediate eggs were numerous. In this case, also, the occurrence of intermediate eggs was determined to be associated with a prolonged spawning period, which allows time for the small, yolked eggs to reach maturity before the close of spawning.

Reighard (1906), in the small-mouthed bass, described three groups of eggs; those large, opaque and yellow, 2.5 mm. in diameter; others white, opaque, 0.5–1.5 mm., and still others small, transparent, colorless, 0.25 mm. He considered that the white opaque group would probably be spawned the next season and the transparent group in subsequent years.

Kuntz (1914), in the vivaparous fish Gambusia affinis, found ova in various stages of development ranging from almost microscopic dimensions to the diameter of 1.8 mm. attained at maturity. The mature eggs were fertilized and gave rise to a brood of young. After birth, a second lot of ova reached maturity, were fertilized and gave rise to a second brood of young. Thus, he thought, that perhaps all ova required to produce the several broods born during the spring and summer, were present in the ovary at the beginning of the season.

Thompson (1914) found three generations of ova in the Pacific halibut: ripe ova, ova for next season, and ova for future seasons. He traced the growth of the second group of ova between spawning seasons, using for the first time the statistical methods employed in this present paper, and thus definitely established the fact that this group would mature the next season. The ripe ova were further divided into translucent and opaque groups. The translucent ones ready to be spawned, and the opaque ones to be spawned later in the season.

Gudger (1919) suggested that in Felichthys felis more than one spawning might take place in a season. In some instances he found, in fish which had already spawned, small ova, empty follicles and a few large ova, and in one case in which the fish had not spawned, almost mature ova of about 20 mm. in diameter, others 10 to 12 mm. in diameter, and small ova. It was the presence of this second group of larger ova which led him to believe that a second spawning might occur in the same season.

Hildebrand (1922) observed eggs of several sizes present at one time in the ovary of the atherine fishes Menidia m. menidia and in "M. beryllina" (=Ischnomembras beryllina beryllina.) When one lot was spawned out, the next lot was large enough to be seen with the naked eye. This, he felt, strongly suggested more than one and perhaps several spawnings during the season.

It is evident from these several investigations that the number of generations of ova during the spawning season apparently varies in different species, and conclusions drawn from one form will not necessarily hold true for another. However, Fulton's classification, in which the presence of an intermediate group of eggs is associated with a prolonged spawning season, probably has a general application. Certainly it holds for Leuresthes, which is a small fish and which sheds its eggs in small batches over a considerable period of time.

The segregation and extrusion of the ova.—During the prespawning growth and between spawning periods the immature, intermediate and maturing ova show no segregation in the ovary. In surface views and cross-sections of the gonad all three groups were found intermingled without suggestion of stratification. However, immediately before spawning the mature ova were freed from their follicles and collected in the lumen of the ovary. Figure 1 shows dorsal and ventral views of the ovaries from a mature fish taken May 3. The shaded area represents the region occupied by the immature and intermediate eggs, the unshaded, the mature. The former lie in the stroma, which at this time is confined to a region on the inner surface, and which extends from the anterior tip to the posterior opening of each ovary. The remainder of the gonad is filled by the maturing eggs lying in the lumen.

Figures 2, 3 and 4 show microphotographs of cross-sections of ovaries from fish taken July 26, 1923, November 14, 1923, and January 11, 1924, respectively. Each of these figures shows the stroma attached to the wall of the ovary along a relatively narrow zone and separated from the lumen by a very delicate epithelial membrane. Figure 3 shows the laminated character of the stroma.

The length of time that the ripe eggs lie in the lumen of the ovary before extrusion is probably relatively brief. Fish in such a condition were found only in collections taken on dates when the tides were favorable for spawning. The collections were made during the day, and such fish would presumably have spawned the same night.

This segregation of the ripe eggs just before spawning may be correlated with the fact that the actual extrusion of the ova is very rapid. Thompson (1919*b*) states that only about 30 seconds elapse from the time a female grunion digs into the sand until she has deposited her eggs and flapped away.

Microscopic study of sections of the ovaries revealed the fact that the walls were composed of a circular and a longitudinal layer of smooth muscle. The thickness of this muscular wall varied with the time of year and the maturity of the fish. The ovarian wall of a young fish taken in November averaged 0.01 mm. in thickness; in an adult taken on the same date 0.13 mm. In a fish taken May 3, 1923, in which the mature eggs were segregated in the lumen, the wall of the ovary averaged only 0.06 mm.

The function of this muscular wall can only be surmised. It seems plausible to assume that it is the chief agent in the extrusion of the ova. It may also provide the greater elasticity necessary to allow the required expansion when the ovary is filled with mature ova. Owsiannikow (1885) mentioned smooth muscle in the ovarian wall of Perca fluviatilis and suggested that it serves to free and force the eggs from their follicles.

Such a muscular wall is apparently common to the ovaries of fishes in general. Sections were made of the ovaries of the atherine fishes Atherinops affinis, Atherinopsis califoriensis and Labidesthes sicculus. A muscular ovarin wall was found in all. Brock (1878), in a general discussion of the structure of sex organs in fishes, stated that the ovarian wall is composed of smooth muscle fibres, connective tissue and elastic fibres. Franz (1910) described muscles in the wall of the ovary of Pleuronectes platessa. Eigenmann (1894) found smooth muscle in Cymatogaster aggregatus; Lane (1903), in Lucifuga and Stygicola; Wallace (1903), in Zoarces, and Williamson (1911), in Helicolenus dactylopterus. However, Cymtogaster, Lucifuga, Stygicola and Zoarces are all viviparous fishes which fact may have a modifying influence on the ovarian structure. Calderwood (1892), in a general discussion, stated that the ovarian wall of fishes consists of fibrous tissue which varies in thickness as the ova increase in size and are spawned out. The fibrous wall contracts rapidly after spawning. Gudger (1919) found the ovarian wall of the catfish Felichthys felis to be composed of an inner germinal layer and an outer peritoneal layer. But this is an exception to the conclusions of other workers and it is probable that the ovarian wall of most fishes is muscular.

The ripe ovum.—The eggs of Leuresthes are deposited in the sand of ocean beaches and, therefore, do not adhere to the surface of submerged objects as in the case of other Atherinidae, as far as recorded. In correlation with this specialization in the habit of depositing the eggs, the ova of Leuresthes do not bear filaments as do those of many species in this family. These filaments vary in structure in different species, and may be grouped as follows: (1) a simple tuft at one pole, (2) a specialization in structure of the whole tuft, (3) a decrease in number and enlargement of one filament, (4) a further reduction to one greatly elongated filament, and (5) total absence of filaments.

Hildebrand (1922) described a bundle of gelatinous threads at one pole of the eggs of Menidia m. menidia, and Kuntz (1916) mentioned a small tuft of threads in the eggs of "Kirtlandia vagrans" (=Membras vagrans laciniata). These illustrate the first type, a simple tuft. Pagenstecher (1861) described in Atherina hepsetus filaments arranged in a circle around one pole, united in a network at the base, the whole forming a funnel-like structure; an example of a specialization of the whole tuft. Ryder (1883) found four filamentous threads in Menidia menidia notata although Kuntz and Radcliffe (1918) describe a tuft of threads in this form. In "Menidia beryllina" (=Ischnomenbras beryllina beryllina) Hildebrand (1922) found the filaments reduced in number, and one much enlarged; a condition obviously derived from that found in Menidia m. menidia and supplying a transition to one in which only one filament remains. The latter condition has been described by Hubbs (1921*b*) for Labidesthes sicculus, in which the one remaining filament is many times longer than the diameter of the egg. Finally, in Leuresthes tenuis, the filaments remain entirely undeveloped at all stages.

Frequency of spawning.—After measurements were made of the ova from a number of fish, a familiarity with the external appearance of the ovary was acquired that made it possible to determine by inspection, whether a fish contained only immature, or also intermediate, or both these groups plus maturing ova. In this manner all females taken in the collections made from March to August, 1923, were grouped into three classes; those with immature ova only, those with immature and intermediate, and those with immature, intermediate and maturing ova.

TABLE 2.—Female Fish Taken at San Pedro During the Spawning Season, Classified According to the Groups of Eggs Found In the Ovary.

Date	Immature eggs only		Intermediate eggs also		Maturing eggs also		Total	
1923	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent
March 13	9	15	32	51	21	34	62	100
April 8	6	7	26	27	62	66	94	100
April 10	2	11	2	11	15	78	19	100
April 12	0	0	2	6	34	94	36	100
April 14	2	8	3	12	21	80	26	100
April 17	1	3	2	7	27	90	30	100
April 19	0	0	18	72	7	28	25	100
April 21	0	0	26	96	1	4	27	100
April 23	0	0	24	100	0	0	24	100
April 25	0	0	5	21	19	79	24	100
April 28	0	0	1	3	32	97	33	100
May 1	0	0	2	8	22	92	24	100
May 3	0	0	2	5	36	95	38	100
May 5	0	0	49	100	0	0	49	100
May 9	0	0	0	0	31	100	31	100
July 24	34	71	10	21	4	8	48	100
July 26	81	80	15	14	7	6	103	100
August 24	116	100	0	0	0	0	116	100
April 8-17	11	5	35	17	159	78	205	100
April 25-May 3	0	0	10	8	109	92	119	100
July 24-26	115	76	25	17	11	7	151	100

TABLE 2.—Female Fish Taken at San Pedro During the Spawning Season, Classified According to the Groups of Eggs Found In the Ovary

Table 2 gives the results of this classification. The first collection was made March 13 at the beginning of the spawning season. Thirty-four per cent of the females taken on this date contained maturing eggs. The average size of this maturing group, in measurements made on ova from five fish, ranged from 1.09 mm. to 1.20 mm. This maturing class corresponded in size to the maturing class for April 28, Graph II, and would undoubtedly have been spawned on the favorable tides of March 17, 18 and 19. In the remainder of the collection for March 13, 51 per cent contained intermediate eggs and 15 per cent immature eggs only. These would undoubtedly have spawned later in the season.

From April 8 until May 5, collections were made every two or three days. The per cent of females containing maturing eggs showed significant fluctuation. From April 8 to April 17, the percentage varied from 66 to 90. During this time the maturing group increased constantly in size. On April 17, two of the 27 females contained ripe ova, segregated in the lumen of the ovary; these two fish were ready to spawn. On April 19, the percentage of fish with maturing eggs dropped to 28 and in all seven fish the mature eggs were ripe and segregated in the ovary. On this same date, the per cent of fish with only immature and intermediate eggs rose to 72. of these 18 fish, at least 10 were very recently spent.

The criterion for a recently spent fish is a condition of the ovary in which a few ripe eggs remain in the lumen. This number varies from three or four to, in exceptional cases, approximately one hundred. These remaining ripe eggs were evident in the gonads during only four or five days immediately after spawning. Whether they are resorbed or extruded, it is impossible to say, but no degenerating ripe eggs were noted.

On April 21, 4 per cent (only one fish of the collection) contained ripe ova and 96 per cent contained immature and intermediate eggs only. Since the tides suitable for spawning occurred on April 17–19, there can be no question that the fish spawned at this time.

On April 23, all the fish were placed in the intermediate group, but Graph II shows that the growth of the next maturing class had started on this date. This class continued to grow up to May 3 in the same manner as from April 8 to April 17. From April 25 until May 3 the percentage of fish containing maturing eggs fluctuates between 79 and 95. On May 3, 8 of the 36 fish contained ripe ova segregated in the lumen and were, therefore, ready to spawn. Two days later, May 5, the fish contained immature and intermediate groups of eggs only, and at least seven of the 49 were recently spent. The suitable spawning tides occurred on May 1–4, and again there is no question that the fish spawned at this time. By May 9, the percentage of fish with a maturing group of eggs rose to 100. Thus it would seem that a main spawning run of Leuresthes occurs every two weeks instead of every four, as Thompson concluded (1919*b*).

The view that there may be two distinct spawning runs, a larger one occurring on the lower series of favorable tides and a smaller occurring on the higher series, can not be substantiated. From the above data, it was found that immediately after spawning, the growth of another group of maturing eggs began and continued in a regular manner up to the next spawning period. The argument may be advanced that spent fish disappear from the regions in which the collections were made, and that the fish taken on April 21 and May 9 showing the beginning of growth of a new maturing class were ones which had spawned two weeks previous and had again migrated into the region of collection. However, the presence of a few mature eggs in the lumen of the ovary showed that these fish had spawned in the past three or four days, and yet a new maturing group was being differentiated from the intermediate class. It seems certain, therefore, that the grunion spawn on one series of high tides; immediately growth of a second group of maturing ova begins; this growth continues until the eggs are ripe, and the fish spawn on the next series of high tides, two weeks after the first spawning. This two-week cycle continues throughout the spawning season.

Eleven of the females taken July 24 and 26, 1923, contained a group of maturing eggs. Measurements were made of eggs of this group from seven of these fish. The average size of the group varied from 0.95 to 1.13 mm, a condition approximating that of April 25, Graph II. Apparently six or seven more days would be required for the maturing group in these fish to reach maturity. The tides suitable for spawning, occurred on July 27–30, several days before the fish would be ready to spawn. In 1924 a parallel condition was found. Measurements of maturing ova in four fish taken July 2, 1924, showed the average size of the group to range from 1.17 to 1.33 mm., a size midway between that of April 28 and May 1 (Graph II). The eggs would not be fully ripe for three or four days, yet the favorable tides occurred on July 1–3.

This relation of the mature eggs to the tides in July, led to a calculation of the probable time required for the maturing of a batch of eggs. Fish with ripe eggs segregated in the lumen of the ovary were first taken April 17, 1923, and again May 3, 1923, but since so many females contained mature eggs on May 3, it was assumed that had collections been made May 2, fish with ripe eggs would have been found. April 17 to May 2, represents a period of fifteen days, and the assumption was made that a period of fifteen days would elapse from the time a fish spawned until she would have matured a second batch of eggs and be ready to spawn again. Thompson (1919*b*) records his first observed spawning run on April 16, 1919. Beginning with this date and calculating on a basis of a fifteen-day interval between spawning periods, a table of the expected dates of the beginning of the spawning runs for 1919 was made up and compared with Thompson's recorded dates.

Table 3 shows the results of such calculations for 1919, and also for 1923 and 19245. The dates on which actual runs were observed are italicized. Those for 1919 were taken from Thompson's data, and those for 1924 from observations made by the staff of the California State Fisheries Laboratory. Thompson in 1919 recorded a run beginning at 12.30 a.m. June 1 instead of May 31, but as the high tide occurred at 10.24 p.m. on the thirty-first this represents the same night, and for convenience the calculated date of May 31 has been considered to coincide with the observed date. Thompson made careful observations of the beginning of the spawning run on the lower series of high tides during April and May and recorded the run as commencing April 16 and May 16, dates agreeing with those calculated. The calculations

TABLE 3.—Relation of a Series of High Tides to the Calculated Time for the Beginning of a Spawning Run.

High tide			Calculated beginning of spawning run			Lag in hours*
Date	Height in feet	Time p.m.	Date	Height of tide in feet	Time of high tide p.m.	
1919			1919			
April 13	5.4	8:15				
April 14	5.4	8:40				
April 15	5.4	9:04				
April 16	5.4	9:28	*April 16*	5.4	9:28	0.0
April 30	6.6	9:09	May 1	6.5	9:52	24.6
May 14	5.7	8:33	*May 16*	5.5	9:25	47.9
May 28	6.9	8:06	*May 31*	6.3	10:24	74.3
June 13	6.0	8:41	June 15	5.7	9:43	49.0
June 26	7.1	7:54				
June 27	7.1	8:41	June 30	5.8	10:54	74.2
July 12	6.3	8:28	*July 15*	5.8	10:13	73.8
July 25	7.0	7:46				
July 26	7.0	8:32	July 30	5.0	11:13	98.7
August 10	6.4	8:14				
August 11	6.4	8:51	*August 14*	5.3	10:51	74.0
1923			1923			
April 15	5.3	8:58				
April 16	5.3	9:23				
April 17	5.3	9:47	April 17	5.3	9:47	0.0
April 30	6.4	8:58				
May 1	6.4	9:38	May 2	6.2	10:21	24.7
May 16	5.7	9:17	May 17	5.5	9:45	24.5
May 29	6.8	8:35	June 1	6.0	10:45	74.2
June 14	6.1	8:57	June 16	5.9	10:06	49.2
June 27	7.0	8:20	July 1	5.6	11:10	98.8
July 13	6.5	8:42				
July 14	6.5	9:19	July 16	6.0	10:39	49.3
July 25	6.9	7:26				
July 26	6.9	8:10	July 31	5.1	11:26	123.3
August 11	6.7	8:28				
August 12	6.7	9:07	August 15	5.5	11:24	74.3
1924			1924			
April 20	6.2	9:53	April 20	6.2	9:53	0.0
May 2	5.5	8:31				
May 3	5.5	8:56				
May 4	5.5	9:22	*May 5*	5.3	9:47	24.4
May 18	6.7	8:48				
May 19	6.7	9:30	May 20	6.5	10:15	24.7
June 1	5.8	8:54				
June 2	5.8	9:22	June 4	5.5	9:51	48.5
June 16	7.1	8:31				
June 17	7.1	9:15	June 19	6.3	10:50	49.6
July 1	6.1	8:35	*July 4*	5.8	10:10	73.6
July 15	7.3	8:20	July 19	5.7	11:22	99.0
July 30	6.3	8:19				
July 31	6.3	8:52	August 3	5.7	10:39	73.8
August 13	7.1	8:11	August 18	4.8	11:46	123.6

* Lag in hours is calculated as the difference between the time of high tide on the date of calculated beginning of spawning and the time of high tide on the last date of a given series of high tides.

TABLE 3.—Relation of a Series of High Tides to the Calculated Time for the Beginning of a Spawning Run

are also in perfect agreement with his observations of runs commencing July 15 and August 14. On May 5, 1924, spawning runs of grunion were reported to the staff of the California State Fisheries Laboratory, and on May 6, Mr. Greene and Miss Miller saw a few small schools. On June 5, one day after the predicated date of the beginning of spawning, Mr. Hill of the Los Angeles Museum found spawning grunion at Long Beach. On June 19, the staff of the Fisheries Laboratory made careful search at Long Beach but observed no grunion between 9.30 and 11.30 p.m. On June 2, Mr. Thompson and Mr. Greene found several schools between 11.45 and 12.30 p.m. On July 4 and 5 runs of grunion were reported to the Laboratory but not observed by the staff. These scattered observations substantiate fairly well the calculation that a fifteen-day period is necessary for a second lot of eggs to reach maturity after a batch has been spawned.

From Table 3 it will be seen that, as a result of this fifteen-day interval, a lag occurs between the last date of the high tide of a series and the date of the beginning of the spawning run. This lag shows an irregular tendency to increase as the spawning season advances, and accounts for the fact that the maturing ova from the females collected in July were not large enough to have been spawned at the expected dates if tides alone are considered.[6]

If the calculation, that a fifteen-day period is necessary for the maturing of a batch of eggs, is valid, probably one of the most significant facts revealed by Table 3 is that the lag is greater on the higher series of tides than it is on the lower series, and, as a result, fish spawning on the higher series spawn later in the evening than they do when spawning on the lower series. On the calculated dates of the beginning of spawning, the time of high tide during the lower series of high tides varies from nine to eleven, while the time of high tide during the higher series varies from ten to twelve. Since the fish do not begin to spawn until the tide turns, they would thus spawn later at night on the higher series of high tides than on the lower series of high tides.

Some evidence is at hand that the fish do actually spawn earlier on the lower series of tides than they do on the higher series. Thompson recorded the run for April 18, 1919, as beginning at 10.30 p.m. and ending at 11.40 p.m. This was the third night of spawning on a lower series of high tides. On May 16, 1919, the run began at 9.15 p.m. and ended at 10.00 p.m. On May 17, it began at 10.00 p.m. and ended at 11.00 p.m. On May 18, it began at 10.20 p.m. and ended at 12.01 a.m. These three nights constituted the dates of spawning on the next series of lower high tides for 1919. Spawning, even on the third night, was completed by midnight. On June 1, 1919, Thompson observed a run of grunion between 12.30 and 12.40 a.m. This was a run on the higher series of high tides and it occurred late at night. On June 20, 1924, Mr. Thompson and Mr. Greene of the Fisheries Laboratory observed a run between 11.45 p.m. and 12.30 a.m. This again was a run late at night on a higher series of high tides.

This tendency to spawn later at night on the higher series of high tides than on the lower series may account for the general opinion that spawning occurs only every four instead of every two weeks. Fish spawning after eleven o'clock would be much less frequently observed by the crowds on the beaches than would fish spawning from nine to eleven.[7]

The popular belief is that the grunion spawn only on the tides associated with the full of the moon. In 1919, these tides constituted the lower series, but in 1923, and 1924, the reverse was true, and the higher series of high tides accompanied the full of the moon. If the fish spawn only on moonlight nights, this would mean that some years they would spawn on the higher series of high tides and in other years they would spawn on the lower series. However, Thompson's work and present data show that the tides and not the phase of the moon constitute the limiting factor on which depends the appearance of the spawning fish.

The probability of a greater lag between the date of the beginning of spawning on the higher series of tides than on the lower series verifies Thompson's suggestion in regard to the possibility of a run on this higher series. He stated: "There seems no obvious reason, however, why eggs could not be laid during the tides coming in the dark of the moon (the higher series), if the run should be during a very late part, when the series was receding and the eggs could be laid where the eroding area of the succeeding lower series could reach them."8

Length of the spawning season.—In order to deal with larger numbers, and thus obtain more significant percentages of maturing fish, data for April 8–17 were combined, and similarly that for April 25–May 3. The justification of such combinations is based on the evidence that fish showing a maturing class of eggs during the first period would have spawned on April 17–19, and during the second period such fish would have spawned on May 2–4; therefore each constitutes a homogenous developing group. The results of these combinations are given in Table 2.

If the collections can be considered representative of the population in the sea, it may be assumed, from the data of Table 2, that about 30 per cent of the fish spawned in March, 75 per cent spawned the latter part of April, and 90 per cent the early part of May. By April 19, all females contained ova larger than the immature class, and on May 9 no females lacked a maturing class. Therefore we may assume that practically the whole population was spawning by the middle of May. In the collections of July 24 and 26, 7 per cent of the females still contained maturing ova, but on August 24 only an immature group was present in all females. Thus in general we may conclude that spawning begins in March, with possibly one-third of the fish spawning; the number of spawners increases through April; reaches its maximum in May; and decreases in June. By the last of July a mere remnant of spawners is left, and the middle of August marks the close of the season.

Size of early spawners.—For March 13 and April 8, 1923, the females were classified according to the groups of ova which they contained and their lengths averaged, with the following results:

	Average length in mm.	
Group	March 13	April 8
With immature eggs only	114.6	116.3
With intermediate eggs also	138.3	120.0
With maturing eggs also	146.2	121.2

It is clear that the largest fish spawn first in the season. The fish with intermediate eggs were larger on the average than those with immature eggs only, and would undoubtedly have spawned before the latter. Probably the very smallest fish do not spawn much before the middle of the season. The maturing of the large fish earlier and of the smaller fish later in the spawning season has been observed by Eigenmann (1894) for Cymatogaster aggregatus, by Hubbs (1921*a*) for Amphigonopterus aurora, by Barney and Anson (1923) for Lepomis humilis, and by Hubbs (1925) for Clupea pallasii, and probably represents a general law.

It was also found that the larger fish matured a greater number of eggs at each spawning than did the smaller fish. A few counts comparing the number of maturing eggs with the length of the fish are as follows:

Length of fish in mm.	No. of maturing ova	
118	1613	
130	2309	Av. 2117
134	2115	
135	1559	
135	2259	
135	2345	
144	3097	
158	3579	

In viviparous fishes, the production of a greater number of young by the larger females has been shown by Eigenmann (1894) for Cymatogaster aggregatus, by Hubbs (1921*a*) for Amphigonopterus aurora and Micrometrus minimus, and by Henn (1916) for Poecilia vivipara, Pseudopoecilia fria, Phalloceros caudomaculatus and Cnesterodon decemmaculatus. Among the oviparous fishes, Barney and Anson (1920, 1923) found that the larger females of Elassoma zonatum and Lepomis humilis matured more eggs than did the smaller ones. In the plaice, Reibisch (1899), Hensen (1884), Apstein (1901) and Franz (1910) have shown that the number of eggs produced increases with the size and age of the fish. Earll (1880) reported a similar increase in the cod, haddock and pollock, and Thompson (1917) found the same condition in the Pacific halibut. In the brown trout, Bean (1901) indicated an increase in the number of eggs in the older fish, and Leach (1923) found a similar condition in the rainbow trout. Finally, Fulton (1890) concluded, from counts made of the number of ova from about twenty-five species of fishes, that in general the larger the individual of a species the greater the number of eggs produced.

3.3. 3. The fate of the intermediate class of ova

In the collections made July 24 and 26, 1923, 17 per cent of the females contained an intermediate group of ova, but no maturing group. In the collection for August 24, the intermediate group had disappeared entirely and only the immature group remained. Obviously the 35 females, with an intermediate but no maturing group of ova, taken the last of July, would not have spawned again that season, and the disappearance of the intermediate group must be accounted for in some other way than by spawning.

Cytological studies were made of ovaries from fish taken in July and which still contained an intermediate ova. In all cases, eggs in the intermediate group were undergoing a process of degeneration and resorption. Figure 5 shows a cross-section of a normal growing ovum from the intermediate group; unfortunately somewhat distorted by preservation and fixation. On the outer surface is found the theca folliculi, a single layer of flattened cells. Next the theca folliculi lies the follicular epithelium, a single layer of columnar cells with large deeply staining nuclei. The zona rariata, the only egg membrane demonstrated for this species, lies directly in contact with the follicle and the yolk. The striations of the zona radiata are very fine and could be seen only with an oil immersion lens.

Contrasted with the normal growing ovum shown in Figure 5, are the degenerating ova in Figures 6, 7 and 8. In this process of resorption the follicular epithelium becomes much thickened and vacuolated, the cells lose their definite structure, and the nuclei alone remain discernible. As the follicular epithelium thickens, the zona radiata breaks down and the vacuoles, normally present in the yolk, disappear. At this time follicular cells appear to migrate into the egg. A late stage in the process of degeneration in which definite structures are no longer apparent, is shown in Figure 8.

During the spawning season the gonads are highly vascular, but, while this abundant blood supply continues throughout the process of degeneration, no evidence was obtained that the leucocytes participated in the process. The tearing down is apparently accomplished by the follicle cells alone.

Cunningham (1898) described the resorption of aborted eggs in spent ovaries of Trigla hirundo, and considered the follicle cells were the chief agents. He thought, however, that the cells which took part in the degeneration were derived from the connective tissue of the wall of the follicle and not from the follicular epithelium.

Barfurth (1886) decided that, in the brook trout, the leucocytes played no part in resorption until a late stage. Similarly, Wallace (1903) after a study of the degenerating ova in Zoarces, claimed that only the follicular epithelium cells function in the process. He saw no blood cells in the dead egg or amongst cells of the proliferated follicular epithelium, and concluded that the leucocytes probably only remove the ultimate products of degeneration, the non-adipose granules.

This degeneration, after the spawning season, of partially matured ova is common among fishes. In addition to the references cited above, Brock (1878) found such eggs in Perca, Franz (1910) in Pleuronectes platessa, and Cunningham (1894) described them for the plaice, flounder and turbot.

3.4. 4. Size of ova from August to January

In Leuresthes the degeneration and resorption of the intermediate ova is completed by the last of August and in collections taken October 17, 1919; October 9, 1922; August 24, September 9 and November 14, 1923; and August 4, 1924, no female was found with ova larger than those of the immature class. This condition prevails during the fall and early winter, but January marks the beginning of growth beyond the immature class. The months of September, October, November and December may thus be said to constitute a resting period for the sexual organs.

3.5. 5. Summary of the history of the maturing ova

1. In Leuresthes tenuis activity of the sex organs begins early in January. At this time the ovary contains only an immature group of

eggs. During January and February, the eggs grow beyond the immature group and an intermediate group is formed which, by the last of February, has reached an upper limit of 0.78 mm.

2. A third group, the maturing class, is differentiated from the intermediate group, this class reaches maturity in about two weeks and is spawned out. At once, a second maturing class starts to grow, matures in two weeks and is again spawned out. This two-week cycle is continued throughout the spawning season.

3. As maturing groups are differentiated from the intermediate group, growth probably takes place from the immature to the intermediate class, but this growth does not entirely compensate for the loss due to the continual moving out of new maturing groups and the number of ova in the intermediate class gradually diminishes with the advance of the spawning season.

4. When the maturing ova are ripe they are freed from their follicles and segregated in the lumen of the ovary.

5. Leuresthes spawns on every series of high tides, but probably requires a trifle more than fourteen days in which to mature a second batch of eggs after a previous spawning. This results in a slight lag between the last date of the high tide of a series and the date on which a spawning run commences. As the season advances this lag increases slightly, especially in relation to the higher series of high tides.

6. The spawning season begins in March, reaches its height in May, and ends by the middle of August. The larger fish constitute the early spawners. They also develop a larger number of eggs.

7. At the close of the spawning season a remnant of the intermediate class is left in the ovary. These eggs undergo degeneration. The resorption is apparently accomplished by the follicular cells.

8. From August to January, only immature eggs are present in the ovary. This time may be regarded as a resting period for the sexual organs.

4. IV. AGE

Age determinations for Leuresthes were based on evidence derived from a study of the scales. This method of ascertaining the age of fishes has been used by numerous workers and a vast literature published on the subject. Thomson (1904), Taylor (1916), Lee (1920) and Creaser (1925), discussed the findings of the many workers in this field and give excellent bibliographies. The numerous authors have employed a varying terminology to designate different structures of the scale. In this paper the word *ridges* has been applied to the concentric striations on the outer surface of the scale, and *annulus* to the mark formed upon the resumption of growth following a period of growth cessation. The age of the fish was determined by the number of annuli. As interpretations were not always clear, no fish with scales in which the number of annuli was questioned was included in the age groups. Approximately 4.5 per cent of the material was omitted for this reason.

In Leuresthes the annulus appears as a fine line running parallel to the scale margin. By a careful focusing of the microscope, this line can usually be traced throughout the anterior and lateral regions of the scale. In the posterior region, the upper layer of the scale does not extend to the margin. The termination of this upper layer forms a scar which runs parallel to the periphery of the exposed portion, and is evident on all scales except those of young fish less than 100 mm. in length. The annulus joins this scar at right angles.

The annulus is not preceded by a band of narrowed ridges such as has been described for some fish, especially the salmon. However, in the anterior region of the scale, immediately preceding the annulus, a very narrow zone of broken ridges is usually apparent. In the lateral regions, the annulus runs obliquely to the preceding ridges and marks their termination. The ridges formed after the annulus run parallel to it. Undoubtedly a slow growth continues in the anterior region of the scale longer than in the lateral portions. This results in the deposition of the broken ridges just previous to the complete cessation of growth. The resumption of the growth of the scale occurs simultaneously in all three regions; thus the annulus is formed and succeeding ridges are laid down parallel to the new scale margin, but obliquely to previously formed ridges. After the first six or eight months of the life of the fish, little growth, apparently, takes place in the posterior portion of the scale.

As a result of the study of the scales, four age groups have been differential for Leuresthes: the O, I, II and III groups. Fish were placed in the O group until they had passed their first winter, in the I group until the second winter was completed, and in the II group until the end of the third winter. March first has been considered the termination of the winter period.

4.1. 1. Formation of a breeding annulus

The collection for March 13, 1923, contained fishes with three types of scales: Those with no annulus, those with one annulus, and those with two annuli. Since all the fish had passed one or more winters, they were placed in the I, II and III groups, respectively (see Table 4). The same three classes were again found in the collections for April and May.

In the case of the I group scales were first found with an annulus, very near the margin, in collections for July 24 and 26, 1923. Since, until July, the I group had shown no annulus, its occurrence on the margin of the scale at that time suggested the possibility that the annulus was normally formed during July and August.

In order to indicate the time of the formation of the annulus, the proximity of the annulus to the scale margin was measured. As a basis for further comparisons, measurements were made of scales with two annuli. The distances from the center of the scale to the first annulus, and from the first to the second annulus, were ascertained from measurements made along the anterolateral radius of the scale, as indicated in Figure 9. The distance between the two annuli was then expressed as a percentage of the distance from the center to the first annulus. This gave an index of the amount of scale growth taking place between the time of the formation of the first and second annulus. Measurements of all scales with one annulus, taken from the collections of July and August, were made in a similar manner. In these scales the distance from the annulus to the scale margin was expressed as a percentage of the distance from the center to the annulus. Thus it was possible to compare the distance between the two annuli on scales of the first type with the distance between the one annulus and the margin on scales of the second type.

TABLE 4.—Age Groups of Leuresthes.

Date	O Group			I Group			II Group			III Group		
	No.	Mean, mm.	P.E.M. ±	No.	Mean, mm.	P.E.M. ±	No.	Mean, mm.	P.E.M. ±	No.	Mean, mm.	P.E.M. ±
1922												
October 9 M.	-----	-----	-----	34	124.71	0.70	10	128.50	1.32	-----	-----	-----
F.	-----	-----	-----	62	134.61	0.68	13	145.77	1.76	-----	-----	-----
1923												
March 13 M.	-----	-----	-----	8	117.25	1.15	40	136.32	0.56	28	136.32	0.74
F.	-----	-----	-----	24	122.25	1.35	29	145.97	0.68	8	151.50	1.63
April 8 M.	-----	-----	-----	44	113.93	0.54	46	132.54	0.69	22	132.41	0.90
F.	-----	-----	-----	86	121.92	0.34	4	123.75	1.09	1	127.00	
April 10 M.	-----	-----	-----	58	117.22	0.54	51	134.49	0.61	49	137.12	0.68
May 9 F.	-----	-----	-----	263	128.19	0.24	80	143.17	0.78	14	150.64	1.10
July 24-26 M.	-----	-----	-----	50	120.92	0.48	25	140.40	0.77	-----	-----	-----
F.	-----	-----	-----	84	129.80	0.42	48	148.54	1.12	-----	-----	-----
August 24 M.	-----	-----	-----	35	121.03	0.74	-----	-----	-----	-----	-----	-----
F.	-----	-----	-----	62	131.45	0.65	-----	-----	-----	-----	-----	-----
September 4 M.	214	79.09	0.26	106	121.88	0.52	31	141.93	0.48	-----	-----	-----
F.	331	81.02	0.23	101	132.38	0.53	35	148.46	1.12	-----	-----	-----
November 14 M.	390	88.03	0.31	23	122.91	1.13	19	139.79	0.88	2	148.50	0.71
F.	510	94.10	0.22	51	133.67	0.64	38	150.55	0.94	4	159.75	2.12
1924												
January 10,11 M.	539	98.06	0.14	32	123.06	0.62	1	134.00	-----	-----	-----	-----
F.	544	100.08	0.17	19	132.95	1.46	4	153.25	1.82	-----	-----	-----
January 15 M.	563	102.31	0.15	22	125.45	0.88	4	135.75	2.08	-----	-----	-----
F.	978	104.16	0.12	16	132.81	1.34	5	134.80	1.66	-----	-----	-----
January 31 M.	886	99.80	1.32	-----	-----	-----	-----	-----	-----	-----	-----	-----
F.	502	100.61	1.86	-----	-----	-----	-----	-----	-----	-----	-----	-----
February 6 M.	698	105.13	0.13	79	126.15	0.49	5	144.40	1.27	-----	-----	-----
F.	614	107.88	0.14	27	140.37	0.90	5	153.00	0.74	-----	-----	-----
February 20 M.	267	109.33	0.21	95	128.54	0.37	9	138.55	1.96	2	143.50	0.24
F.	840	114.08	0.12	25	135.56	0.87	6	141.50	1.99	-----	-----	-----
April 4, 5, M.	-----	-----	-----	6	112.17	1.37	6	130.50	1.45		-----	-----
23 F.	-----	-----	-----	9	126.11	1.36	10	150.70	1.43	9	154.67	1.57
May 17 M.	-----	-----	-----	1	110.00	-----	2	137.00	5.25	-----	-----	-----
F.	-----	-----	-----	3	131.00	1.27	3	153.33	0.66	-----	-----	-----
June 20 M.	-----	-----	-----	5	109.40	2.50	-----	-----	-----	-----	-----	-----
F.	-----	-----	-----	2	128.00	1.84	1	143.00	-----	-----	-----	-----
July 2, 25 M.	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
F.	-----	-----	-----	3	128.33	2.88	3	153.67	1.75	2	155.00	3.82
August 4, 20 M.	-----	-----	-----	2	116.00	0.48	-----	-----	-----	-----	-----	-----
F.	-----	-----	-----	5	128.80	1.37	-----	-----	-----	-----	-----	-----
	No.	%	Ratio	No.	%	Ratio	No.	%	Ratio	No.	%	Ratio
Totals M.	3563	45.12	100	600	41.61	100	247	46.51	100	105	24.00	100
F.	4333	54.88	122	842	58.39	140	284	53.49	115	40	76.00	38
M. and F.	7896	100.00	-----	1442	100.00	-----	531	100.00	-----	145	100.00	-----

TABLE 4.—Age Groups of Leuresthes

TABLE 5.—Growth of Scale from the Time of the Formation of the First Until the Formation of the Second Annulus, or from the First Annulus to the Margin, Expressed in Percentage of the Growth from the Center to the First Annulus.

* Percentage	Scales with two annuli	Scales with one annulus	
	Distance, first to second annulus	Distance first annulus to margin	
		July, 1923	August, 1923
1	-	-	-
2	-	5	3
3	-	3	3
4	-	3	4
5	-	2	12
6	-	1	13
7	-	4	17
8	-	-	13
9	-	4	6
10	-	2	9
11	1	3	8
12	5	5	3
13	3	8	5
14	5	4	2
15	8	6	4
16	6	6	1
17	10	5	-
18	5	6	-
19	3	5	-
20	2	5	1
21	1	5	-
22	5	3	-
23	7	-	1
24	6	2	-
25	1	1	-
26	4	-	-
27	5	-	-
28	1	-	-
29	2	2	-
30	2	-	-
Totals	82	90	105

TABLE 5.—Growth of Scale from the Time of the Formation of the First Until the Formation of the Second Annulus, or from the First Annulus to the Margin, Expressed in Percentage of the Growth from the Center to the First Annulus

These comparisons are shown in the percentages given in Table 5. The percentages for the distance between the first and second annulus in scales with two annuli are given in the first column. The range was from 11 per cent to 30 per cent. This indicated the amount of scale growth that might be expected in a year, the period of time elapsing between the formation of the first and second annulus. In the second column are given the percentages of the distance from the annulus to the margin for scales with one annulus taken July 24 and 26, 1923. For July, the range was from 2 per cent to 29 per cent, and obviously this group of fish, the scales of which showed only one annulus, was composed of two year-classes. Those scales in which the percentage of the distance from the annulus to the margin ranged from about 10 to 29, came from fish of the II group. The annulus on these scales had been formed a year previous, and was located an appreciable distance from the scale margin. On the other hand, those scales in which the percentage of the distance from the annulus to the margin ranged from 2 to about 10, came from fish of the I group, and the annulus on these had been formed very recently. In the third column are given the percentages of the distance from the annulus to the margin for scales with one annulus taken August 24, 1923. On this date the range was from 2 per cent to 23 per cent, and again two year-classes were involved. But, by the latter part of August, an annulus had been recently formed on the scales of most of the fish, as is indicated by the large numbers with less than 10 per cent of growth between the annulus and the scale margin. Only a small remnant of the fish of the II group had scales with only one annulus, and no fish of the I group were found in which the scales lacked an annulus, while in the July collections there were many scales from fish of the latter group without an annulus.

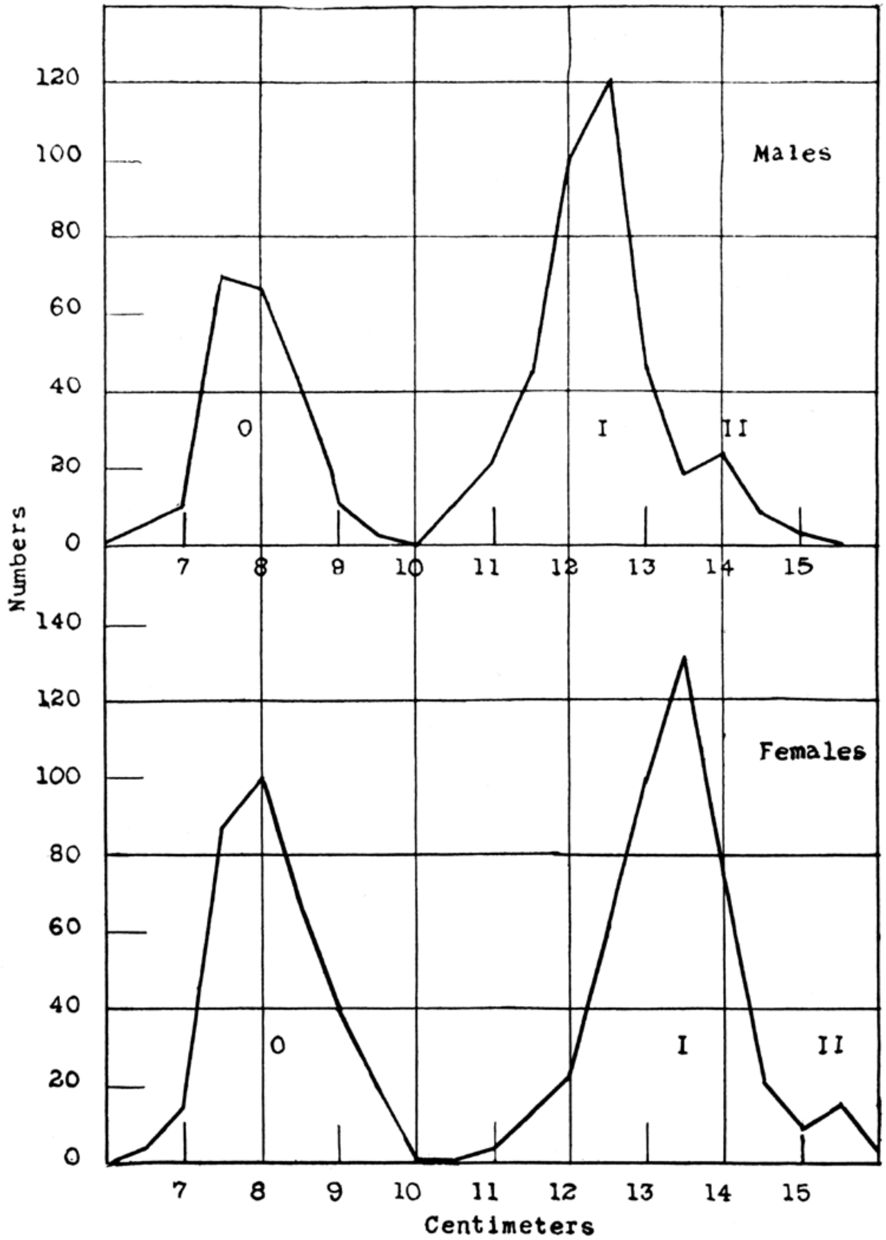
Since a group of spawning fish, the scales of which bore no annulus, was found in all collections taken from March to July; since the scales of a few fish from this group taken in July had an annulus very near the margin; since most of the scales of the fish taken in August showed an annulus near the margin; and since there were no fish in the August collection whose scales had no annulus; it appears evident that the annulus on the scale of Leuresthes is formed during a period comprising the latter part of July and August. Since August marks the close of a long, protracted spawning season which undoubtedly places a sufficient drain on the metabolism of the fish to stop growth; this annulus has been termed a breeding annulus in contrast to the winter annulus formed in the spring on the scales of many fishes.

Hubbs (1921*a*, p. 199) found that the annuli in certain embiotocid fishes (viviparous perches) are doubled, this condition "suggesting the possibility that two annual checks in growth are registered on the scales, one during the winter and the other during the breeding season." Mohr (1921), in a study of the scales of seven species of fishes from the Malay Peninsula and Ceylon found year rings on the scales on which he based age determinations. He offered the suggestion that these year rings are due to breeding, assuming that variation of the temperature of the water would not be sufficient to cause a cessation of growth during the winter and a formation of a winter ring.

At the time that the first annulus appears on the margin of the scales of fish in the I group, a second annulus is formed on the scales of the fish in the II group, and a third on those of the III group. Since growth is very slight after the first year, succeeding annuli lie so close to the margin of the scale that it is impossible to determine from inspection whether an annulus has been recently formed or whether it was formed a year previous. To separate the fish of the II and III groups in the August collection, a series of measurements similar to those made for the I and II groups would have been necessary. But due to this lessened growth the measurements would not have given clear cut results and would have proved unsatisfactory. For this reason the II and III groups for August 24, 1923, have been omitted from Table 4. Presumably a new annulus had been formed on the scales of all fish by September, and in the collection for September 4, fish with one annulus were placed in the I group and those with two annuli in the II group. In the collection for this date there were no scales showing three annuli. But on November 14, six fish with scales of this type were found and these were placed in the III group.

4.2. 2. The winter annulus

While the formation of a breeding annulus on the scales of Leuresthes can be demonstrated, this does not preclude the possibility of the formation of a winter annulus in addition. To determine this point, a study was made of the scales of the young fish. The first collection of immature fish was made September 4, 1923. The scales of the 133 young fishes examined showed no annuli, and these fish were placed in the O group. In Graph III are given the frequency polygons for the lengths of each sex which comprised the September collection. At this time the young fish formed a homogeneous group entirely distinct from the one-year group.



GRAPH III. Frequency polygons showing numbers of fish at nearest half centimeter of length. Total collection of September 4, 1923.

GRAPH III. Frequency polygons showing numbers of fish at nearest half centimeter of length. Total collection of September 4, 1923

In the collection for November 14, 1923, examination was made of the scales of 97 specimens comprising the O group. These were still without annuli. On January 10 and 11, 1924, two fish from among

121 examined from the O group had scales with an annulus on the margin. Two more were found among 65 in the collection for January 15, one out of 70 in the February 6 collection, and one among 182 in the February 20 collection. In the February 6 and 20 collections, four fish of the 226 comprising the I group were found with an annulus near the margin of the scale in addition to the breeding annulus, which at this time lies a short distance from the periphery.

An acceleration in the growth of the fish begins during the latter part of January (see discussion on rate of growth), and if there had been a preceding cessation of growth, the winter annulus would have been formed on the scales at this time. But such an annulus was seldom found. Only 43 of the 3130 fish examined (these having been taken at all seasons of the year) had scales with a clear winter annulus. It is thus evident that a winter annulus is formed on the scales of only one fish among about 74.

Fortunately the winter annulus differs somewhat in appearance from the breeding annulus. It is not as clear cut and is never preceded by the zone of broken circuli usually found associated with the breeding annulus. Nevertheless, many transitional stages are to be found, and the possibility of confusing a winter annulus with a breeding annulus makes age determination for Leuresthes especially difficult. Most of the 4.5 per cent of fish omitted were thrown out because of the difficulty of determining whether the particular annulus in question was a winter or a breeding annulus. However, by thus omitting all questionable cases it was felt that on the whole the final determinations were accurate.

4.3. 3. Age at first maturity

Measurements were made of ova from seven females of the O group taken January 10 and 11, 1924. Some of these fish showed an intermediate as well as an immature class of ova, and by the last of February practically all females of this group contained these two classes of eggs. In February, gonads of the males of the O group also appeared to be nearly mature. This group of fish would undoubtedly have spawned during the months following, if not in March at least in April, May and June. This indicates with considerable certainty that Leuresthes spawns at the end of the first year. However, since age determination is based on a breeding and not on a winter annulus, it must first be established that the O group taken in January and February of 1924 was spawned in 1923, and had passed but one winter.

In September this group averaged approximately 80 mm. in length. On the assumption that these fish were spawned during the summer of 1923, their growth per day from May 15 to September 4 was calculated. This gave an average daily increase of 0.73 mm., not an unusual growth for young fishes. Hubbs (1921*b*) found that Labidesthes sicculus, of the same family, grew approximately a millimeter a day during early growth and maintained an average of 0.40 mm. during the first growing season (which was colder than normal). Hubbs also computed the daily increments of growth over a period of 30 days for fourteen other species and found averages ranging from 0.30 to 2.33 mm.

If, on the other hand, it be assumed that the O group taken in September was spawned during the summer of 1922, the daily growth increment would have been only 0.17 mm., a very much slower rate;

in fact hardly as fast as from September 4 to February 20. During this second period the average daily growth was 0.18 mm., a rate which would be quite plausible for the first fall and winter of the life of the fish, but hardly conceivable for the second fall and winter if the previous rate had been only 0.17 mm. per day. Therefore, the fish of the O group taken in January and February were, almost without doubt, passing through their first winter, having been spawned the previous summer.

Finally, the occasional occurrence of a winter annulus on scales of fish of the O group taken in January, indicates with fair certainty that these fish were in their first winter. If they had already passed one winter, such an annulus should also have been found on the scales of at least a few of the 230 young fish examined from the September and November collections.

Since fish of the O group at the end of their first winter have practically mature sex organs, and, since this group is also found in collections of spawning fish, it may be definitely stated that Leuresthes matures at the age of one year.

4.4. 4. Age limits

In a comparison of the total number of fish for each age as given in Table 4, the O group shows a great preponderance over the other three. However, this disproportionate size of the O group is due to artificial selection, and can not be taken as a criterion for the relation between the numbers of this group and of other groups; although it is undoubtedly safe to assume that the young fish are present in greater numbers than those of other age classes. If the O group is disregarded, the I group stands out as representing by far the greatest numbers. With the exception of the collection of March 13, 1923, the dominance of this group is evident in all the numerous collections made. In the same way the II group shows excess over the III group.

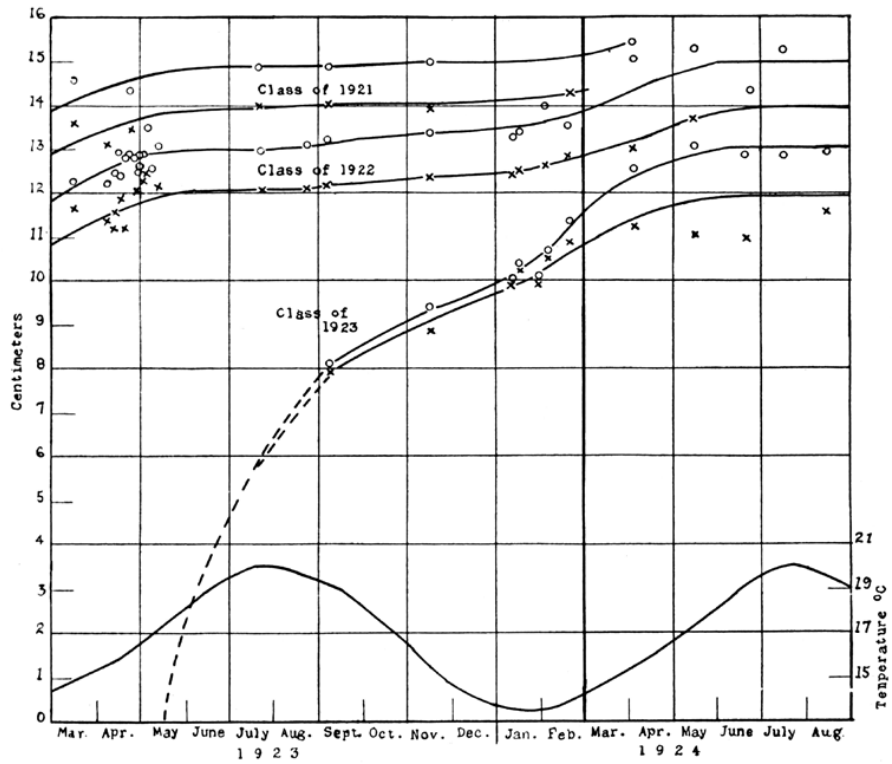
In a study of the scales only eight fish were found whose scales had three annuli. One of these, a female, taken on November 11, 1923, was 170 mm. in length; the largest fish found in any of the collections studied. After the spawning season very few fish were found in the III group and at no time was a fish found which would have been in a IV group. The oldest fish observed were two males taken February 20, 1924. These were in the III group, but had practically completed their fourth year.

This rapid falling off of numbers in the older year classes can be interpreted in either of two ways. First, it seems probable that the life cycle of Leuresthes is relatively short; maturity comes at the end of the first year, and spawning continues during one, two, and at the most, three seasons. However, before the fourth year most of the fish have either fallen prey to their enemies or run out their life course. Hubbs (1912*b*) described an even briefer life cycle of Labidesthes sicculus, another Atherinid. That fish is "characterized by an annual life-cycle, breeding but once at the age of one year, then dying and leaving the young-of-the-year as the only link over the winter connecting the generation of one year with that of the next."9

The alternative explanation is that the lack of numbers in the older year classes has resulted from depletion. One of the first signs of over-fishing is the disappearance of the older fish. When Thompson made his observations at Long Beach in 1919, the spawning grunion were found in great numbers, but at the present time lack of spawning fish on this beach indicates strongly that Leuresthes is being subjected to over-intensive fishing. Age determinations have been made on 115 fish taken by Thompson from April to October, 1919. These fish were classed as follows: O group, 20; I group, 24; II group, 57; III group, 4. In these collections the II group contained the largest numbers, a fact which may indicate that depletion has played some part in the reduction of the older year-classes. However, since the III group contained few fish, and none were found of more than three years, it is apparent that Leuresthes very seldom completes the third year and practically never the fourth.

5. V. RATE OF GROWTH

A basis for an estimation of the rate of growth of Leuresthes has been obtained from the average length of the fish in each year-group in the collections taken from March, 1923, to August, 1924. These averages are given in Table 4, and the growth curves in Graph IV. In this graph the circles represent the average length of the females and the



GRAPH IV. Average length of the year-classes at different seasons of the year, showing the growth rate during the first three years. Below, the average monthly surface-water temperature, San Diego, California. x—x—x males. o—o—o females.

GRAPH IV. Average length of the year-classes at different seasons of the year, showing the growth rate during the first three years. Below, the average monthly surface-water temperature, San Diego, California. x—x—x males. o—o—o females

crosses the averages for the males. The year-classes are indicated by the date of spawning. Thus the 1923 class comprised the O group until March, 1924, when it was considered the I group. The average seasonal variation in the surface-water temperature as given for Coronado Beach, California, by McEwen (1916), is shown on the same graph. As no water temperature data were available for the San Pedro region, this data for San Diego has been employed as a probable indication of the general trend of seasonal temperature fluctuations.

5.1. 1. Growth during the first year

The first young fish were taken September 4, 1923. The males of this collection averaged 79.09 mm. in length and the females 81.02 mm. These points on Graph IV have been connected with the base line at May 15, by hypothetical lines indicating the probable growth rate from the time of hatching until September. From September to the latter part of January, this 1923 year-class continued to grow, but at a slower rate than during the previous summer. The last of January and early February, marked the beginning of a second period of rapid growth, which continued until April.

Data for growth of the 1923 year-class were very incomplete for the months following February, 1924, but the curve has been continued through August on the basis of averages from small collections taken at intervals during the 1924 spawning season. The first year in the life-history, considered as terminating on March 1, was characterized by a rapid growth during the first summer, a slowing-down but not complete cessation of growth during the fall and winter, and an acceleration beginning in the late winter and continuing throughout the spring.

In September the females were but little longer than the males. During the winter they showed a slightly greater growth rate, which increased rapidly during the spring acceleration of growth, so that by April the females averaged approximately 10 mm. longer than the males. This 10 mm. difference was maintained throughout the adult life.

5.2. 2. Growth during mature life

The first fish of the 1922 year-class were taken in March, April and May, 1923. These collections comprised small samples taken at frequent intervals. As a result of the small size of the individual collections, the averages show considerable fluctuation. However, the spring acceleration of growth which characterized the 1924 year-class was also apparent for the 1923 class. This rapid growth continued through April but showed a slackening during early May.

No collections were made between May 9 and July 24, but the average length of the May collection equaled that of the July. This indicated that a complete cessation of growth occurred during the latter part of May, June and July. For the 1923 year-class a similar cessation was indicated, from May to July, 1924. The fish of the 1922 class averaged slightly longer in August than in July and this slow increase in size was maintained until January. Again, during the latter part of January an acceleration in growth began and continued until May. Data beyond this point suggested a cessation during the summer of 1924, the third summer in the life of the fish. The cessation of growth during the summer months occurs at the time of spawning and explains the formation of the breeding annulus in July and August, at the close of the long breeding season. As an obvious result of the frequently repeated spawning, the fishes do not grow during the warmest part of the summer, but as indicated on Graph IV, begin to grow again in August. The continuation of growth through the winter explains the absence of a winter annulus on the scales of practically all the fishes. Since there is no cessation in the growth of the fish, the growth of the scale continues, the course of the ridges is not interrupted, and no annulus is formed. Growth-rate during the winter is slower than in the spring and early fall, and in a few individuals a complete cessation apparently does occur, since in these a winter annulus is formed. However, these few fish comprise a very small percentage of the whole population.

As far as known, a cessation of growth during the height of the growing season has been demonstrated for no other fish. In fact, the growth cycle of Leuresthes stands out in marked contrast to the findings of other workers. Hubbs (1921*b*) found that the growth of Labidesthes sicculus in Michigan took place from June to October and ceased entirely from October to May. For the plaice of the North Sea, Dannevig (1899), Johansen (1910) and Allen (1917), found that growth began about April, went on vigorously until September, slowed down in October and practically ceased from October to April. For Clupea harengus off the east coast of Canada, Huntsman (1919) and Lea (1919) found that growth occurred from May to September, and for the herring of the North Sea, Lea (1911) considered the growing season to be from April to October. In aquarium specimens of Coregonus clupeaformis, Van Oosten (1923) found a growth of the scales from April to September, but no growth from October to March. Rich (1920) found that young salmon, Oncorhynchus tschawytscha, from the Columbia River, grew rapidly during their first summer but showed no growth from November to March. The growth of the older salmon in the ocean, Rich (1925), "progresses at a maximum rate during the warmer part of the year, May to September, and slows materially, if it does not stop entirely during the colder months." Pearse (1919) showed that Pomoxis sparoides, from a Wisconsin lake, grew rapidly from July to November, but ceased growing from November to February. Shann (1910) claimed a rapid summer growth and a winter slackening for Gobius mintus, however, his data were inconclusive. Barney and Anson (1920) found that young Elassoma zonatum from Louisiana grew rapidly from April to November, and very slowly from December to March.

During the first summer Leuresthes maintains the rapid growth common to fishes in general, and shows a slackening but not an entire cessation during the first winter. This continuation of growth through the winter differs from the condition obtaining in most other fishes as far as ascertained, and is probably due to the lessened range of temperature variation and the higher winter temperature of the waters in which the grunion lives. Most of the data obtained by other workers are from fishes taken in more northern waters, where the extremes of temperature are much greater and the winter temperatures much lower. Spring acceleration of growth occurs by the first of February, thus earlier for Leuresthes than for any other fish for which data are obtainable. This spring acceleration continues to May, when as a result of the first spawning, growth stops entirely until July. In August, growth is resumed and continues slowly during the second winter. In February, a second spring acceleration begins and is maintained until May, when growth again stops as a result of the second spawning season. The few fish which survive the second breeding season repeat the growth fluctuation during the third fall, winter and spring.

For Leuresthes, as for other fishes, growth during the first year is very rapid and decreases constantly during the following years. At the end of the first year the length of the males averages approximately 110 mm., and that of the females 119 mm.; at the end of the second year, 129 mm. and 140 mm.; and at the end of the third, 143 mm. and 154 mm. Thus, the average growth increment for the combined sexes is 115 mm. for the first year, 20 mm. for the second, and 14 mm. for the third.

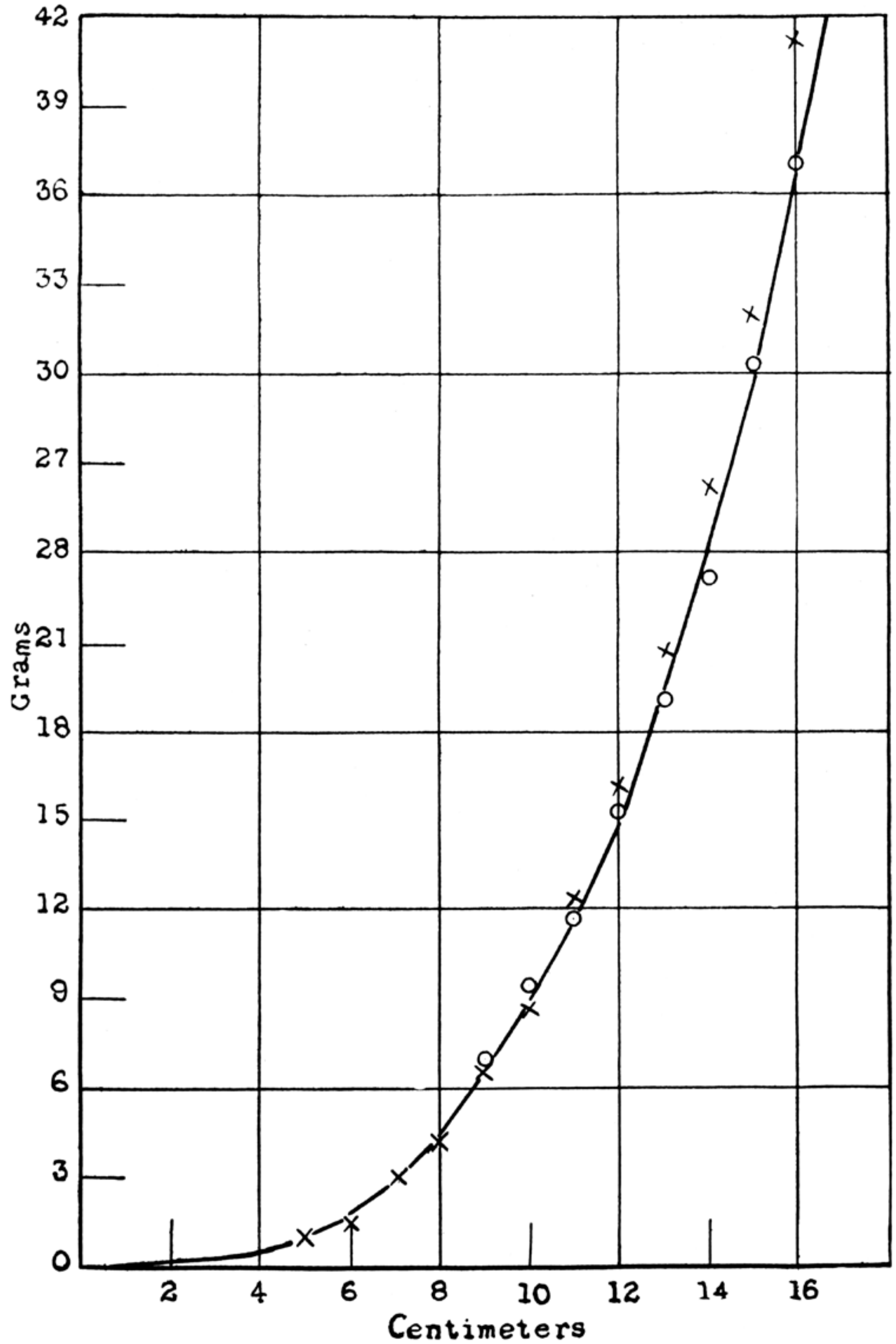
5.3. 3. Growth in weight

Weights were ascertained for fish from the collection taken September, November, January and February. From these data the average weight for each half centimeter of length was compiled. September and November data were combined, and similarly those for January and February; thus making possible a comparison of the weight of the fall fish and the winter fish. Table 6 and Graph V give the results of such compilations. Data for the fall fish are indicated by crosses, and for the winter fish by circles. No sexual differences were found and the curves represent a combination of both sexes.

TABLE 6.—Weight at Nearest Half Centimeter of Length for Fall and Winter Fish.

Length, cm.	September, November			January, February			Difference in weight fall minus winter		Calculated weight
	Number	Mean wt. Grams	P. E. M ±	Number	Mean wt. Grams	P. E. M ±	Difference Grams	P. E. D. ±	$W=0.0089L^3$
5.0	12	1.00							1.11
5.5									1.48
6.0	2	1.50	0.24						1.92
6.5	6	2.00							2.44
7.0	7	3.00							3.05
7.5	34	3.32	0.05						3.75
8.0	43	4.39	0.05						4.55
8.5	56	5.32	0.04						5.45
9.0	41	6.56	0.07	87	6.70	0.05	–0.14	0.09	6.47
9.5	58	7.72	0.06	139	8.02	0.04	–0.30	0.07	7.61
10.0	35	8.80	0.07	140	9.33	0.03	–0.53	0.08	8.88
10.5	13	10.15	0.09	143	10.54	0.04	–0.39	0.10	10.28
11.0	3	12.33	0.18	156	11.81	0.05	0.52	0.19	11.82
11.5	19	14.58	0.15	133	13.50	0.07	1.07	0.17	13.50
12.0	26	16.96	0.16	121	15.21	0.07	1.75	0.17	15.34
12.5	53	18.98	0.12	93	17.31	0.10	1.67	0.15	17.34
13.0	41	21.44	0.17	71	19.31	0.17	2.13	0.24	19.51
13.5	39	24.10	0.16	53	22.45	0.15	1.65	0.22	21.85
14.0	17	26.06	0.23	24	23.00	0.23	3.06	0.33	24.37
14.5	8	27.62	0.26	29	26.72	0.33	0.90	0.42	27.07
15.0	2	32.00		11	30.18	0.34	1.82		29.97
15.5				6	32.33	0.81			33.07
16.0	1	41.00		1	37.00		4.00		36.37
Totals	516			1207					

TABLE 6.—Weight at Nearest Half Centimeter of Length for Fall and Winter Fish



GRAPH V. Length-weight relationships for fall and winter fish. x x x September, November fish. o o o January, February fish. —— Calculated weight.

GRAPH V. Length-weight relationships for fall and winter fish. x x x September, November fish. o o o January, February fish. — Calculated weight

In January and February no fish were taken less than 9.0 cm. in length. At 9.0 to 10.5 cm. length, the winter fish were slightly heavier than the fall fish. This slight excess in weight is probably significant, as, with one exception, the differences exceed the probable errors by four times. Since these lengths comprised fish of the O group, the data may thus indicate that, during the winter, the immature fish increase slightly more rapidly in weight than length.

At lengths of 11.0 cm. and more, the fall fish are consistently heavier than the winter fish. The differences, where the numbers involved were sufficient to make comparisons reliable, exceeded their probable errors by six to eleven times. Thus, for adult fish, the average weight for each unit of length was greater in the fall than at the end of the winter.

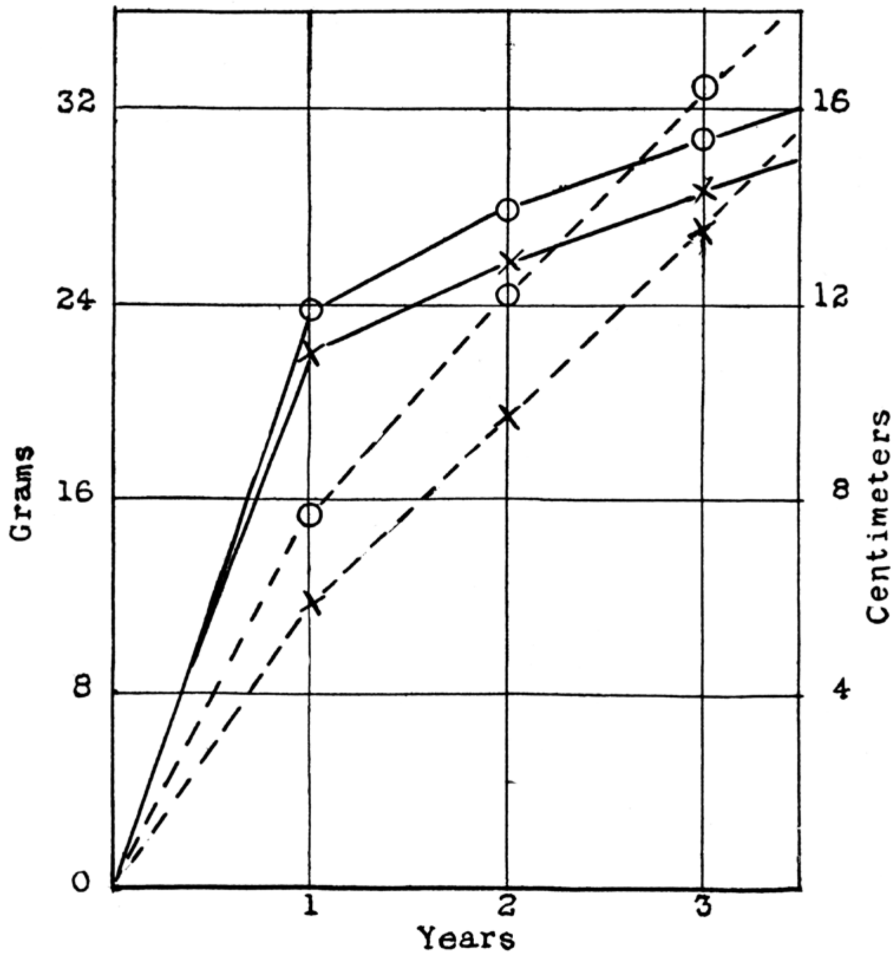
The curve obtained by calculating the weight from the formula $W=0.0089\ L^3$ fits the ascertained weights for the immature fall fish and for the winter fish, but falls below the observed weights of the adult fall fish. To obtain a curve which would give the accurate weight of the adult fish in the fall, the constant 0.0096 would have to be used. Using this constant for the immature fall fish would give a calculated weight higher than the observed value. The fluctuating value of the constant K at different seasons, as found from the formula $K = 100\ W/L^3$ has been used by many workers as an index of the condition of the fish. Reibisch (1908; 1911) used the formula [q] = 40000 G/L3 and obtained a value for [q] which he termed a "Dicken-koeffizienten." G is the weight of the fish without the gonads and L, the length. The values of [q] in the formula showed the plaice of the Baltic to be in the poorest condition from January to April, April marking the close of the breeding season. Johnstone (1910) used the formula $K = 100\ W/L^3$ and found for the plaice of the Irish Sea that the value of K fluctuated with the season and varied for different localities. Similarly, Johansen (1910) used the same formula and obtained the same results for the plaice of the North Sea. Hecht (1916) in a general paper on the form and growth of fishes used the formula $A = 100\ W/L^3$. The constant A differed for different species and fluctuated with the seasons of the year.

For Leuresthes, K has the value of 0.89 for winter fish and 0.96 for fall fish. This difference in the condition of the fish in the two seasons of the year depended, to a large extent, at least, on the fat content. Fat was present in the body cavity of the fall fish in considerable quantities, while in the winter fish or, in fact, in fish taken at any season of the year except in the fall, very little fat was evident.

Pearse (1925) by chemical analysis, found that the fat content of perch and brook trout increased slightly during the first year, but in the following years fluctuated with the seasons. The highest percentage of fat was found in the summer and the lowest in the winter. Clark and Almy (1918), from an analysis of twenty species of fishes, concluded that a large number of the common food fishes have a greatly increased fat content in late summer and autumn. In Leuresthes the highest percentage of fat is found in the fall; the long spawning season preventing the accumulation of fat during the summer months.

Unfortunately very few weights were obtained for fish taken during the spawning season. At the time when the sex products are ripe the weight at each unit of length would be greater than for any other season of the year. The scant data obtained indicated a sexual difference with a possible value for K of 1.0 for the males and 1.1 for the females.

The average lengths and weights of each sex at the end of the first, second and third years are compared in Graph VI. During the first



GRAPH VI. Average length and weight for each sex at the end of the first, second and third year. —x—x length of males. —o—o length of females. - - -x - - -x weight of males. - - -o- - -o weight of females.

GRAPH VI. Average length and weight for each sex at the end of the first, second and third year. —x—x length of males. —o—o length of females. - - -x - - -x weight of males. - - -o- - -o weight of females

year the increase in both weight and length was greater than for succeeding years although the gain in weight was not as great as in length. After the first year, the gain in length fell off rapidly, while the weight increase continued at a very slightly diminished rate throughout the life of the fish.

6. VI. SUMMARY

By a series of measurements of the ova from Leuresthes tenuis, the following facts were ascertained.

1. Growth of the ova toward maturity begins as early as January and continues throughout the spawning season.

2. As soon as one batch of eggs matures and is spawned out, another batch begins to develop, is matured, and spawned out two weeks later. Thus, after an individual fish starts spawning it continues to spawn periodically on each series of high tides throughout the breeding season.

3. The interval between spawnings is apparently fifteen days instead of two weeks. This condition results in the fishes spawning on later and lower tides during the higher series of high tides than on the lower series of high tides.

By a study of the scales and length-frequency data, it was found that Leuresthes matures at the end of the first year. For the population studied, approximately 25 per cent of the fish spawn again at the end of the second year and 7 per cent at the end of the third year. No fish were found spawning at the end of the fourth year.

Leuresthes grows rapidly during the first year, the males reaching an average length of 110 mm. and the females of 119 mm. After the first year and the resulting attainment of sexual maturity, increase in length falls off rapidly, but increase in weight continues at only a slightly diminished rate.

As a result of the long protracted spawning season, growth of the mature fish ceases during the months of May, June and July, and is resumed again in the fall. This cessation of growth during the summer months results in the formation of a breeding annulus on the scales. Growth continues during the winter and a winter annulus is formed only in rare cases.

7. VII. LITERATURE CITED

Allen, E. J. 1917. The age of fishes and the rate at which they grow. Jour. Mar. Biol. Assoc., N. S., Vol. 11, 1916–1918, pp. 399–424.

Apstein, C. 1901. Zur Lebensgeschichte des Goldbutts. Vortrag auf der 24. General versammlung des Central=Fishcherei=Vereins für Schleswig=Holstein, pp. 1–14.

Barfurth, D. 1886. Biologische untersuchengen über die Bachforelle. Archiv für Mikrosckopische Anatomie, Bd. 27, pp. 128–179.

Barney, R. L. and Anson, B. J. 1920. Life history and ecology of the pigmy sunfish Elassoma zonatum. Ecology, Vol. 1, pp. 241–256.

1923. Life history and ecology of the orange-spotted sunfish Lepomis humilis. Rept. U. S. Fish Comm., Appendix XV, 1922, pp. 1–16.

Bean, Tarleton H. 1901. Food and game fishes of New York. Forest, Fish and Game Comm., New York, 7th Rept., pp. 251–460.

Brock, J. 1878. Beiträge zur Anatomic und Histologic der Geschlechsorgan der Knockenfischi. Morph. Jahrbuch, Bd. 4, Heft 4, pp. 505–578.

Calderwood, W. L. 1892. A contribution to our knowledge of the ovary and intra-ovarian egg in Teleosteans. Jour. Mar. Biol. Assoc., N. S., Vol. 2, pp. 298–313.

Clark, Ernest D. and Almy, Loyd H. 1918. The analysis of twenty common food fishes with especial reference to a seasonal variation in composition. Journ. Biol. Chem., Vol. 33, pp. 483–498.

Creaser, Charles W. and Clench, W. J. 1923. The use of sodium silicate as a mounting medium. Trans. Am. Micr. Soc., Vol. 42, pp. 69–71.

Creaser, Charles W. 1925. The structure and growth of the scales of fishes in relation to the interpretation of their life history, with especial reference to the sunfish Eupomotis gibbosus. Misc. Pub. Mus. Zool., Univ. Mich. In press.

Cunningham, J. T. 1894. The ovaries of fishes. Jour. Mar. Biol. Assoc., N. S. Vol. 3, 1893–1895, pp. 111–118.

1898. On the histology of the ovary and of the ovarian ova in certain marine fishes. Quart. Jour. Micr. Sci. N. S., Vol. 40, pp. 101–163.

Dannevig, H. C. 1899. On the rate of growth of plaice. Seventeenth Ann. Rept. Fishery Board, Scot., Pt. III, 1898 (1899), pp. 232–247.

Earll, R. E. 1880. A report on the history and present condition of the shore cod-fisheries of Cape Ann, Mass., together with notes on the natural history and artificial propagation of the species. Rept. U. S. Fish. Comm., 1878 (1880), pp. 685–740.

Eigenmann, Carl H. 1894. On the viviparous fishes of the Pacific Coast of North America. Bull. U. S. Fish. Comm., Vol. 12, 1892 (1894), pp. 381–478.

Franz, Viktor. 1910. Die Eiproduktion der Scholle. Wiss. Meeresuntersuchungen, N. F., Bd. 9, Abth. Helegoland, pp. 59–141.

Fulton, T. Wemyss. 1890. The comparative fecundity of sea-fishes. Ninth Ann. Rept. Fishery Board, Scot., pp. 243–268.

1899. The growth and maturation of the ovarian eggs of Teleost fishes. Sixteenth Ann. Rept. Fishery Board, Scot., Pt. III, 1898 (1899), pp. 88–124.

Gudger, E. W. 1919. The ovary of Felichthys felis, the galf-topsail catfish: Its structure and function. Carnegie Institute Wash., Vol. 13, pp. 111–128

Hecht, Selig. 1916. Form and growth in fishes. Journ. Morph., Vol. 27, pp. 379–400.

Henn, Arthur W. 1916. On various South American Pœciliid fishes. Ann. Carnegie Mus., Vol. 10, pp. 93–142.

Hensen, V. 1884. On the occurrence and quantity of the eggs of some of the fish of the Baltic, especially those of the plaice (Platessa platessa), the flounder (Platessa vulgaris), and the cod (Gadus morrhus). Rept. U. S. Fish Comm., 1882 (1884), pp. 427–454.

Hildebrand, Samuel F. 1922. Notes on habits and development of eggs and larvae of the silversides Menidia menidia and Menidia beryllina. Bull. U. S. Bur. Fish., Vol. 38, 1921–1922, pp. 113–120.

Hubbs, Carl L. 1921a. An ecological study of the life-history of Amphigonopterus aurora and of other viviparous perches of California. Biol. Bull., Vol. 40, pp. 181–209.

1921b. An ecological study of the life-history of the fresh-water atherine fish Labidesthes sicculus. Ecology, Vol. 2, pp. 262–276.

1925. Seasonal and age variation in the Pacific herring, California sardine and California anchovy. Calif. Fish and Game Comm., Fish Bull. No. 8, pp. 1–23.

Hunstman, A. B. 1919. Growth of the young herring (so-called sardines) of the Bay of Fundy. Canadian Fisheries Expedition, 1914–1915, pp. 165–171.

Johansen, A. C. 1910. Bericht ueber die Daenischen Untersuchungen ueber die Schollenfischerei und den Schollenbestand in der Oestlichen Nordsee, dem Skagerak und dem Noerdlichen Kattegat. Meddel. Komm. Havundersøgelser, Ser. Fiskeri, Bd. 3, pp. 1–142.

Johnstone, James. 1910. Report on measurements of the Irish Sea plaice during the year 1909. Proc. and Trans. Liverpool Biol. Soc., Vol. 24, pp. 100–184.

Kuntz, Albert. 1914. Notes on the habits, morphology of the reproductive organs, and embryology of the viviparous fish Gambusia affinis. Bull. U. S. Bur. Fish., Vol. 33, 1913 (1915), pp. 177–190.

1916. Notes on the embryology and larval development of five species of teleostean fishes. Bull. U. S. Bur. Fish., Vol. 34, 1914 (1916), pp. 407–429.

Kuntz, Albert, and Radcliffe, Lewis. 1918. Notes on the embryology and larval development of twelve teleostean fishes. Bull. U. S. Bur. Fish., Vol. 35, 1915–1916 (1918), pp. 89–134.

Lane, Henry H. 1903. The ovarian structure of the viviparous blind fishes Lucifuga and Stygicola. Biol. Bull., Vol. 6, pp. 38–54.

Lea, Einar. 1911. A study on the growth of herrings. Conseil Perm. Intern. Explor. Mer, Public. de Circonstance, No. 61, pp. 35–57.

1919. Report of age and growth of the herring in Canadian waters. Canadian Fisheries Expedition, 1914–1915, pp. 77–164.

Leach, Glen C. 1923. Artificial propagation of brook trout and rainbow trout, with notes on three other species. Rept. U. S. Fish. Comm., Appendix VI, 1923, pp. 1–74.

Lee, Rosa M. 1920. A review of the methods of age and growth determination in fishes by means of scales. Fisheries Eng. and Wales, Ministery Agri. and Fish., Fishery Invest., Ser. II, Vol. 4, No. 2, pp. 1–32.

McEwen, George F. 1916. Summary and interpretation of the hydrographical observations made by the Scripps Institution for Biological Research of the University of California, 1908–1915. Univ. Calif. Publ. in Zool., Vol. 15, pp. 255–356.

Mohr, E. 1921. Altersbestimmungen bei tropischen Fischen. Zoologischer Anzeiger, Bd. 53, pp. 87–95.

Owsiannikow, Ph. 1885. Studien über das Ei, hauptsächlich bei Knochenfischen. Mém. Acad. Sci. St. Pétersb., 7 Serie, Tome 33, pp. 1–54.

Pagenstecher, H. A. 1861. Ueber das Ei von Atherina hepsetus. Arch. für Anatomie, Physiologie, und Wissen. Medicin, 1861, pp. 631–634.

Pearse, A. S. 1919. Habits of the black crappie in inland lakes of Wisconsin. Rept. U. S. Fish. Comm., Appendix III, 1918 (1919), pp. 1–16.

1925. The chemical composition of certain fresh-water fishes. Ecology, Vol. 6, pp. 7–16.

Reibisch, Johannes. 1899. Ueber die Eizahl bie Pleuronechthes platessa und die Altersbestimmung dieser Form aus den Otolithen. Wiss. Meeresuntersuchungen, N. F., Bd. 4, Abth. Kiel, pp. 230–248.

1908. Ein Dickenkoeffizient als Mass für Alter und Ernährungszustand der Fische. De Beteiligung Deutschlands an der internationalen Meeresforshung. Jahresbericht IV und V, pp. 59–65.

1911. Biologische Untersuchungen über Gedeihen, Wanderung und Ort der Entstehung der Scholle (Pleuronectes platessa) in der Ostee. Wiss. Meeresuntersuch., N. F., Bd. 13, Abth. Kiel, pp. 127–202.

Reighard, Jacob. 1906. The breeding habits, development and propagation of the black bass. Bull. Mich. Fish Comm., No. 7, pp. 1–73.

Rich, Willis H. 1920. Early history and seaward migration of chinook salmon in the Columbia and Sacramento rivers. Bull. U. S. Bur. Fish., Vol. 37, 1919–1920 (1920), pp. 1–73.

1925. Growth and degree of maturity of chinook salmon in the ocean. Bull. U. S. Bur. Fish., Vol. 41, pp. 1–90.

Ryder, John A. 1883. On the thread-bearing eggs of the silversides (Menidia). Bull. U. S. Fish. Comm., Vol. 3, pp. 193–196.

Shann, Edward. 1910. Some notes on the life-history and the rate of growth in Gobius minutus. Ann. and Mag. Nat. Hist., Ser. 8, Vol. 5, pp. 217–239.

Taylor, Harden F. 1916. The structure and growth of the scales of the squeteague and the pigfish as indicative of life history. Bull. U. S. Bur. Fish., Vol. 34, 1914 (1916), pp. 287–330.

Thompson, William F. 1914. A preliminary report on the life-history of the halibut. Rept. British Columbia Fish. Comm., 1914, pp. 76–99.

1917. The egg production of the halibut of the Pacific. Report British Columbia Comm. Fish., 1916 (1917), pp. 35–39.

1919a. The spawning of the grunion. Calif. Fish and Game, Vol. 5, p. 201.

Thompson, Will F., assisted by Thompson, Julia Bell. 1919b. The spawning of the grunion (Leuresthes tenuis). Calif. Fish and Game Comm., Fish Bull. No. 3, pp. 1–29.

Thomson, J. Stuart. 1904. The periodic growth of scales in Gadidae as an index of age. Jour. Mar. Biol. Ass., N. S., Vol. 7, 1904–1906, pp. 1–109.

Van Oosten, John. 1923. A study of the scales of whitefishes of known ages. Zoologica, Vol. 2, pp. 381–412.

Wallace, William. 1903. Observations on ovarian ova and follicles in certain Telostean and Elasmobranch fishes. Quart. Journ. Micr. Sci., Vol. 47, pp. 161–213.

Williamson, H. C. 1911. Report on the reproductive organs of Sparus centrodontus, (Delaroche); Sparus cantharus, (L.); Sabastes marinus (L.); and Sebastes dactylopterus (Delaroche); and on the ripe eggs and larvae of Sparus centrodontus (?), and Sebastes marinus. Fisheries, Scot., Sci. Invest., 1910, No. 1, pp. 1–35.

8. VIII. APPENDIX

Tables of frequency distributions on which the graphs given in the text are based. The tables bear the same numbers as the graphs, suffixed by letters.

TABLE 1A.—Diameters of Ova Measured from Five Fish Taken November 14, 1923.

Diameter, mm.	Length of Fish, mm.					
	123	134	134	136	154	Total
0.04	45	45	33	27	45	195
0.08	68	73	77	79	57	354
0.12	43	49	48	64	52	256
0.16	34	21	26	19	36	136
0.195	10	10	9	8	8	45
0.23		2	7	3	2	14
Totals	200	200	200	200	200	1,000

TABLE 1A.—Diameters of Ova Measured from Five Fish Taken November 14, 1923

TABLE 1B.—Diameters of Ova Measured from Five Fish Taken January 10 and 11, 1924.

Diameter, mm.	Length of fish, mm.					
	108	111	139	152	157	Total
0.04	46	22	29	35	39	171
0.08	80	60	60	54	55	309
0.12	39	49	36	39	36	199
0.16	16	27	25	28	42	138
0.195	6	17	20	18	10	71
0.23	6	5	11	12	6	40
0.27	2	9	4	6	6	27
0.31	5	3	5	4	3	20
0.35		4	4	3	2	13
0.39		1	4	1	1	7
0.43		2	2			4
0.47		1				1
Totals	200	200	200	200	200	1,000

TABLE 1B.–Diameters of Ova Measured from Five Fish Taken January 10 and 11, 1924

TABLE 1C.—Diameters of Ova Measured from Five Fish Taken January 15 and 31, 1924.

Diameter, mm.	Length of fish, mm.					
	108	109	109	111	138	Total
0.04	67	37	29	54	41	228
0.08	85	91	93	89	89	447
0.12	47	67	67	88	62	331
0.16	31	46	47	28	40	192
0.195	22	18	16	6	17	79
0.23	11	7	10	2	10	40
0.27	11	5	10	9	12	47
0.31	7	8	7	5	8	35
0.35	4	4	4	3	7	22
0.39	3	9	5	5	8	30
0.43	12	3	6	5	6	32
0.47	3	5	4	6	3	21
0.51	2	2	3	2		9
0.55			2			2
Totals	305	302	303	302	303	1515

TABLE 1C.–Diameters of Ova Measured from Five Fish Taken January 15 and 31, 1924

TABLE 1D.—Diameters of Ova Measured from Five Fish Taken February 6, 1924.

Diameter, mm.	Length of fish, mm.					
	108	108	113	120	160	Total
0.04	49	37	52	54	62	254
0.08	74	80	100	100	93	447
0.12	65	59	71	56	54	305
0.16	40	41	22	37	22	162
0.195	17	20	12	14	18	81
0.23	11	8	5	3	10	37
0.27	7	6	6	5	8	32
0.31	7	4	2	3	3	19
0.35	10	4	5	3	10	32
0.39	4	9	4	6	8	31
0.43	5	6	4	8	5	28
0.47	7	6	6	2	2	23
0.51	4	11	5	3	2	25
0.55	1	5	7	8	5	26
0.585	2	4	2	1	3	12
0.62	---	1	2	---	---	3
Totals	303	301	305	303	305	1517

TABLE 1D.–Diameters of Ova Measured from Five Fish Taken February 6, 1924

TABLE 1E.—Diameters of Ova Measured from Five Fish Taken February 20, 1924.

Diameter, mm.	Length of fish, mm.					
	116	127	135	137	145	Total
0.04	56	60	54	62	36	268
0.08	117	164	129	132	133	675
0.12	77	82	108	95	135	497
0.16	69	66	71	63	70	339
0.195	34	26	41	40	33	174
0.23	20	10	16	16	15	77
0.27	13	9	12	10	3	47
0.31	6	10	8	12	13	49
0.35	10	4	4	7	8	33
0.39	11	11	11	7	6	46
0.43	9	11	4	8	2	34
0.47	5	6	9	14	5	39
0.51	12	7	7	7	4	37
0.55	11	5	4	3	11	34
0.585	9	9	11	4	11	44
0.62	4	11	4	1	4	24
0.66	12	8	5	6	4	35
0.70	9	2	6	2	8	27
0.74	9	1	1	6	2	19
0.78	8	1	1	3	1	14
0.82	3	---	---	3	---	6
0.86	1	---	---	2	---	3
Totals	505	503	506	503	504	2521

TABLE 1E.–Diameters of Ova Measured from Five Fish Taken February 20, 1924

TABLE 2A.—Diameters of Ova Measured from Five Fish Taken April 19, 1923.

Diameter, mm.	Length of fish, mm.					
	118	121	136	138	150	Total
0.04	51	69	35	25	66	246
0.08	110	144	72	95	172	593
0.12	76	68	75	62	70	351
0.16	45	30	65	48	28	216
0.195	31	23	45	21	25	145
0.23	20	16	30	20	14	100
0.27	16	11	19	27	11	84
0.31	12	12	11	20	5	60
0.35	10	19	16	11	11	67
0.39	22	10	12	13	11	68
0.43	18	14	13	8	9	62
0.47	14	16	10	15	9	64
0.51	14	19	14	11	3	61
0.55	10	12	12	15	15	64
0.585	21	12	10	20	9	72
0.62	11	10	9	18	9	57
0.66	8	11	5	22	5	51
0.70	5	6	12	14	3	40
0.74	2	2	13	5	3	25
0.78	1	1	5	7	3	17
0.82	2		2	6		10
0.86	2			2		4
0.90				1		1
0.94						
0.975						
1.01						
1.05						
1.09						
1.13						
1.17						
1.21						
1.25						
1.29						
1.33						
1.365						
1.40				1	1	2
1.44					1	1
1.48				1	1	2
1.52					3	3
1.56	1		1	1	4	7
1.60				7	1	8
1.64			4	3	6	13
1.68	4		4		1	9
1.72			4	1	2	7
1.755			4	5	2	11
1.79			1	1		2
1.83			1			1
1.87			1			1
Totals	506	505	505	506	503	2,525

TABLE 2A.–Diameters of Ova Measured from Five Fish Taken April 19, 1923

TABLE 2B.—Diameters of Ova Measured from Five Fish Taken April 21, 1923.

Diameter, mm.	Length of fish, mm.					
	113	121	135	147	152	Total
0.04	61	53	45	45	62	266
0.08	139	138	123	113	124	637
0.12	97	94	82	85	85	443
0.16	50	56	46	53	34	239
0.195	25	33	31	22	19	130
0.23	22	17	15	21	24	99
0.27	12	12	18	15	11	68
0.31	12	4	10	13	9	48
0.35	4	7	10	9	10	40
0.39	7	7	10	10	10	44
0.43	10	11	8	13	8	50
0.47	9	9	27	16	15	76
0.51	8	10	13	9	7	47
0.55	15	11	12	12	14	64
0.585	2	5	7	6	10	30
0.62	7	3	3	5	16	34
0.66	6	2	----	7	7	22
0.70	2	----	7	5	14	28
0.74	10	----	8	14	7	39
0.78	6	1	8	12	8	35
0.82	2	1	12	10	----	25
0.86	1	15	6	8	1	31
0.90	----	6	4	1	1	12
0.94	1	6	3	1	----	11
0.975	----	----	----	1	----	1
1.01	----	1	----	----	----	1
Totals	508	502	508	506	496	2,520

TABLE 2B.–Diameters of Ova Measured from Five Fish Taken April 21, 1923

TABLE 2C.—Diameters of Ova Measured from Five Fish Taken April 23, 1923.

Diameter, mm.	Length of fish, mm.					
	120	131	133	134	149	Total
0.04	44	78	51	56	42	271
0.08	114	109	114	110	96	543
0.12	87	81	63	74	97	402
0.16	65	60	43	35	69	272
0.195	28	31	24	19	19	121
0.23	17	16	11	14	20	78
0.27	11	17	16	8	10	62
0.31	14	7	8	17	9	55
0.35	10	9	20	14	11	64
0.39	12	5	18	13	13	61
0.43	13	7	21	11	5	57
0.47	14	9	14	17	13	67
0.51	14	9	13	19	17	72
0.55	10	11	15	19	14	69
0.585	6	9	4	17	9	45
0.62	8	6	8	9	9	40
0.66	1	3	2	11	10	27
0.70	----	3	2	5	4	14
0.74	1	2	2	14	9	28
0.78	2	2	4	15	20	43
0.82	----	4	4	3	5	16
0.86	3	3	14	5	2	27
0.90	6	6	8	1	2	23
0.94	5	3	12	----	----	20
0.975	11	8	6	1	----	26
1.01	6	4	----	----	----	10
1.05	3	1	4	----	----	8
1.09	----	1	----	----	----	1
1.13	----	----	1	----	----	1
Totals	505	504	502	507	505	2,523

TABLE 2C.–Diameters of Ova Measured from Five Fish Taken April 23, 1923

TABLE 2D.—Diameters of Ova Measured from Five Fish Taken April 25, 1923.

Diameter, mm.	Length of fish, mm.					
	119	131	133	135	139	Total
0.04	81	95	78	50	50	354
0.08	126	170	155	93	148	692
0.12	55	68	76	52	56	307
0.16	55	40	34	27	42	198
0.195	35	26	17	30	24	132
0.23	21	9	16	18	10	74
0.27	15	12	14	17	16	74
0.31	11	11	8	16	6	52
0.35	16	6	9	15	10	56
0.39	24	4	5	14	14	61
0.43	8	6	13	21	12	60
0.47	15	5	11	15	12	58
0.51	9	7	12	17	20	65
0.55	8	6	9	14	14	51
0.585	4	7	10	16	12	49
0.62	4	10	3	13	5	35
0.66		1	3	4	1	9
0.70	2	2	1	2		7
0.74				1		1
0.78			1		1	2
0.82		1		1		2
0.86			1	2	1	4
0.90		3	4	4	2	13
0.94		3		8	8	19
0.975	1	4	1	14	6	26
1.01	4	4	9	11	15	43
1.05	3	2	3	17	11	36
1.09	3	3	9	6	4	25
1.13	4	4	2	5	2	17
1.17	1	1		1	2	5
1.21						
1.25		1	1			2
Totals	505	511	505	504	504	2,529

TABLE 2D.–Diameters of Ova Measured from Five Fish Taken April 25, 1923

TABLE 2E.—Diameters of Ova Measured from Five Fish Taken April 28, 1923.

Diameter, mm.	Length of fish, mm.					
	121	123	130	135	149	Total
0.04	52	66	109	47	48	322
0.08	104	125	153	97	99	578
0.12	75	71	63	60	87	356
0.16	45	40	25	37	58	205
0.195	29	25	25	12	39	130
0.23	17	19	13	15	19	83
0.27	14	13	15	10	7	59
0.31	6	10	6	10	2	34
0.35	18	12	11	13	9	63
0.39	14	7	6	16	11	54
0.43	15	14	9	14	9	61
0.47	19	7	8	14	11	59
0.51	15	7	5	14	15	56
0.55	12	8	5	20	5	50
0.585	23	16	11	12	13	75
0.62	9	10	9	13	9	50
0.66	4	8	4	18	11	45
0.70	1	5	2	4	5	17
0.74	1	2	1	1	7	12
0.78		1		3	2	6
0.82		1			1	2
0.86			1		1	2
0.90						
0.94		1		3	1	5
0.975	1		1		1	3
1.01		1		1		2
1.05	3	4	2	1	2	12
1.09	5	5	3	11		24
1.13	4	4	4	18		30
1.17	6	10	7	9	2	34
1.21	7	7	2	14	4	34
1.25	6	9	5	10	5	35
1.29	2	3	1	4	3	13
1.33			1	1	7	9
1.365	1	1			5	7
1.40	1			1	4	6
1.44					1	1
Totals	509	512	507	503	503	2,534

TABLE 2E.–Diameters of Ova Measured from Five Fish Taken April 28, 1923

TABLE 2F.—Diameters of Ova Measured from Five Fish Taken May 1, 1923.

Diameter, mm.	Length of fish, mm.					
	119	130	134	149	156	Total
0.04	48	54	48	36	55	241
0.08	96	113	97	98	88	492
0.12	73	61	69	73	90	366
0.16	54	58	49	65	39	265
0.195	32	21	25	30	29	137
0.23	26	25	21	17	29	118
0.27	23	11	20	17	10	81
0.31	11	11	9	21	11	63
0.35	13	18	20	15	12	78
0.39	14	13	21	10	10	68
0.43	6	13	17	11	9	˙6
0.47	15	14	21	10	13	73
0.51	15	8	18	12	13	66
0.55	9	13	19	13	11	65
0.585	18	11	18	12	7	66
0.62	12	9	6	12	11	50
0.66	7	16	10	8	11	52
0.70	3	3	1	6	12	25
0.74	1	3		3	9	16
0.78	2				4	6
0.82		1			1	2
0.86		1				1
0.90						
0.94						
0.975						
1.01						
1.05						
1.09		1		1		2
1.13		1				1
1.17	1			2		3
1.21		1				1
1.25	1	5	1	1	1	9
1.29		2		8	2	12
1.33	1	2	4	9	2	18
1.365	3	8	6	7	1	25
1.40	7	3	5	3	6	24
1.44	7	3	1	2	5	18
1.48	2	1	2	3	5	13
1.52	5	2		2	1	10
1.56	2				2	4
1.60					5	5
1.64					2	2
1.68					1	1
Totals	507	506	508	507	507	2,535

TABLE 2F.–Diameters of Ova Measured from Five Fish Taken May 1, 1923

TABLE 2G.—Diameters of Ova Measured from Five Fish Taken May 3, 1923.

Diameter, mm.	Length of fish, mm					
	119	131	134	136	150	Total
0.04	53	53	43	48	50	247
0.08	104	130	94	86	121	535
0.12	64	70	35	66	56	291
0.16	62	49	42	40	41	234
0.195	33	21	27	28	32	141
0.23	21	22	28	20	15	106
0.27	7	15	18	18	12	70
0.31	8	7	14	18	12	59
0.35	11	7	15	14	10	57
0.39	15	7	10	21	11	64
0.43	16	10	18	10	15	69
0.47	7	11	14	16	11	59
0.51	9	9	14	7	14	53
0.55	16	10	20	20	13	79
0.585	9	16	23	12	15	75
0.62	7	19	22	11	19	78
0.66	7	10	21	10	17	65
0.70	7	7	3	11	7	35
0.74	11	3	4	15	2	35
0.78	5			13	3	21
0.82	3	1		5		9
0.86	1			1	1	3
0.90						
0.94						
0.975						
1.01						
1.05						
1.09						
1.13						
1.17						
1.21						
1.25						
1.29			1			1
1.33			1			1
1.365		1	3			4
1.40			3			3
1.44	3	4	3			10
1.48		2	6	1		9
1.52	2	7	1	1	4	15
1.56	7	8	6	4	4	29
1.60	4	3	9	2	4	22
1.64	4	1	1	3	7	16
1.68	4	2	3	1	3	13
1.72	1	1		2	2	6
1.755				1	2	3
1.79			1			1
1.83						
1.87	1					1
1.91		1				1
Totals	502	507	503	505	503	2,520

TABLE 2G.–Diameters of Ova Measured from Five Fish Taken May 3, 1923

TABLE 2H.—Diameters of Ova Measured from Five Fish Taken May 5, 1923.

Diameter, mm.	Length of fish, mm.					
	119	130	134	139	143	Total
0.04	71	80	42	85	84	362
0.08	119	131	101	161	125	637
0.12	78	86	78	84	81	407
0.16	43	43	38	31	59	214
0.195	27	20	46	17	19	129
0.23	14	17	27	27	16	101
0.27	11	9	17	15	10	62
0.31	13	10	13	6	7	49
0.35	16	5	8	5	14	48
0.39	7	10	12	7	11	47
0.43	11	14	11	8	8	52
0.47	5	13	7	8	9	42
0.51	10	7	6	2	10	35
0.55	10	10	7	8	3	38
0.585	8	11	10	8	4	41
0.62	12	2	8	15	5	42
0.66	10	4	10	8	2	34
0.70	10	14	9	5	3	41
0.74	3	12	17	6	9	47
0.78	6	4	24	-	5	39
0.82	1	3	8	1	4	17
0.86	-	1	3	-	2	6
0.90	-	-	2	-	6	8
0.94	-	-	1	-	4	5
0.975	-	-	-	-	1	1
1.01	-	-	-	-	4	4
1.05	-	-	-	-	1	1
1.09	-	-	-	-	1	1
Totals	485	506	505	507	507	2,510

TABLE 2H.–Diameters of Ova Measured from Five Fish Taken May 5, 1923

TABLE 3A.—Lengths of Fish Taken September 4. 1923, Grouped to Nearest Half Centimeter.

Length, cm.	Number		Length, cm.	Number	
	Males	Females		Males	Females
6.0	1		12.0	100	22
6.5	6	4	12.5	120	61
7.0	11	15	13.0	46	98
7.5	70	87	13.5	19	131
8.0	67	100	14.0	24	74
8.5	42	66	14.5	8	21
9.0	15	40	15.0	3	9
9.5	3	19	15.5	1	15
10.0	-	1	16.0	-	4
10.5	11	1			
11.0	22	3	Totals	614	784
11.5	45	13			

TABLE 3A.–Lengths of Fish Taken September 4, 1923, Grouped to Nearest Half Centimeter

9. EXPLANATIONS OF FIGURES.

Abbreviations

b. a. breeding annulus.
d. o. Degenerating ovum.
gran. Follicular epithelium.
im. o. Immature ovum.
in. o. Intermediate ovum.
th. fol. Theca folliculi.
w. a. Winter annulus.
z. r. Zona radiata.

PLATE I. Figs. 1a, 1b, 2, 3, and 4.

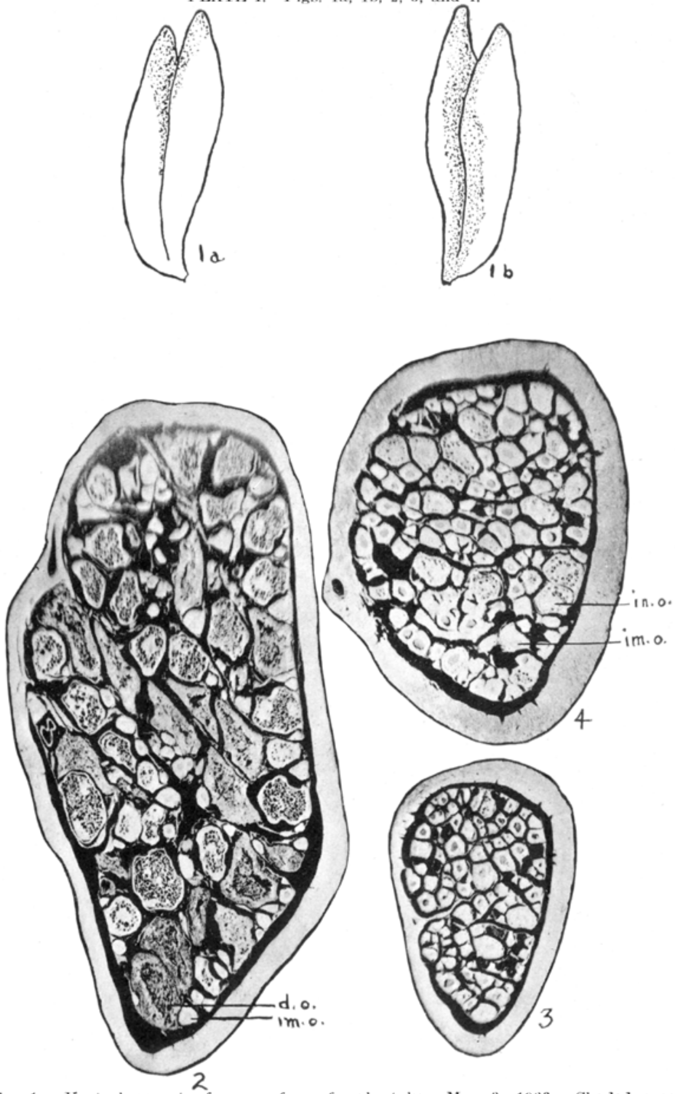


FIG. 1a. Ventral aspect of ovary from female taken May 3, 1923. Shaded area represents region occupied by immature and intermediate groups of eggs. Unshaded area, mature eggs segregated in lumen.
1b. Dorsal aspect of same.
FIG. 2. Photomicrograph of a cross-section of an ovary from an adult female taken July 26, 1923, showing degenerating intermediate eggs.
FIG. 3. Photomicrograph of a cross-section of an ovary from an adult female taken November 14, 1923, showing immature eggs only.
FIG. 4. Photomicrograph of a cross-section of an ovary from an adult female taken January 11, 1924, showing immature and a few intermediate eggs.

PLATE I. Figs. 1a, 1b, 2, 3, and 4

FIG. 1a. Ventral aspect of ovary from female taken May 3, 1923. Shaded area represents region occupied by immature and intermediate groups of eggs. Unshaded area, mature eggs segregated in lumen.

1b. Dorsal aspect of same.

FIG. 2. Photomicrograph of a cross-section of an ovary from an adult female taken July 26, 1923, showing degenerating intermediate eggs.

FIG. 3. Photomicrograph of a cross-section of an ovary from an adult female ta ken November 14, 1923, showing immature eggs only.

FIG. 4. Photomicrograph of a cross-section of an ovary from an adult female taken January 11, 1924, showing immature and a few intermediate eggs.

PLATE II. Figs. 5a, 5b, 6a, 6b, 7a, 7b, 8a and 8b.

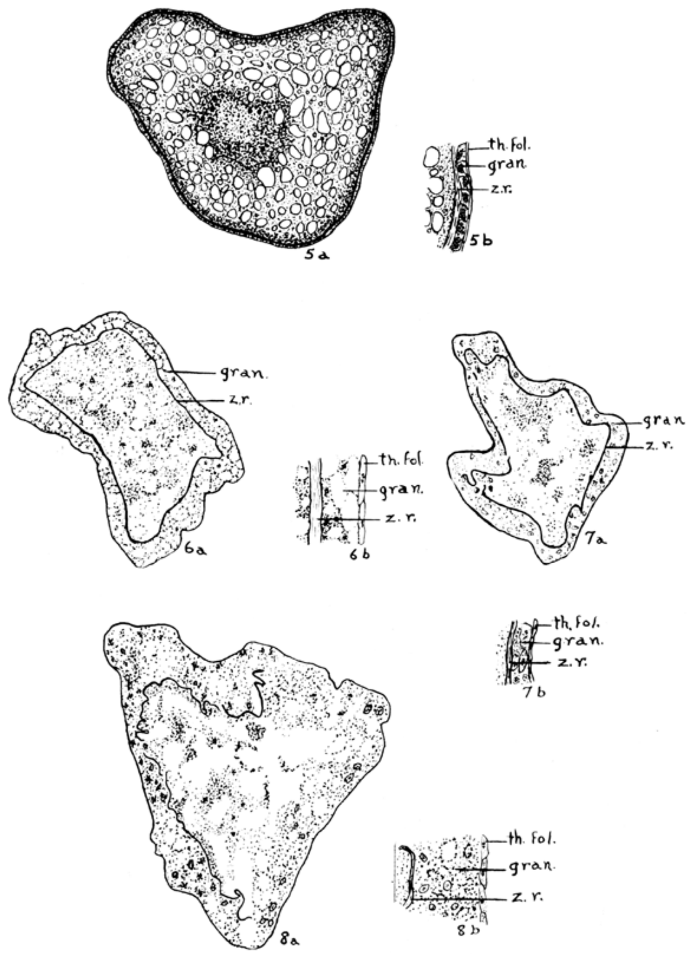
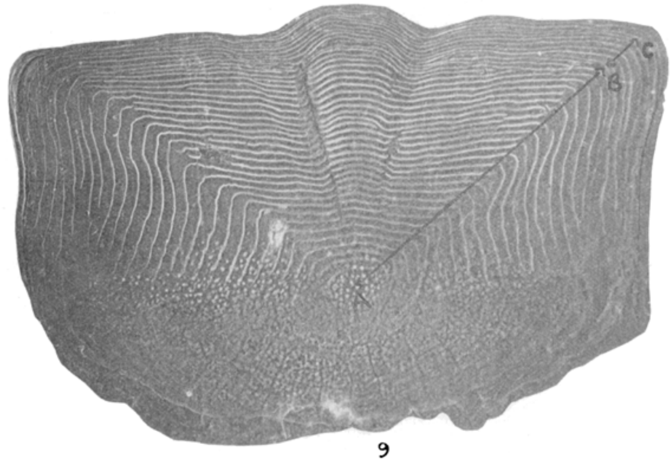


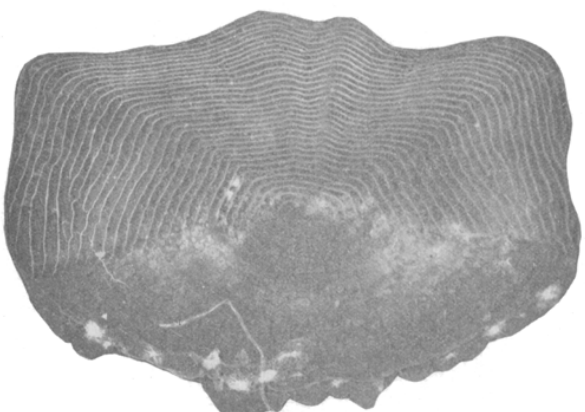
FIG. 5a. Cross-section of a normal growing ovum.
5b. Follicle and egg membrane of same.
FIG. 6a. Cross-section of an ovum in an early stage of degeneration.
6b. Follicle and egg membrane of same.
FIG. 7a. Cross-section of an ovum in a later stage of degeneration.
7b. Follicle and egg membrane of same.
FIG. 8a. Cross-section of an ovum in a late stage of degeneration.
8b. Follicle and egg membrane of same.

PLATE II. Figs. 5a, 5b, 6a, 6b, 7a, 7b, 8a and 8b
FIG. 5a. Cross-section of a normal growing ovum.
5b. Follicle and egg membrane of same.
FIG. 6a. Cross-section of an ovum in an early stage of degeneration.
6b. Follicle and egg membrane of same.
FIG. 7a. Cross-section of an ovum in a later stage of degeneration.
7b. Follicle and egg membrane of same.
FIG. 8a. Cross-section of an ovum in a late stage of degeneration.
8b. Follicle and egg membrane of same.

PLATE III. Figs. 9 and 10.



9



10

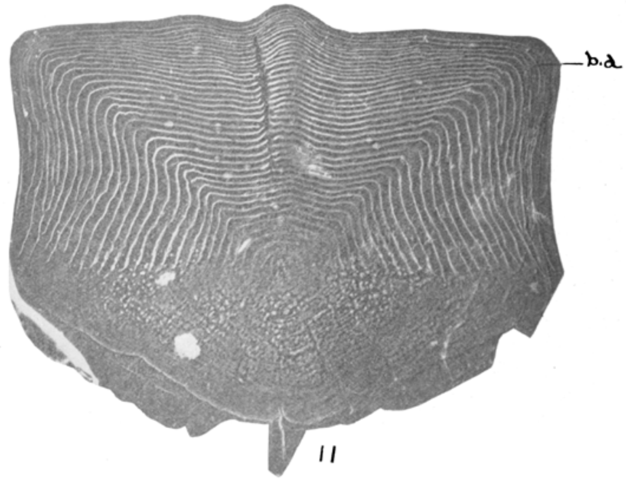
Fig. 9. Scale from a male fish 149 mm. in length, of the II group, taken November 14, 1923, showing region of scale measured. A–B distance from center to first annulus; B–C distance between first and second annulus.
Fig. 10. Scale from a female fish 137 mm. in length, of the I group, taken July 24, 1923, showing no annulus.

PLATE III. Figs. 9 and 10

FIG. 9. Scale from a male fish 149 mm. in length, of the II group, taken November 14, 1923, showing region of scale measured. A–B distance from center to first annulus; B–C distance between first and second annulus.

FIG. 10. Scale from a female fish 137 mm. in length, of the I group, taken July 24, 1923, showing no annulus.

PLATE IV. Figs. 11 and 12.



12

FIG. 11. Scale from a male fish 123 mm. in length, of the I group, taken August 24, 1923, showing a breeding annulus near the margin.
FIG. 12. Scale from a male fish 125 mm. in length, of the I group, taken November 14, 1923, showing a breeding annulus a short distance from the margin.

PLATE IV. Figs. 11 and 12

FIG. 11. Scale from a male fish 123 mm. in length, of the I group, taken August 24, 1923, showing a breeding annulus near the margin.

FIG. 12. Scale from a male fish 125 mm. in length, of the I group, taken November 14, 1923, showing a breeding annulus a short distance from the margin.

PLATE V. Figs. 13, 14 and 15.

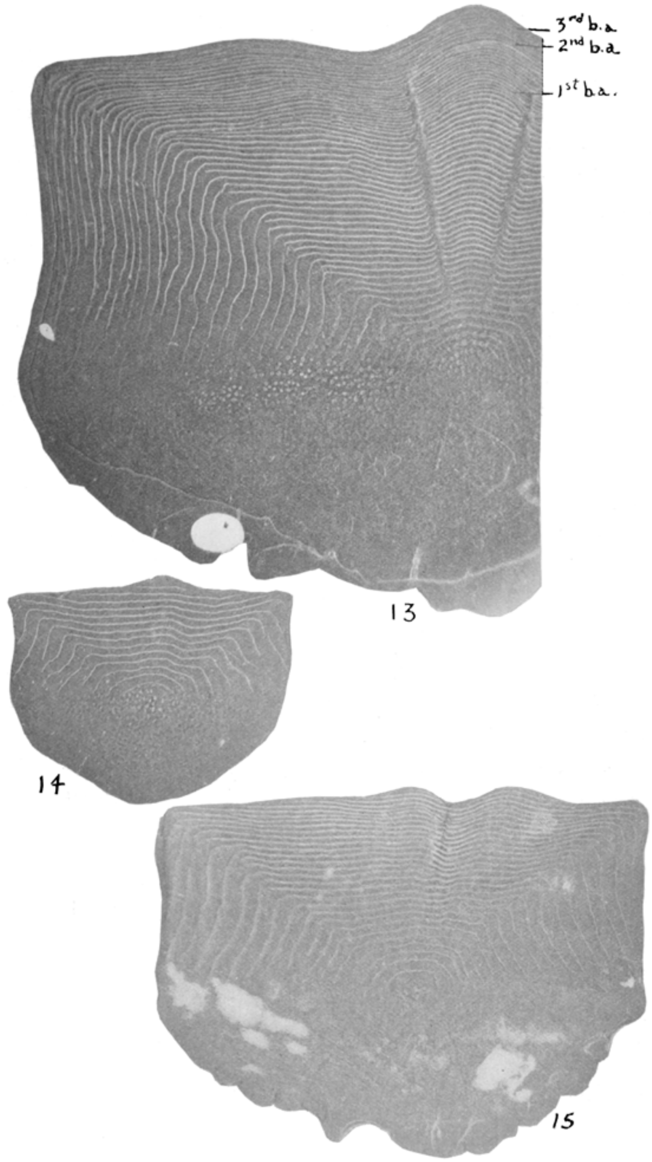


FIG. 13. Scale from a female fish 170 mm. in length, of the III group, taken November 14, 1923, showing three breeding annuli.
FIG. 14. Scale from an immature male 51 mm. in length, of the O group, taken September 9, 1923.
FIG. 15. Scale from an immature female 94 mm. in length, of the O group, taken November 14, 1923.

PLATE V. Figs. 13, 14 and 15

FIG. 13. Scale from a female fish 170 mm. in length, of the III group, taken November 14, 1923, showing three breeding annuli.

FIG. 14. Scale from an immature male 51 mm. in length, of the O group, taken September 9, 1923.

FIG. 15. Scale from an immature female 94 mm. in length, of the O group, taken November 14, 1923.

PLATE VI. Figs. 16 and 17.

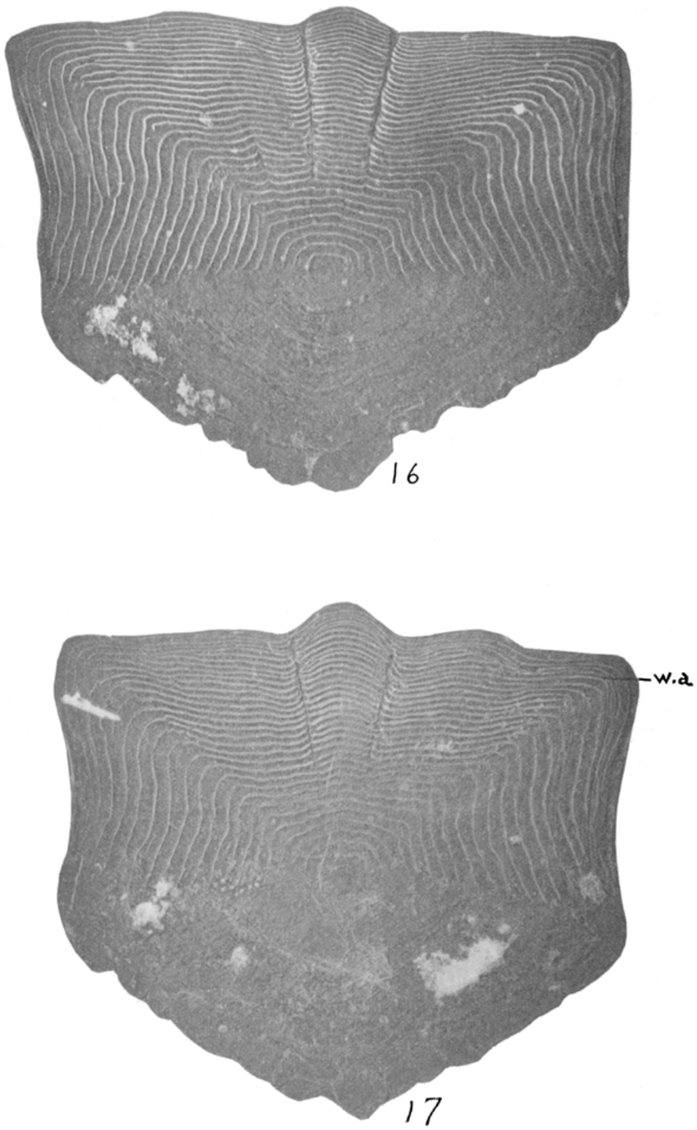


FIG. 16. Scale from a male fish 102 mm. in length, of the O group, taken January 10, 1924, showing no annulus.
FIG. 17. Scale from a female fish 110 mm. in length, of the O group, taken February 20, 1924, showing a winter annulus.

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PLATE VI. Figs. 16 and 17

FIG. 16. Scale from a male fish 102 mm. in length, of the O group, taken January 10, 1924, showing no annulus.

FIG. 17. Scale from a female fish 110 mm. in length, of the O group, taken February 20, 1924, showing a winter annulus.

1 Thompson (1919*b*) p. 20.

2 Under enemies of the eggs are listed one isopod, Tylos punctatus, maggots of two species of flies, and a beetle, Saprinus sulcifrons, which was found very frequently in the midst of the eggs.