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ERRATA

Page 37, second line from bottom: *heat* should be *beat.*

Page 149, second paragraph, seventh line: *cemtimeters* should be *centimeters.*

Page 174, table 17: The box head should read *Percentage of fish that had eaten*—.

Figure 5, Document 1047: In the legend *1926* should be *1916.*

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

Figure 33, opposite page 354: In the legend the word "female" should occur after the length and before the age.

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

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

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

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

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

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

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

EXPERIMENTAL STUDY OF THE FUNCTION OF THE OYSTER GILLS AND ITS BEARING ON THE PROBLEMS OF OYSTER CULTURE AND SANITARY CONTROL OF THE OYSTER INDUSTRY

By PAUL S. GALTSOFF, Ph. D.

Aquatic biologist, United States Bureau of Fisheries

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INTRODUCTION

A study of the physiology of the oyster is of great practical importance for the oyster industry and at the same time it presents a broad and interesting field for research that hardly has been touched by scientific investigation. The present paper deals with the function of the gills of the American oyster.

The gill may be regarded as one of the most conspicuous of the organs that take part in the feeding and respiration of the oyster. The fact that great quantities of oysters are consumed raw makes the questions of what constitutes the food of an oyster and how it is taken in of great practical importance. Because the mode of feeding consists in straining great volumes of water through the gills and ingesting the microscopical material suspended therein, the purity of the oyster meat is correlated closely with the character of the water running over the oyster beds.

It has been known for many years that the general appearance of the oyster, the thickness and shape of its shell, and the quality and flavor of its meat reflect readily the conditions of the environment under which the organism grew. The constantly increasing pollution of our inshore waters caused by the discharge of domestic sewage and trade wastes has ruined many thousands of acres of profitable oyster grounds and in many instances has rendered the oysters grown in the vicinity of large cities unfit for human consumption. Long before the discovery of bacteria

as the cause of infectious diseases, a French physician, Pasquier, attributed the epidemic of intestinal illness to the eating of raw oysters taken from sewage-polluted bottoms. Since 1816, the year when his investigation was made (Pasquier, 1818), and up to the present time, oysters and other shellfish often were held responsible for the outbreaks of acute gastrointestinal disturbances and typhoid fever.

Realizing the danger to the public health brought about by the consumption of infected oysters, and conceiving the damages to the oyster industry caused by the loss of public confidence in the safeness of the oyster, the various States gradually have placed the harvesting and handling of oysters under the supervision of the municipal and State health authorities and shellfish commissions. In 1909 the Federal Government took a step in the same direction when the United States Department of Agriculture, acting under the authority of the Federal food and drugs act, issued Food Inspection Decision No. 110, which declared it to be unlawful to ship or to sell polluted shellfish in interstate commerce. In the following year, by another act (Department of Agriculture, Food Inspection Decision No. 121), it prohibited the shipment or sale of oysters floated in polluted waters. In 1927 Food Inspection Decision No. 110 was reaffirmed and it was declared unlawful to ship or to sell in interstate commerce oysters or other shellfish that have been subjected to "floating" or "drinking" in brackish water or water containing less salt than that in which they are grown. (Department of Agriculture, Food Inspection Decision No. 211). At present all the oyster-producing States have adopted a system of issuing certificates to the respective oyster growers and dealers under the supervision and with the approval of the United States Public Health Service. According to this plan every bed from which oysters are taken for the market is examined from a sanitary point of view and must conform to the established bacteriological and chemical standards of purity.

The question of standards in the sanitary control of shellfish was much discussed and is of great importance to the industry. For many years bacteriologists were using various schemes of bacteriological examination of the oysters, with the result that various Federal, State, and municipal authorities gave preference to one or another standard and enforced their regulations accordingly. In 1922 the American Public Health Association (Committee on Standard Methods for the Bacteriological Examination of Shellfish, 1922) adopted a standard method for the bacteriological examination of shellfish, which at present is widely though not universally employed in the sanitary control of the shellfish industry. Briefly speaking, it consists in determining the relative abundance of *Bacterium coli* in the shell liquor of the mollusks and expressing the results by an arbitrary numerical system known as the American Public Health Association method of scoring oysters. The technical procedure consists in making a composite sample from at least five oysters and incubating the fermentation tubes filled with lactose broth with 0.1 and 0.01 cubic centimeter of the composite liquor. The water required for dilution purposes is either sterile sea water or tap water containing 2 per cent sodium chloride. For each dilution five fermentation tubes are used; altogether 15 fermentation tubes are required for every test. Upon the formation of gas, confirmatory tests are made in accordance with the standard methods of water analysis. The presence of *Bacterium coli* in each tube, if confirmed, is to be given the value representing the reciprocal of the greatest

dilution in which the test for *B. coli* is positive. If, for instance, *B. coli* is present in 1 cubic centimeter but not in 0.1 cubic centimeter the value is 1; if present in 0.01 cubic centimeter the value is 100. The score for the whole sample is the total of these values. Sometimes, however, one or more tubes show results, for instance in 0.01 cubic centimeter, while the other tubes show negative results in 0.1 cubic centimeter. In this case the recession of values is made; the 0.01 tube is given the value 10 instead of 100, while the tube showing absence of *B. coli* is given the value 10 instead of 1. The results of the test are expressed in a tabular form.

TABLE 1.—*Method of scoring*

Tubes	1 cubic centimeter	0.1 cubic centimeter	0.01 cubic centimeter	Values
1	+	+	−	10
2	+	+	−	10
3	+	+	+	100
4	+	+	−	10
5	+	+	−	10
Score				140

The weak point in the method of scoring consists in the fact that the figures of the score do not represent exact quantitative values and are used simply as symbols to express the relative abundance or scarcity of a given microorganism. Sometimes instead of a standard method a so-called "individual" method of scoring is used. It consists in planting shell liquor from five separate oysters instead of making one composite sample. The counting is done in the same manner as prescribed by the standard method. The comparison between the two methods made by Hasseltine (1926) shows that the scores obtained by the individual method may be much lower than that obtained by the standard. For instance, the sample of five oysters tested by the individual method scored 5 while the same examined by the standard method gave a score of 5,000. Such a discrepancy is undoubtedly due to the error in the method of sampling. In order to get reliable results many more oysters should be examined, but this involves so much labor and time as to make it impracticable.

The question of the standards of purity of the oyster was much discussed during the past 17 years and different standards of purity were proposed by several laboratories. The bacteriological examinations of oysters were supplemented by an inspection of the beds from which the oysters were obtained and by the bacteriological examination of the water. Finally, the *B. coli* score not exceeding 50 was accepted by all parties interested in shellfish control as a permissible standard of purity. The committee on standard methods of the American Public Health Association (1922) failed, however, to recommend a definite standard of purity, and the members of the committee have limited their report to a description of the methods of examination without committing themselves to any definite figure. For many years various State and municipal authorities regarded oysters produced under satisfactory circumstances and having a *B. coli* score of not over 50 as safe. In 1925 the Committee on Sanitary Control of the Shellfish Industry of the United States Public Health Service recommended that pending the collection and analysis of further data the standard of a *B. coli* score not exceeding 50 be continued, with the understanding that if the facts collected warrant it this recommendation would be altered.

The question of a definite criterion of purity is of great practical importance, yet the problem has never been studied experimentally; the proposed score of 50 was accepted as standard, although no significance was established for either figure by a comprehensive investigation.

In introducing the standard of purity of shellfish the bacteriologists have followed the practice established in the sanitary control of drinking water and milk. They met with difficulties, however, which at the beginning were not fully recognized and which are caused by the very nature of the product. The oyster is a living organism and can not be treated in the same manner as milk, water, or other food products. It is capable of adjusting itself to new conditions in which it may be placed and responds quickly to changes in environment. The first difficulty encountered in the application of the *B. coli* score method to the sanitary control of the oyster consisted in sudden and wide fluctuations in score, which sometimes occurred after the oysters were taken from the water, and consequently the possibility of their further pollution was excluded. It has been found that the *B. coli* score of the shell liquor of the oyster kept in storage does not remain constant but increases and decreases rather irregularly. It happened, for instance, that oysters tested in New York and found to have a low score were shipped to Chicago, where they were condemned because of a very high score. Recently Elliot (1926) made a study of the changes in the bacterial content of market oysters and found that shucked and shell oysters kept at room temperature show a sudden and maximum rise in total count of bacteria from the second to the fourth day of storage. Unfortunately the author failed to make temperature readings but specifies that the oysters were kept in a "cool basement when the outside temperature was below freezing point." Sudden increase in the *B. coli* score indicates that the microorganism was propagating in the oyster liquor, but the increase in score after the oyster was taken from the water had no relation to the sanitary conditions under which it was grown.

It has been observed, also, by a number of investigators that there exists a definite relation between the temperature of water and the *B. coli* score in the oysters. Gorham (1912), Pease (1912), and Gage and Gorham (1925) have shown that in winter the bacterial content of oysters taken from polluted waters is abnormally low. Discussing this phenomenon, the investigators attributed it to the slowing down of biological activity of the oyster as a result of a reduction of temperature and came to the conclusion that with the decrease in temperature the oyster passes into a state of hibernation. Round (1914), working on the bacteriology of oysters, came to the conclusion that oysters close their shells for varying periods of time, depending on temperature. According to his opinion the opening and closing of the shell is controlled by the rapidity of metabolic processes, which in turn are controlled by temperature. He failed to support this statement with the experimental data, however. Cumming (1916) has shown that January and February were the months when the *B. coli* content of water taken at the mouths of rivers was highest and the lowest for oysters taken from the same locality.

The study of the effect of temperature on the *B. coli* score in the oyster was handicapped by the lack of knowledge of the relation between the abundance of *B. coli* in the water and in the oysters taken from the same locality. So little was known regarding this important question that the Committee on Sanitary Control

of the Shellfish Industry (1925) failed to recommend any precise bacterial standards for waters from which the taking of shellfish is permitted until additional data are assembled and considered. It was regarded as unnecessary, however, to apply to such waters the rigid standards that are established for drinking-water supplies in interstate commerce. It is known at present that because of the mode of feeding, the oyster is able to concentrate in the shell liquor the microorganisms present in the sea water. Undoubtedly the process is dependent on the rate of filtration of water through the gills and on the rate of ejection of the accumulated material. Both processes very likely are affected by changes in the environment. Wells (1926), working at the United States Public Health Laboratory at Fishermans Island, arrived at the conclusion that the number of *B. coli* in the shell liquor is higher as compared to that of the water, where the *B. coli* concentration was low, and that the ratio decreased as the abundance of *B. coli* in the water increased. The same relation was observed by Tarbett (1926) in the waters of lower Chesapeake Bay. He has shown that with water scoring from 0 to 0.5, the ratio of water score to oyster score was 1 to 600; in water scoring 1.4 to 5 the ratio was 1 to 44.8; and in water scoring from 14 to 50 the ratio was 1 to 7.6. Tarbett admits that the relation between the *B. coli* content in water and in the oyster is not a simple one and that temperature is an important factor. Neither Wells nor Tarbett give any explanation for the differences in the ratios they have observed. It is very likely that a number of factors, like temperature, pH, and changes in the chemical composition of water, should be held responsible for the differences in the ratios observed by these investigators. It is difficult to believe that merely the fluctuation in the abundance of *B. coli* may affect the activity of the oyster. It is very likely that the increase or decrease in *B. coli* content in shallow and polluted waters where the observations were carried out are accompanied by physical and chemical changes in the water, which in turn affect the activity of the oyster gills.

In a study of seasonal fluctuations in *B. coli* score in the oyster, and in discussing the questions of feeding and hibernation, some of the investigators (Round, 1914; Nelson, 1921, 1923) regarded the oyster as feeding whenever its shells are open. As it will be shown in the present paper, the fact that the shells are open does not necessarily mean that the oyster is feeding. The two phenomena namely, the contraction of the adductor muscle and the ciliary activity of the gill epithelium—are independent from one another and should be studied separately.

The crisis of the oyster industry in 1924 caused a revision of the methods of sanitary control of shellfish. At the same time, the question of the effect of temperature on the activity of the oyster was taken up again by the bacteriologists engaged in the sanitary inspection of shellfish and by the oyster growers interested in the safety of their product. It is the author's belief that the solution of the practical problem concerning the standard of purity of the oyster should be based on a profound knowledge of the functions of the organism and its relation to its environment. On the other hand, understanding of the activity of the organism is essential for the oyster growers who, by adopting methods that permit self-purification of the oyster, are trying to insure the cleanliness of their product.

The present investigation was made for the purpose of filling the gap in our knowledge of the physiology of the oyster and to supply information concerning the

effect of temperature on the activity of the gill. An effort was made to put the experimental work on a quantitative basis and whenever possible to give an accurate measurement of the reaction of the organism. The experiments were carried out at the United States Fisheries Biological Station at Woods Hole, Mass., in the summers of 1925 and 1926 and the winter of 1926, and in the Pease Laboratories in New York. The author wishes to acknowledge his gratitude to Dr. H. D. Pease for extending the privilege of using his laboratory and supplying technical assistance in several bacteriological experiments performed in connection with this investigation.

The oysters used in the experiments were received from Long Island Sound, Wellfleet Harbor, Mass., Wareham River, Mass., and Chesapeake Bay. No differences in the behavior of oysters from these localities were noticed.

STRUCTURE OF THE OYSTER GILL

The gill of an oyster is a complex, ciliated organ that takes part in three important functions of the organism—respiration, feeding, and excretion. One of its most noticeable activities consists in producing a strong current of water, which passes through numerous branchial chambers and insures the exchange of gases between the tissues of the organism and the surrounding medium. The material suspended in water and brought in with the current constitutes the food of the oyster. It settles on the surface of the gill and, after being entangled in the mucus excreted by numerous gland cells, is pushed by the ciliary epithelium toward the distal edges of the gill laminæ and is conveyed to the labial palps, where it is either rejected or enters into the digestive tract. When the oyster is not feeding and keeps its valves closed the gland cells of the gills continue to excrete mucus, which accumulates in a large quantity on the surface of the gills and is discharged into water at the first opportunity. The structure of the lamellibranchiate gill has been the object of numerous investigations, and for a detailed anatomical and histological description the reader is referred to the works of Peck (1877), Kellog (1892), Janssens (1893), Ridewood (1903), and Yonge (1926). It is necessary, however, for the purpose of the present paper, to give a brief account of its essential features.

The oyster has two gills, each formed by one outer and one inner demibranch. In a transverse section the gill presents the figure of the letter W. Each demibranch consists of one descending and one ascending lamella, leaving a space between them and being united at their lower ends. The upper edges of the ascending lamellæ of the inner demibranchs are united in the middle line, those of the outer are fused with the mantle. The spaces above the gill lamellæ are called epibranchial or suprabranchial chambers; they open posteriorly into one large exhalant chamber (cloaca). The spaces below the lamellæ (so-called infrabranchial chambers) are completely shut off from the epibranchial chambers, and communication between them is possible only through numerous minute pores in the gill.

The gill lamellæ are made up of numerous parallel filaments (fig. 1, *fl.*) arranged in rows, alternatingly forming crests and grooves. There are from 10 to 16 filaments to each crest. According to Herdmann (1899) there must be over 2,000 filaments for each surface of each gill, or from 8,000 to 10,000 filaments in all. Due to the peculiar arrangement of the filaments, the surface of the gill is plicate, the crests of the

plicæ being visible to the naked eye. The neighboring filaments are connected by an interfilamental junction (*int. fl. j.*) formed by a band of connective tissue running round the inner surface of the plicæ. In every groove between the two adjacent filaments there is a water pore (*p.*), through which the water enters into the interfilamental spaces. The two lamellæ of each demibranch are, in turn, united by the interlamellar junctions (*int. lm. j.*), having a form of septa and subdividing the

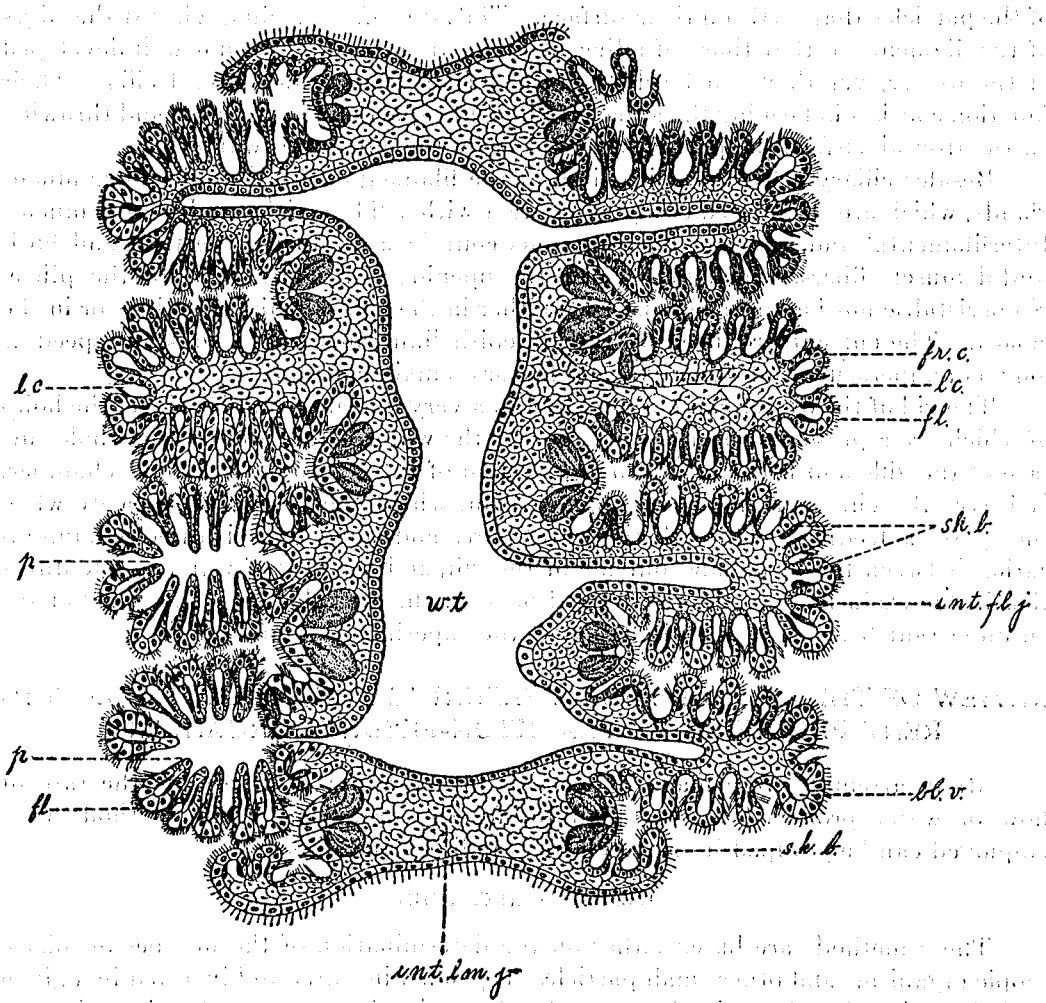

FIG. 1.—Cross section of the gill lamellæ of the oyster. Semidiagramatic. *bl. v.*—blood vessel; *fl.*—filament; *fr. c.*—frontal cilia; *l. c.*—lateral cilia; *int. lm. j.*—inter lamellar junction; *int. fl. j.*—inter filamentar junction; *sk. b.*—skeletal bar; *p.*—water pores; *wt.*—water tubes. (Slightly modified from Kellog)

epibranchial chambers into canal-like compartments or "water tubes" (*w. t.*), very narrow at their distal ends but reaching several millimeters in diameter in the proximal portion of the gill. In an adult oyster there are about 30 tubes in each demibranch, or about 120 tubes altogether. Each filament of the gill has one blood vessel (*bl. v.*), lined by a thin layer of connective tissue, and has two skeletal bars (*sk. b.*). The surface of the filament is covered with a ciliated epithelium forming

three groups of cells, frontal, (*fr. c.*) latero-frontal, and lateral (*l. c.*), the relative positions of which are shown in Figure 1. It has been fully established by the work of Orton (1912) and Gray (1922) that the ingoing current of water, passing through the water pores into epibranchial chambers and cloaca, is produced by the activity of the lateral cilia, which beat inward; i. e., across the surface of the gill. The frontal cilia beat parallel to the surface of the gill and are concerned solely with the transport of the particles that settle on their surface. The latero-frontal cilia, lying at the edges of the filaments so that those of adjacent filaments interlock, are not well developed in the oyster, yet they can be distinguished from frontal and lateral cilia. Their function consists in keeping the adjacent filaments apart and in stopping and throwing on the frontal surface the particles carried in by the current of water.

Besides ciliary cells, the epithelium of the filaments contains unicellular mucus glands, which are stimulated easily by contact with solid particles and secrete mucus. Interfilamental and interlamellar junctions contain a number of vertical and horizontal muscle fibers, which may cause the opening and contraction of the plicæ. No peristaltic motion has been observed either in the epibranchial chambers or in the cloaca. The current produced by the gill epithelium runs with a constant speed as long as temperature and other external factors remain constant.

The gill of the oyster can be compared to a very fine and complex sieve, the holes of which are represented by the water pores; the water is taken in by the whole surface of the gills and is driven through a system of tubes into one exhalant chamber. It leaves the gills as a single outgoing stream, which can be observed easily when the oyster is feeding. Through the water pores and tubes there is direct communication between the inside and outside of the gill, and the flow of water in one direction is due exclusively to the rhythmical beats of the lateral cilia. These facts have an important bearing on the discussion of the experimental data.

REVIEW OF THE METHODS FOR MEASURING THE STRENGTH OF CURRENT PRODUCED BY PLANKTON-FEEDING ORGANISMS

Many attempts were made by various investigators to determine the rate of flow of water produced by the plankton-feeding organisms. The methods they employed can be grouped into two classes—indirect and direct.

INDIRECT METHODS

These methods are based either on the determination of the number of microscopic organisms and other small particles suspended in water and ingested in a given period of time by the animal, or on the determination of the rate of respiratory exchange of a given organism. One of the first estimations of the rate of flow of water through the gills of an oyster was made by Grave (1905). He kept the oysters in filtered sea water for three days until their digestive tract became devoid of any plankton organisms. Then the oysters were placed in the natural sea water and at convenient intervals were taken up, contents of their stomachs were removed, and the number of diatoms in them counted. Knowing the average number of diatoms per liter during the three consecutive summers, and having obtained the number of diatoms collected by the oyster in a given period of time, Grave estimated the rate of

flow of water through the gills. His method is open to several objections. First, because of the seasonal and daily fluctuations in the abundance of diatoms in water the average figure may differ greatly from the diatom content at the time of observation. Second, not all of the diatoms strained by the gills are ingested; certain numbers of them may be rejected into the pallial cavity and do not reach the digestive tract.

Virtually the same method as that employed by Grave was used by Moore (1913) in studying the oysters of Mississippi. Nelson (1921), studying the feeding of oysters in Barnegat Bay, adopted the following procedure: At ebb tide oysters were placed on a platform built in the bay; when the tide began to run the investigator watched for the opening of the shells and kept them continuously under observation for one hour. Meanwhile, every two minutes a sample of the water that was passsing over the oysters was taken and the number of Tintinnopsis (a protozoan, which was taken as an index) was counted. At the close of the hour two oysters were opened, the stomachs washed out, and the contents counted. The number of Tintinnopsis collected by the two oysters compared with the number in the water gave the rate of current produced by the oyster. Nelson assumes that the stomachs of the oysters he examined were empty because, according to his observations, when an oyster opens after a period of closure of one hour or more its stomach is virtually empty of food.

An entirely different method was employed by Viallanes (1892) and Ranson (1926) in experiments on European oysters and mussels. Their method is based on the determination of the amount of clay precipitated by the mollusks during a period of 24 hours. The mollusks are kept in the crystallizing dishes placed on the bottom of a tank filled with water, to which a known quantity of clay (0.0546 gram per liter) is added. Several dishes are placed in the same tank for control without the animals. After 24 hours the sediment that has accumulated on the bottoms of the dishes is collected, dried, and weighed. The figures thus obtained are corrected by subtraction of the amount of precipitate by gravity (in the controls), and the rate of filtering of water through the gills is thus computed. These authors used their method chiefly for the determination of the relative filtering ability of European and Portuguese oysters. They fail, however, to give a record of the temperature of the water and do not state whether the shells of the mollusks were open all the time during the experiment. The possible source of error in this method lies in the fact that the mucus discharged by the gills may cause the agglutination and precipitation of the clay, and therefore the amount of precipitate on the bottom is not a safe measure of the activity of the gills.

In a series of papers Pütter (1909, 1911, 1924) has estimated the rate of flow of water by measuring the CO_2 production and O_2 consumption by various marine organisms. As a result of this study he arrived at the conclusion that in order to receive a required amount of carbon from plankton the organisms in question should filter tremendous volumes of water. Thinking that this is impossible he advanced the hypothesis, which was much criticized by other investigators (Moore, Edie, Whitley, and Dakin, 1912), that the marine organisms feed by absorption of organic matter dissolved in sea water.

DIRECT METHODS

The first measurement of the rate of flow of water through the plankton-feeding organisms was made by Parker (1914). Experimenting with the siliceous sponge Stylotella, he adopted the following method: A glass tube was inserted into the osculum and the flow of water in the tube was determined by measuring the velocity of floating particles, such as grains of carmine, that were carried up the tube by the current. By placing the tube introduced into the osculum in a vertical position he was able to observe the rise of water in the tube above the level of water in the tank where the sponge was kept and thus measured the pressure produced by the ciliary motion of the cells.

A similar method was used by Allen (1914) in a study of the feeding habits of fresh-water mussels. He introduced one end of the rubber tubing in the excurrent siphon; the other end was connected to a calibrated glass tube having a capacity of 2 cubic centimeters between given marks. A neutral coloring matter was added into the rubber tubing through a pipette thrust into it just outside the siphon and the rate of flow of colored substance in the tube was measured. Because of the contraction of the siphon, Allen had considerable difficulty in measuring the velocity of the outgoing current and made only one determination. Both Parker and Allen failed to note that the velocity of the current running in a circular pipe varies along the cross section of the pipe, the maximum velocity being at the center, with minimum velocity close to its walls. Consequently, no discharge of water can be computed from their data unless the position of the particle, the speed of which is being measured, is known. When the carmine grains flow in water they settle on the bottom gradually and are carried out at different speeds depending on the distance from the center of the tube.

METHODS EMPLOYED IN THE PRESENT INVESTIGATION

Two methods of measuring the rate of flow produced by the gills of the oyster were described by the author in 1926 (Galtsoff, 1926). It is desirable to give a more complete description of them here.

TANK METHOD

This method is designed primarily to collect the water after it had passed through the gills and to measure the pressure inside the gill cavity. The valves of the oyster are forced apart and a glass rod is placed between them to prevent their closing; a rubber tube 6 to 7 millimeters in diameter is inserted in the gill cavity and made fast by packing all the spaces around with cotton. The outgoing water passes through the tube; leakage, if any, can be noticed easily by adding a few drops of carmine suspension and watching the produced currents. The oyster is then placed in a tank (fig. 2) of about 10 liters capacity; the tank is connected through a horizontal glass tube (*b*) of 6 millimeters diameter, with a small vessel (*v*) of about 50 centimeters capacity. A vertical tube (*c*), 8 millimeters in diameter, passes through the bottom of a small vessel and serves as an overflow; its upper level is about 1 centimeter above the upper level of the horizontal tube *b*. The tank is made of celluloid, ⅛ inch thick; the walls are cemented with a solution of celluloid in acetone.

The large tank is filled with water up to the level of the vertical tube *c*. When equilibrium is established the rubber tube inserted into the oyster is connected to the horizontal tube *b* and the water from the gills begins to flow into the small vessel. The overflowing water is collected in a graduate.

The hydrostatic pressure inside the gill cavity can be measured by plugging the vertical tube *c* and watching, in the water gauge (*g*), the rise of the level in the small vessel. In a few minutes a maximum difference is reached and the flow of water through the tube *b* ceases. This indicates that there is no more difference in pressure between the inside of the gill cavity and the end of the tube *b*.

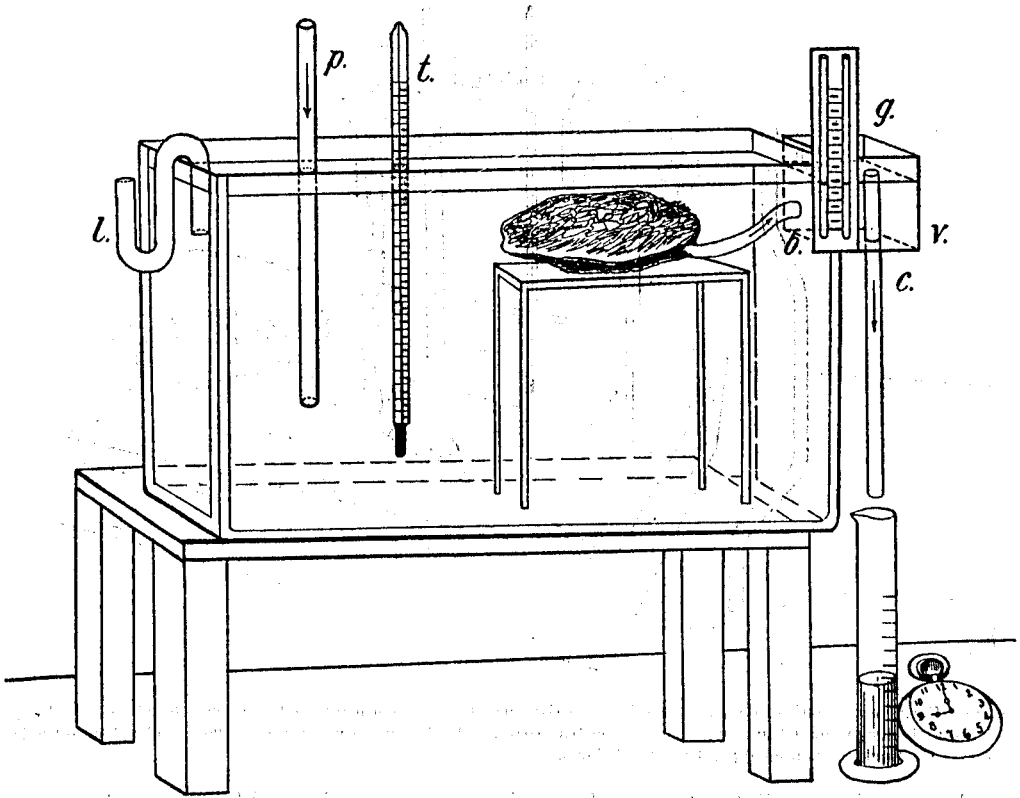

FIG. 2.—Tank for collecting the water after it passed through the gills, and measuring the hydrostatic pressure inside the gill cavity. *b*.—tube connecting the two vessels; *c*.—overflow; *g*.—water gauges; *l*.—constant level arrangement; *p*.—pipe supplying fresh sea water; *t*.—thermometer. Approximately one-third natural size

The difficulty in employing the tank method lies in the necessity of being very careful to keep the water in both vessels at a constant level. The rise of level in the large tank forces the water to flow by gravity through the gills, while a rise in the level in the small vessel retards the rate of flow because the gill epithelium is forced to work against the pressure. The method is indispensable, however, for collecting the water that had passed by the gills.

CARMINE METHOD

The rate of flow of water can be determined easily by the carmine method (Galtsoff, 1928), which is as follows: The oyster is rigged up in the same manner as in the

tank method and is placed in a glass tray of about 4 liters capacity. (Fig. 3.) The end of the rubber tube inserted in the gill cavity is connected to a ⊥ tube, the upper end of which is attached to a funnel filled with a fine suspension of carmine in sea water. The third end of the tube is connected with a graduated glass tube (*t*) 6 millimeters in diameter and 17 centimeters long. Releasing the clamp (*C*) a very small amount of carmine is allowed to enter the tube, where it forms a distinct cone moving inside the tube. The rate of movement of the apex of the cone is measured by recording, with a stop watch, the time required for it to pass from 0 to the 15-centimeter mark.

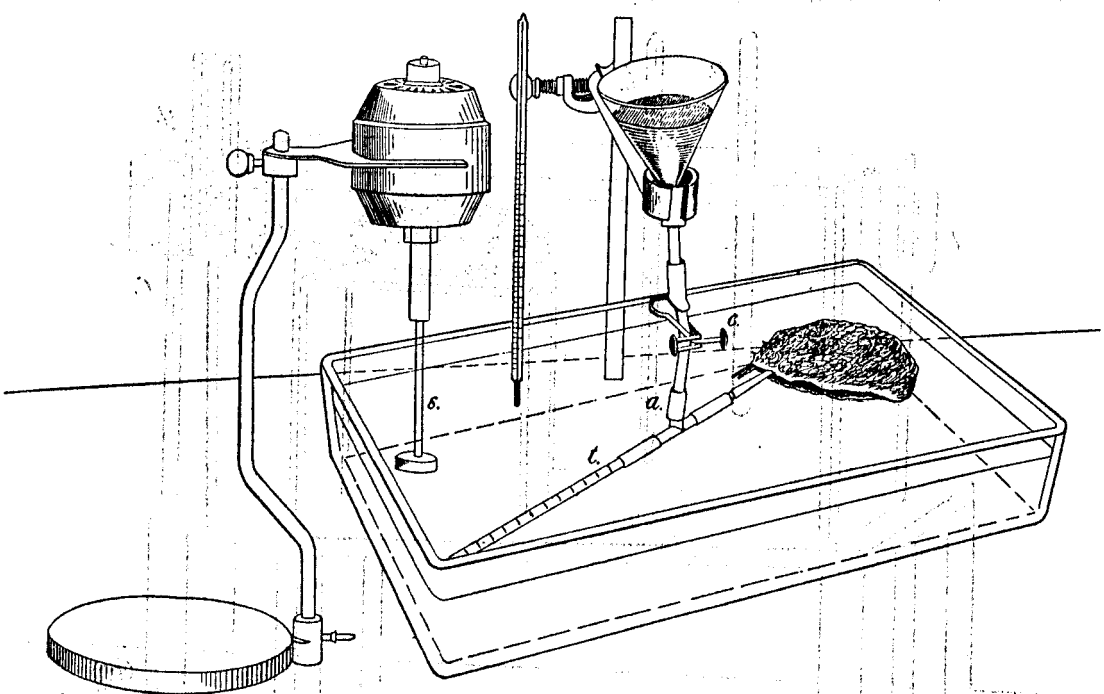

FIG. 3.—"Carmine method" to measure the velocity of the current. *a.*—vertical tube with rubber connections; *c.*—clamp; *t.*—horizontal tube graduated in centimeters; *s.*—electric stirrer. The drawing is made from a photograph taken in the laboratory. Heating and aeration apparatus are not shown

Inasmuch as a distinct cone of carmine suspension is visible, it may be assumed that in this case we have a viscuous flow or stream line, to which the Poiseuille's formula

$$S=\frac{D^2\Delta p}{16\mu l} \qquad (1)$$

is applicable. In this formula S = speed at the axis of the tube; D = diameter and l length of tube in centimeters; Δp = pressure drop between the two marks in dynes per cm^2; μ = viscosity in poises.

As the mean velocity S_m of the whole cross-sectional area of the tube is one-half the velocity at the axis (see Gibson, 1925, p. 63)

$$S_m=\frac{S}{2} \qquad (2)$$

the rate of discharge, V, in cm^3 per second is

$$V=\frac{\pi D^2 S}{8} \qquad (3)$$

For accurate measurement of the velocity of the current in the tube (t) the quality of the carmine suspension is of great importance. The suspension must be very fine and should contain no particles that may settle inside the tube; it must have the same specific gravity as that of the sea water in which the oyster is kept, and its color must be sufficiently deep to be noticeable when a small amount of the suspension is allowed to enter the tube and forms a cone.

To make up a suspension that will conform with these requirements the following procedure should be followed: The carmine powder is ground in a glass mortar with a few drops of sea water; after a very fine paste is formed more sea water is added and the suspension is poured into a glass bottle, is well shaken, and is allowed to stand undisturbed for five minutes. Then the upper half of it is poured into another bottle, to be used in the experiments. Only fresh suspension should be used, because after 24 hours the carmine particles settle more quickly and have a tendency to form lumps.

In a study of the effect of temperature and other external factors on the function of the gills the carmine method has several advantages over the tank method. First, no error is introduced by the possible fluctuations in the levels of water in the two vessels; second, the water in the tray where the oysters are kept can be changed easily without disturbing the animals; and third, the measurement of the rate of flow can be made in a few seconds instead of several minutes, as is required by the tank method. It is interesting, however, to show how the two methods check each other. The following figures were obtained with an oyster that was placed first in a tank, where the rate of flow of water through its gills was measured; then it was transferred to a tray and after 30 minutes of rest the rate of flow of water was measured again. In both cases 10 readings were made and the arithmetic mean was computed. The results of this test are shown in the following table:

TABLE 2.—*Rate of flow of water determined by "tank" and "carmine" methods*

Method	Rate of flow (liters per hour)	Temperature, ° C.	Time
Tank	1.40	20.3	2.07–2.21 p. m.
Carmine	1.66	20.8	2.51–2.54 p. m.

It has been found that in all cases where such a comparison was made that the figures obtained by the tank method are a little lower than those obtained with the carmine method. This is due probably to the additional resistance in the tube (b) connecting the two vessels. It is obvious that the rate of flow can be measured more accurately by employing the carmine method, while the tank method makes it possible to measure the hydrostatic pressure in the gills and to collect the water after it has passed by the gills.

In the experimental study of the effect of one of the external factors on the biological reaction, particular care should be exercised in eliminating the influence

of other variables that may affect the function of the organism. Gray (1922, 1924, 1924a) has shown that not only temperature but changes in the hydrogen-ion concentration, oxygen and carbon dioxide contents, and concentration of various salts in sea water affect the ciliary activity. In the present experiments the salinity of the water, its oxygen content and the pH value were kept constant. There are two factors, however, the control of which presented certain difficulties and which may be responsible for considerable fluctuation in the experimental data. In some of the oysters, especially in those that had been exposed for a long time to a low temperature, the gills were covered with a thick layer of mucus, which blocked a free passage of water through the pores. These oysters exhibited wide and irregular fluctuations in the velocity of the current, but after the outside and the inside of the branchial chambers were washed out with sea water the current became steady.

Mechanical stimulation represents another factor that may affect the velocity of the current. Whenever the oyster attached to the apparatus was disturbed, it invariably showed a change in the rate of flow, frequently stopping the current entirely but coming back to normality in a few minutes. The following record of one of the experiments illustrates this fact very clearly.

TABLE 3.—*Effect of mechanical stimulation on the velocity of the current.—Experiment 62, August 10, 1926*

Speed at the axis of the tube (centimeters per second)	Temperature, ° C.	Time	Remarks
1.1	14.2	11.03	
1.1	14.2	11.04	
1.1	14.2	11.05	
1.1	14.2	11.06	
1.2	14.2	11.07	Oyster disturbed
.6	14.2	11.08	
.6	14.2	11.09	
1.1	14.3	11.10	
1.0	14.3	11.11	
1.0	14.3	11.12	

It is very probable that these fluctuations are due to the contraction of the branchial chambers, caused by mechanical stimulus. In the experiments described below the precaution was taken to avoid mechanical stimulation, and in case the oyster was disturbed by accident it was left for 10 minutes before the next readings were made.

The temperature of the water was changed by using either an electric hot-point immersion heater or a battery of jars filled with a freezing mixture. The water in the tray was agitated by an electric stirrer (fig. 3 *s*) and aerated. If necessary, the tray was placed in a water jacket with a mixture of salt and crushed ice packed between the walls. Readings were made after the oyster had been left for 15 minutes at a given temperature. The temperature was maintained constant within 0.5° C. At every given temperature from 10 to 20 readings were made, from which the arithmetical mean was computed. All temperature readings, unless otherwise indicated, were made in centigrade.

EFFECT OF TEMPERATURE ON THE RATE OF FLOW OF WATER THROUGH THE GILLS

SUMMER EXPERIMENTS

We begin the discussion of this problem with an analysis of the results of summer experiments The experimental material consists of the data of 64 experiments performed during the summers of 1925 and 1926, but in the following discussion the data of only 15 experiments, in which the observations were made at not less than five different temperature points, are taken into consideration.

The following technical procedure was followed in all the experiments: The first observations were made at room temperature, which in most cases was around 20° C.; then the water was cooled gradually to 5° and then warmed until the temperature of 35° and in a few cases 45° was reached, and cooled again to 20°. In 5 experiments readings were made at 2° intervals; in 10 experiments 5° intervals were used. Each determination of the rate of flow is a mean of 10 or 20 readings. Altogether 2,470 readings were made.

All the experiments were made with adult oysters varying in size from 3.5 to 5 inches. There exist considerable individual variations in the rate of flow of water that can not be correlated with the differences in size of the oysters and undoubtedly depend on the physiological conditions of the organisms. Some of the small oysters proved to be very active and produced very strong currents, while some of the largest ones were very weak. At present it is impossible to determine the cause of such differences. There was nothing in the appearance of the oysters that could be correlated with the efficiency of their gills.

The range of individual variations in the rate of flow of water at different temperatures is shown in Table 4 and Figure 4. In Table 4 the experimental data are grouped in 14 classes, each at 3° intervals, the figures in the body of the table representing the frequencies; in Figure 4 the frequency distributions for temperature, ranging from 6° to 26.9°, are presented graphically. An examination of the frequency polygons discloses that the individual variations increase with the temperature and reach their maximum between 24° and 26.9° C.

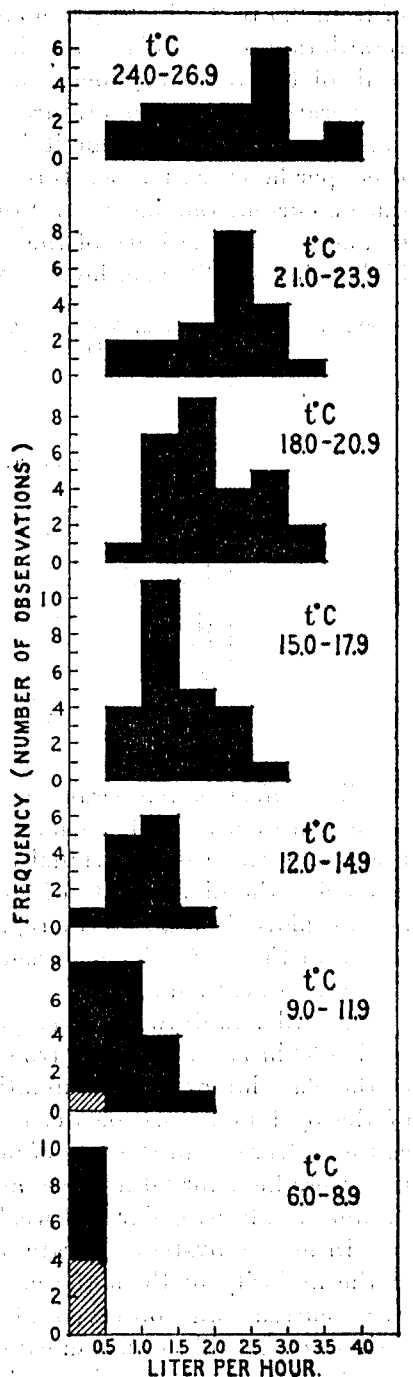

FIG. 4.—Frequency distribution of the rate of flow of water at different temperatures. Cross-hatched areas show the number of oysters that failed to produce any current

At this temperature the rate of flow of water varies in the different oysters from 0.5 to 3.9 liters per hour; the majority of the oysters, however, filter the water at a rate of from 2.5 to 2.9 liters per hour. With the cooling of the water comes a gradual retardation of the ciliary activity of the gills, and, as can be seen in Figure 4, the peak of the frequency polygons moves toward the left, following the decrease of temperature. At temperatures between 9° and 14.9° the range of individual variations is smaller than it is at higher temperatures and varies from 0 to 2.4 liters per hour; at temperatures between 9° and 11.9° the majority of oysters produce a current ranging from 0 to 0.9 liter per hour. At a low temperature between 6° and 8.9° the activity of the gills is greatly reduced and the rate of flow is never higher than 0.4 liter per hour. No current is produced below 5°.

TABLE 4.—*Frequency distribution of the rate of flow of water through the gills at a given temperature. The figures indicate the number of observations*

°C.	Rate of flow (liters per hour)							
	0–0.4	0.5–0.9	1–1.4	1.5–1.9	2–2.4	2.5–2.9	3–3.4	3.5–3.9
5–5.9	2							
6–8.9	10							
9–11.9	8	8	4	1				
12–14.9	1	5	6	5	1			
15–17.9		4	11	5	4	1		
18–20.9		1	7	9	4	5	2	
21–23.9		2	2	3	8	4	1	
24–26.9		2	3	3	3	6	1	2
27–29.9			1		2	2	1	
30–32.9			1		1	1	3	
33–35.9		1	1			2	1	
36–38.9					1			
39–41.9	2							
42–44.9	3							

The effect of temperature on the ciliary activity of the individual oysters can be seen in Figure 5. The curves represent the results of seven experiments and cover the whole range of individual variations from very slow-working oysters to those producing the highest rate of flow. The results of the remaining eight experiments are not plotted because they represent the repetition of one of the types of the curve shown in Figure 5. The average results of all 15 experiments are shown in a curve drawn in a heavy line.

In order to draw the average curve all the data were grouped in 14 classes, each having 3° intervals, and the true mean of each class was plotted against the midvalue of the class interval. Examination of the curves shows that the maximum activity of the oysters occurs between 25° and 30° C. Exposure to higher temperatures causes a decrease in the rate of flow. Below 40° the process is reversible, but oysters that were kept for 20 minutes at 40° and brought back to 20° failed to recover and produced only irregular and weak currents.

In all the oysters the rate of flow decreases with the drop in temperature, and in the majority of them the current stops at 8°. In a few cases, however, a very weak current was observed at 5.1°. Temperatures below 5° inhibit the ciliary activity of the gill to such an extent that no current is produced by the gill epithelium.

Analyzing the experimental data, it has been noticed that under the conditions of the experiments every oyster exhibited certain fluctuations in the rate of flow,

which could not be attributed directly to changes in the surrounding medium. Excluding the cases of accidental mechanical stimulation that may cause the contraction of the muscles in the gill tissue and result in a temporary decrease in the velocity or even in a complete stoppage of the current, the range of the fluctuations observed in all the experiments varied with the temperature. It has been shown in a previous paper (Galtsoff, 1928) that between 15° and 25° the fluctuations are small, ranging from 4.4 to 5.9 per cent, but that they increase considerably both below and above these temperatures. This means that the nearer we approach the temperature limits of the ciliary activity the more irregular becomes the ciliary motion of the gills. It must be borne in mind that the flow of water from the gill cavity is due to the difference in pressure between the inside and the outside of the gills, and that

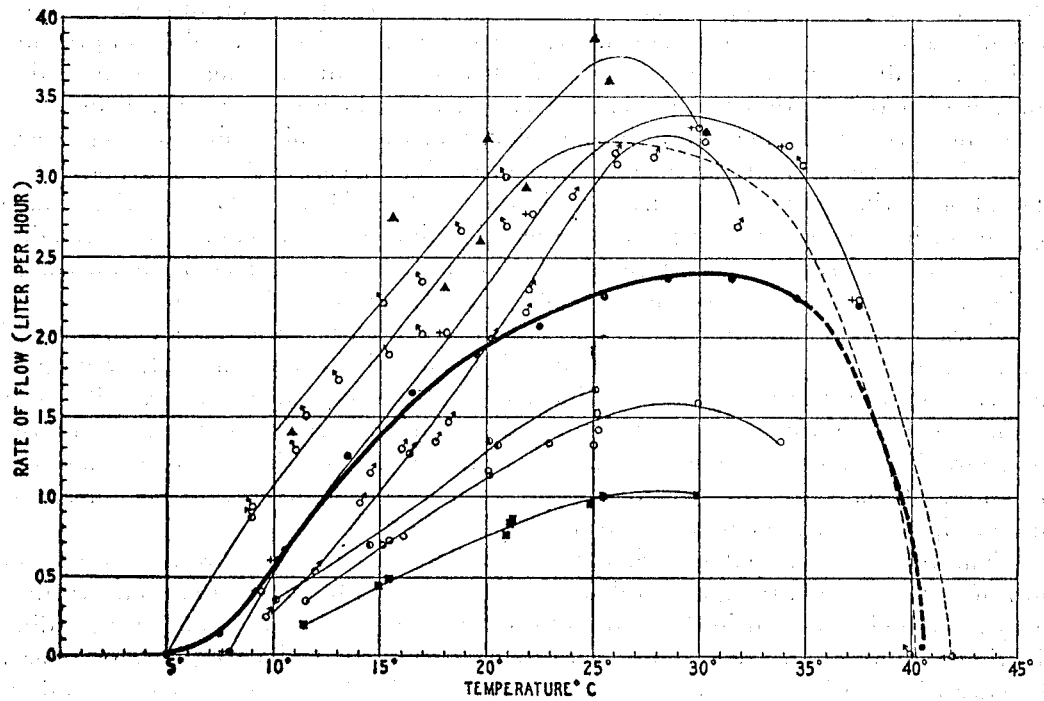

FIG. 5.—Effect of temperature on the rate of flow of water produced by the gills

the velocity of the current is a function of a pressure drop between the two points. The head pressure inside the gill cavity is maintained by the activity of the lateral cilia and is dependent upon the rhythm and coordination of the ciliary motion along the whole surface of the gill.

The beat of the ciliary cell has two distinct phases—a very rapid forward or effective stroke and a slow backward or regressive stroke. It has been shown by Weiss (1909) and Gellhorn (1925) that the work performed by the cilium during one phase is proportional to the cube of the velocity

$$W = KV^3 \qquad (4)$$

where K is a constant, W is work, and V is velocity. The ability of the ciliated cells to transport particles or produce a current depends on the difference in the velocities

of the progressive and regressive strokes. At present we have no means to measure the absolute velocity of the motion of the cilium, but Kraft (1890) has estimated that the velocity of the progressive phase is five or six times greater than that of the regressive period. This means that the work performed during the forward motion is one hundred and twenty five or two hundred and sixteen times greater than that produced during its backward movement. It is obvious that even an insignificant decrease in the ratio between the velocities of the two strokes will result in a considerable loss of efficiency of the ciliary motion.

The coordination of the ciliary activity is another factor that determines the constancy of the current produced by the gill epithelium. The maintenance of a constant pressure inside the gill cavity depends on a definite rhythm of strokes along all the filaments of the gill. As soon as the rhythmic motion in some of them becomes irregular a leakage occurs through the wall of the gill, resulting in a drop of pressure and in retarding or complete stoppage of current. In this manner even small disturbances in the rhythm of the beats of lateral cilia along one or several filaments result in considerable fluctuation in the velocity of the outgoing current. The variations in the velocity of the current that occur both below 15° C. and above 25° should be attributed to the disturbances in the rhythm of beats. Observations made by the author on the excised pieces of the epithelium kept at temperatures ranging from 5° to 15° show that the irregularity in the rhythm of the ciliary motion becomes noticeable under the microscope as soon as the temperature drops to 15°. At 10° the characteristic metachronial wave often is interrupted because the cilia in some of the filaments begin to beat simultaneously instead of in succession, as they do normally. The result is that in certain blocks of the filament all the lateral cilia beat simultaneously at the same phase, while in the other portions of the filament the metachronial rhythm is maintained. At 5° the ciliary motion becomes slow and irregular. Because of the lack of coordination at this temperature no current is produced, although the cilia are beating.

The results of present experiments on the effect of temperature on the rate of flow of water through the gills parallel the data obtained by Gray (1924) on Mytilus. Gray's method consisted in determining the relative speed of the cilia by recording the time required to move at a uniform rate a small circular plate of platinum over a distance of 1 centimeter along the surface of the gill. It should be borne in mind, however, that the transport of a particle over the ciliated surface is accomplished by the frontal cilia, while the current running through the gills is produced by the lateral cilia. As in the case of the oyster, the activity of the frontal cilia of Mytilus is a function of temperature. Gray finds that between 0° and 33° the speed of the cilia increases with the rise in temperature, although the amplitude remains normal. Between 34° and 40° a marked falling off in the amplitude of the beat occurs, followed by the reduction of the rate of beat. Experimenting with oysters, I was unable to observe the changes in the amplitude of the beats, and the attempts to apply Gray's method for measuring the mechanical activity of the frontal cilia were unsuccessful. The gills of the oyster contain numerous mucus glands that are stimulated by contact with metal and secrete mucus, which accumulates on the surface of the gill and increases the resistance to the motion of the plate. On the other hand, repeated mechanical stimulation of the cilia by contact with metal causes a complete

cessation of the ciliary motion on a given area of the gill. Readings obtained with Gray's method were so inconsistent that the method was discarded as unsuitable for the oyster gill. The temperature optimum for Mytilus gills is somewhat higher than that of the oyster. Gray's figures show that the highest activity of the Mytilus cilia takes place at a temperature between 27° and 38°, while the maximum activity of the oyster occurs between 25° and 30°.

A comparison of the results of Gray's work on Mytilus and the data obtained during the present investigation discloses the interesting fact that the curves describing the effect of temperature on the rate of flow of water and on the mechanical work produced by the oyster gills are different from the curve showing the effect of temperature on the relative speed of Mytilus cilia. (Fig. 6.) As has been shown in another

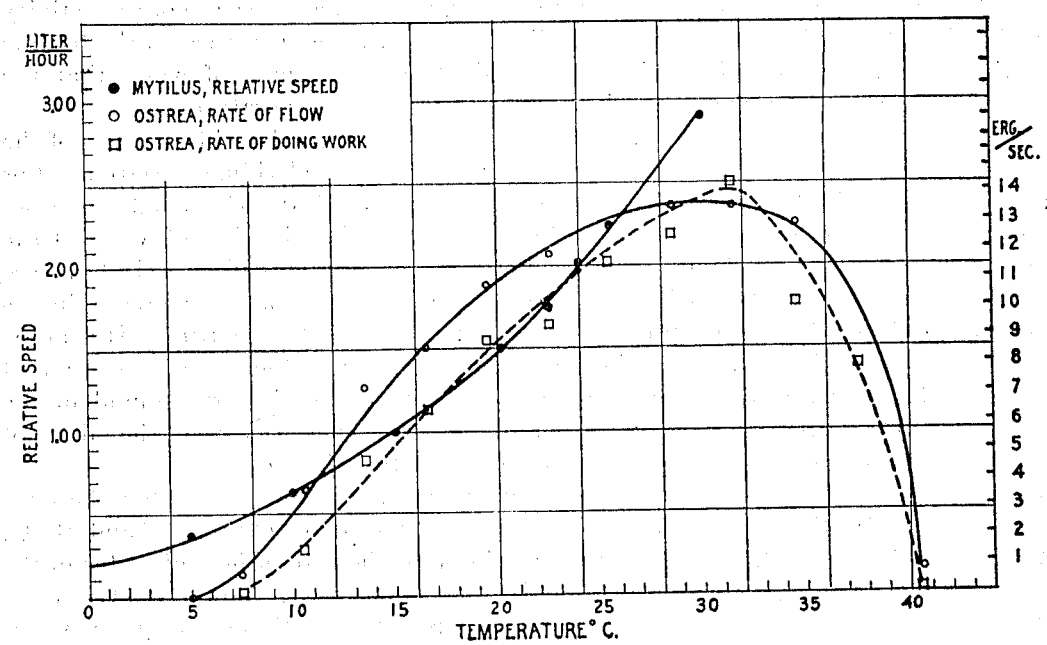

FIG. 6.—Effect of temperature on the relative speed of ciliary activity of Mytilus (Gray's data) and on the rate of flow of water and rate of doing work by the oyster. The vertical scale for the rate of doing work is shown on the right side

paper (Galtsoff, 1928), the rate of flow of water is not a true expression of the mechanical activity of the gills. With the decrease in temperature the viscosity of water increases, and therefore the resistance to fluid motion increases also; consequently more energy is required to propel cold water at a given velocity. The work expended in producing a steady current through the horizontal glass tube can be computed from the following formula (Galtsoff, 1928):

$$W = 2\pi l \mu S^2 \qquad (5)$$

where W = rate of doing work in ergs per second, l = length of the tube in centimeters, μ = viscosity of water in poises, and S = speed at the axis of tube in centimeters per second.

Analyzing the curves of the effect of temperature on the rate of doing work and on the rate of flow of water, one finds that neither curve can be described by the Arrhenius equation, which was found applicable to many instances of the effect of temperature on biological reactions. Crozier (1924) has found, however, that the effect of temperature on the relative speed of the Mytilus cilia follows this equation. The discrepancy undoubtedly is due to the fact that the rate of flow of water is controlled not only by the frequency of the ciliary beats (which may depend on a definite chemical reaction) but also is governed by several other factors, such as rhythm and coordination of the ciliary motion along the whole surface of the gill. The production of a current by the gills is a very complex phenomenon in which several reactions of the organism are involved.

Although the rate of flow of water does not give us a true measure of the activity of the gills, it supplies information regarding the effect of temperature on the feeding of the oyster; the latter is obviously dependent on the volume of water that the oyster is capable of passing through the gills at various temperatures.

It has been shown above that the rate of flow of water produced by oysters of the same age and taken from one locality is subject to wide individual variation. For instance, the highest figure of discharge of water measured at 25° was 3.9 liters per hour, while another oyster at the same temperature produced a flow of water at the rate of only 0.9 liter per hour. The results of the experiments discussed above are consistent in the respect that in all of them there was a decrease or increase in the rate of flow depending on the direction of the changes in the temperature. It is interesting to compare the data obtained in these experiments with the estimates computed by other investigators and based on the counts of planktonic forms found in the stomachs of the oysters. The comparison is difficult, however, because of the failure of the investigators to give temperature readings at the time of their experiments. Assuming that the experiments were made in summer, it is very likely that the temperature at which the observations were made was somewhere between 18° and 24° C. As is shown in Figure 4, at this temperature interval the rate of flow of water in the majority of oysters varies between 1.5 and 2.5 liters per hour. Grave (1905) states that the oyster filters 0.167 liter per hour. Moore (1913) estimates that an oyster takes in water at the rate of 40 quarts (38 liters) a day but fails to state whether the filtering was going on continuously for a 24-hour period. Wells (1916) states that "at feeding temperatures large volumes of water, from 25 to 50 gallons a day, pass through the oyster gills." In another paper (Wells, 1926) he says that "the quantity of water filtered through an oyster gill at moderate temperatures averaged greater than 2 gallons per hour." As has been shown in the present paper, "feeding temperature" covers quite a wide range—from 7° to 40° C. Unfortunately Wells does not state how he arrived at these figures. It is doubtful that there are oysters that are able to take in water at the rate of 7.5 liters (2 gallons) per hour, and Wells's figures should be regarded as guesses not supported by any experimental evidence.

Nelson's (1921) estimate of the rate of flow of water through the oyster is 6 quarts (5.7 liters) per hour. Allen (1914), for a fresh-water mussel, gives a rate of flow of 1.4 liters per hour. The filtering of water by the sea mussel has been studied in Conway Laboratory (England). According to a statement found in the Guide to

the Fisheries Exhibit (Ministry of Agriculture and Fisheries, 1922), "a mussel can pump at least 10 gallons of water through itself in 24 hours." Unfortunately I was not able to find a description of the method employed in Conway Laboratory.

The fact that the estimated figures of the rate of flow through the oyster vary from 0.167 to 7.5 liters per hour is good evidence of the unreliability of the methods employed by previous investigators. The estimation based on the count of the planktonic froms found in the stomach and intestine can not be accurate. Everyone who has had experience with quantitative plankton examination is familiar with the difficulties encountered in obtaining reliable figures. Moreover, in the estimation of the rate of flow by this method an assumption is made that all the microorganisms caught by the gills are ingested by the oyster, which obviously is incorrect, as some of them never reach the mouth of the oyster but are rejected into the pallial cavity.

EXPERIMENTS WITH HIBERNATING OYSTERS

In the experiments described above the oysters were exposed to sudden changes in temperature. Observations have shown that the period of 15 minutes during which the organism was kept at a constant temperature was sufficiently long to produce an effect on the ciliary motion. There arises a question, however, whether long-continued exposure to low temperature would produce different reaction. Nelson (1926) thinks "that with the slowly falling temperatures of autumn and early winter the oyster becomes adapted to a lower range of temperature, so that although there is a sharp decrease in ciliary movement below 5° activity does not entirely cease." For practical purposes it is very important to know whether in winter the oysters respond to the changes in temperature in the same manner as they do in summer.

In order to study this problem, several dozens of oysters were left on the bottom of Woods Hole Harbor, close to the United States Bureau of Fisheries pier, in September, 1926. The daily examination of temperature records taken at 8 a. m., noon, and 4 p. m. shows that since December 5 the temperature of the water was below 40° F. (4.4° C.), and during January and February it varied from 29.6° to 34° F. (−1.4° C. to 1.1° C.). On February 12, 1927, 36 oysters were taken from the harbor, brought into the cold laboratory room (air temperature 3.5° C.), and examined. All the oysters appeared to be healthy and showed a new growth at the edges of the shell.

The purpose of the first experiment was to determine the exact temperature at which the outgoing current begins to flow. The valves of the oysters were forced apart and glass rods were thrust between them to prevent their closing. Then the oysters were placed in cold sea water poured into a large, white enamel tray and the temperature of the water was raised gradually from 1° to 9° C. The oysters were kept from 30 minutes to one hour at a given constant temperature; observations were made at 1° intervals, and the beginning of the flow of water from every oyster was noticed by adding a few drops of carmine suspension. The temperature of the suspension was always the same as that of the water in the tray. The results of this experiment are presented in Table 5 and Figure 7. In order to facilitate a comparison with the results of summer experiments, the latter data are shown in the right column of the table.

The majority of the oysters began to produce a current at a temperature between 8.1° and 9°, though in a few of them the beginning of the flow of water took place either below or above this temperature interval. No current was observed at 5° and below. This result confirms what has been observed in the summer experiments (see right column of the table) and shows that so far as the activity of the ciliated

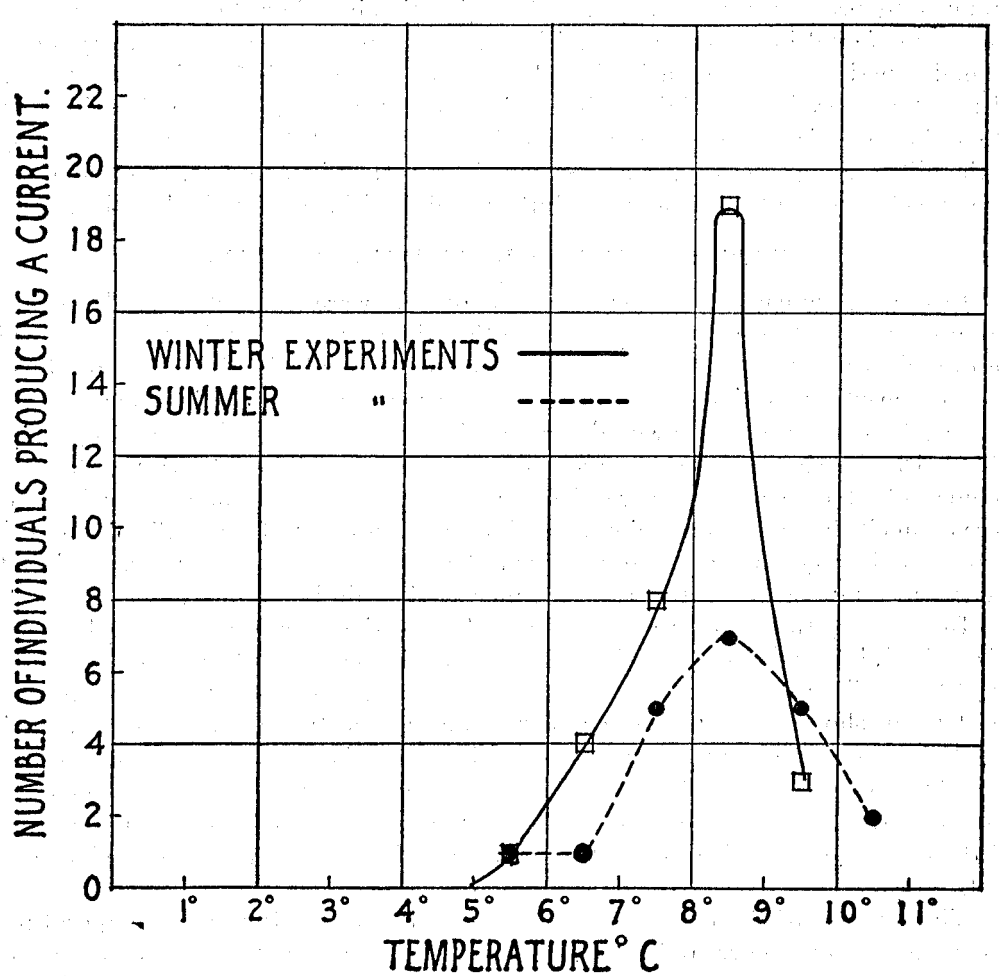

FIG. 7.—Frequency distribution of the beginning of current at different temperatures

epithelium of the gills is concerned there is no special adaptation to low temperatures; in hibernating oysters the current produced by the gills begins and ceases to flow at the same temperatures as in the summer oysters that were chilled suddenly. Examining Figure 7 one notices that in summer oysters the peak of the frequency curve is not so pronounced as it is in winter experiments, but this slight difference is insignificant and should be attributed to the greater number of winter observations.

TABLE 5.—*Temperatures at which the oysters begin to produce a current*

Temperature at which the current begins to flow (° C.)	Number of oysters		Temperature at which the current begins to flow (° C.)	Number of oysters	
	Winter	Summer		Winter	Summer
0–1	0	0	7.1–8	8	5
1.1–2	0	0	8.1–9	19	7
2.1–3	0	0	9.1–10	3	5
3.1–4	0	0	10.1–11		2
4.1–5	0	0			
5.1–6	1	1	Total number of oysters examined	35	21
6.1–7	4	1			

Another question that requires examination is whether the hibernating oysters would respond to the increase in temperature in the same manner as they do in spring or summer. In order to answer this question two experiments were performed at Woods Hole on February 14 and 15, 1927. The oysters were taken directly from the harbor and the rate of flow of water through their gills was measured with the carmine method. The results of these experiments are shown in Table 6 and Figure 8.

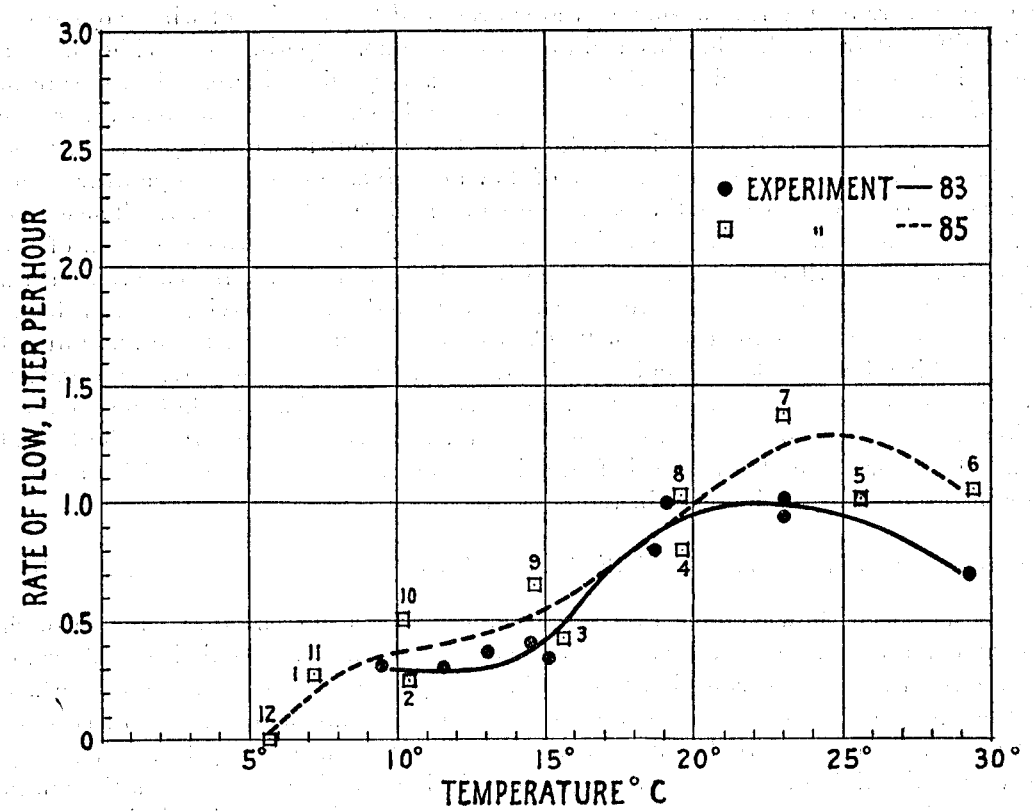

FIG. 8.—Effect of temperature on the rate of flow of water. Two experiments with hibernating oysters

TABLE 6.—*Effect of temperature on ciliary activity—Winter experiments*

Experiment 83, Feb. 14, 1927			Experiment 85, Feb. 15, 1927		
Temperature (° C.)	Speed at the axis of tube (centimeters per second)	Rate of flow (liters per hour)	Temperature (° C.)	Speed at the axis of tube (centimeters per second)	Rate of flow (liters per hour)
9.5	0.5	0.33	7.2	0.43	0.29
11.6	.45	.30	10.5	.39	.26
15.2	.51	.34	15.6	.61	.41
19.2	1.56	1.05	19.5	1.21	.81
24	1.40	.94	25.5	1.56	1.05
29.2	1.02	.68	29.4	1.81	1.22
24.2	1.56	1.05	24	2.03	1.36
18.8	1.16	.78	19.5	1.63	1.09
14.5	.61	.41	14.6	1.03	.69
13 [1]	.57	.38	10.3	.76	.51
			7.8	(2)	
			5.8	0	0

[1] Next day.

[2] Current very slow.

As can be seen from an examination of Figure 8, the curve describing the effect of temperature on the rate of flow of water produced by the gills of winter oysters is quite different from what has been obtained in summer experiments. (Fig. 5.) In both winter experiments (fig. 8) the curves show a very slight increase in the rate of flow of water between 7° and 15°, while in summer the slope of the curve at this range is quite steep. It has been noticed, also, that the current in winter oysters was less regular and the fluctuations in the rate of flow at a given constant temperature were wider than those observed at the same temperature during the summer. The explanation of such a difference in the activity of the gills is found in the condition of the gill epithelium. All the oysters examined in February had the gills covered with a thick layer of mucus accumulated during the periods of inactivity. After being kept in a tank at a temperature of 9° C., the oysters discharged large amounts of mucus, which, being of less specific gravity than water, formed long strings of gelatinous substance suspended in water. It has been mentioned above that the accumulation of the mucus clogs the water pores and interferes with the activity of the lateral cilia. It is very probable that this factor is responsible to a great extent for a slowness in response to the increase in temperature.

TEMPERATURE AT WHICH THE CILIARY MOTION CEASES COMPLETELY

It has been shown above that the production of a current that runs through the gill chambers and which is caused by the beating of the lateral cilia is also dependent on the rhythm and coordination of the ciliary motion along the whole surface of the gill. The fact that at certain low temperatures no current is produced does not necessarily mean that the cilia are at a standstill; the latter may beat irregularly without maintaining a necessary head pressure inside the gill cavity, and although in doing so they produce a certain amount of work, the efficiency of the gill is equaling zero. It is interesting to determine, however, at what temperature a complete cessation of the ciliary activity takes place. In 1926 (Galtsoff, 1926), a series of observations was made with very small pieces of gill epithelium that were kept under a

cover glass in a microaquarium. The temperature of the water in the microaquarium was regulated and kept constant within one-half of 1°. It has been found that with the decrease in temperature below 15° C. the ciliary motion becomes slow and irregular and ceases entirely at 5°. The experiments were repeated many times with the same results. Different results, however, were obtained when observations were made on large pieces of the gill. Portions of the gill lamellæ approximately 6 square centimeters in area were kept in a Stender dish of about 15 centimeters capacity which was placed on a little platform built on the bottom of a finger bowl. The space between the walls was filled with water and the temperature was kept constant. The experiments were made in September, 1926, and February, 1927. The microscopic examination made with a water immersion lens on the large pieces of gill showed that when the temperature drops to 5° C. there is a considerable slowing down of the ciliary activity and the beating continues without a definite rhythm. Due to the lack of coordination and irregularity of the ciliary motion, no current is produced. The activity of some of the cilia continues even at −2° C., when almost all the water in the dish except a narrow space just around the gill is frozen. A complete cessation of ciliary activity occurs only when the water freezes entirely. The process is reversible, and as soon as the ice melts the cilia begin to beat again. It has been noted that at low temperatures some of the cilia cease beating sooner than others; it is impossible, therefore, to speak of a definite critical temperature at which ciliary activity stops. In some of the filaments the motion stops as soon as the temperature drops to 5°; in others it goes on until all the water is frozen. There is also a distinct difference in the behavior of different kinds of cilia; frequently the lateral cilia come to rest first while the frontal cilia continue to beat.

The discrepancy observed in the experiments with small and large pieces of gills should be attributed to the different conditions of the tissues and probably to the lack of blood in the small pieces. Gray (1926) has shown that in the Mytilus gills the cells of the lateral epithelium contain a supply of available energy sufficient to maintain their activity in sea water for a limited period of time. If the gills are thoroughly washed with the sea water the lateral cilia come to rest in about 15 minutes. In a well-fed mussel the period of activity may be considerably longer. The frontal cilia, however, remain active for a very long period.

Several experiments were performed in February, 1927, with the view to determining whether the efficiency of the frontal cilia is affected by low temperature in the same manner as that of the lateral cells. The oysters were taken from the harbor when the temperature of the water was 0.8° C.; after removing the left valves and mantles the oysters, with the gills exposed, were placed in a tray filled with sea water, the temperature of which was raised gradually. A few drops of carmine suspension, having the same temperature as that of the surrounding water, were dropped on the surface of each gill, and the temperature at which the carmine particles began to move was recorded. The following is the record of one of the experiments (February 3, 1927). At 11.45 a. m. eight oysters were taken from the harbor, opened, and placed in water of 0.5° C.

TABLE 7.—*Effect of low temperature on the ciliary activity of frontal and lateral cells*

Time, p. m.	Temperature of water (°C.)	Motion of carmine particles (frontal cilia)	Outgoing current (lateral cilia)
12.37	1.0	No	No.
1.45	2.4	do	Do.
1.55	2.4	do	Do.
2.14	3.0	do	Do.
2.24	3.0	Slow in all oysters	Do.
2.32	4.0	do	Do.
2.48	4.2	do	Do.
2.54	5.2	do	Slight in 1 oyster.
3.13	5.2	do	Do.
3.18	6.4	do	Do.
3.38	6.3	do	Slight in 2 oysters.
3.42	7.0	do	Do.
4	7.2	Active	Current in 5 oysters.
4.07	8.2	do	Current in 7 oysters.
4.17	8.1	do	Do.
4.55	9.5	do	Do.
5.30	9.5	do	Do.
6.15	10.0	do	Do.
6.25	10.2	do	Current in all oysters.

The experiment shows that the frontal cilia can produce mechanical work and transport the particles along the surface of the gill at 3° while the current is produced by the lateral cilia only at temperatures above 5°. This undoubtedly is due to the fact that for the production of a current a coordinated ciliary motion along the whole surface of the gill is essential, while the transport of particles along the surface is accomplished by the coordinated beats of frontal cilia on one or several filaments only. If, for instance, the ciliary motion stops on one of the filaments (which often happens at low temperatures), it would not affect the mechanical activity of frontal ciliæ on the other filaments; as long as a sufficient ratio between the progressive and regressive strokes is maintained, the frontal cilia are pushing the particles toward the distal end of the gill, and the absence of ciliary motion in some of the filaments does not interfere with the transport of the particles by the others although the cessation of motion of lateral cilia in one of the filament interferes with the running of current through the gills.

In connection with these experiments it is interesting to mention the results of the observations that show that when the shell of the oyster is closed at low temperature the ciliary motion may be inhibited completely. The following experiments supply evidence for this statement: On February 15, 1927, six oysters were taken from the shallow water of the harbor; the temperature of the water was 0.8 ° and that of the air 1.7°. The shells were forced apart slightly and a small thermometer was thrust into the oyster meats. It registered the following temperatures: 1.4°, 1.2°, 1.3°, 1.2°, 1.4°, 1.4°. Then the oysters were opened and small pieces of gill epithelium were put in sea water immediately and examined under the microscope. The examination was made on the deck of a boat anchored in the harbor. Air temperature during the examination varied from 1.6° to 1.7°. In all the pieces of epithelium cut from the gills and placed in sea water at 1.4° there was no ciliary motion. Ten minutes later, however, the ciliary motion was active in all of them. The same experiment was repeated next day with six oysters that were taken from the harbor and left for two hours exposed to direct sunlight. The air temperature was 3.8°. When the oysters were opened the temperature of their meats was as follows: 8.6°, 8.5°, 9.6°, 10.1°, 10°, and 10°. In all of them the ciliary motion observed on the excised pieces of the gill epithelium was slow and irregular but became normal in a

few minutes. The experiments show that at low temperature in a closed shell the ciliary motion may be inhibited completely and that when the oyster is exposed to direct sunlight the temperature of its meat becomes much higher than that of the air. These facts should be taken into consideration when the hibernation of oysters is regarded from the sanitary point of view.

STRAINING OF WATER BY THE GILLS

One of the main functions of the lamellibranchiate gills consists in straining the water that passes through its body and catching planktonic organisms and other food particles suspended in it. It is interesting to study this function more carefully and to determine how completely the water is deprived of suspended material after it had passed through the gills. This can be done easily by employing the "tank" method. The oyster is placed in the tank (fig. 2) and is allowed to filter water, which is collected in a graduate. After 1 liter has been collected the water is passed through the high speed (Fœrst's) centrifuge (making about 20,000 revolutions per minute), the sediment is collected and transferred into a small volume of water, and the number of organisms in it is counted in a Sedgwick-Rafter cell. A comparison of the number of organisms present in the water before and after it had passed through the gills gives us a good idea of the efficiency of the latter as a filter. Obviously the number of organisms that can pass through the gills depends on the size and shape of the various forms. Long diatoms like Rhizosolenia or those that have long appendages, like Chætoceras, are easily retained by the gills; while minute forms, and especially bacteria, have a good chance to pass between the lateral cilia. The first experiments made in 1925 (Galtsoff, 1926) have shown that over 99 per cent of certain plankton forms may be caught by the gills. The plankton in these experiments consisted of Chætoceras, Rhizosolenia, and comparatively large dinoflagellates like *Peridinium oceanicum* and Ceratium. Different results were obtained, however, in the summer and autumn of 1926, when the plankton consisted chiefly of small organisms. Following are the results of two experiments made in August and September, 1926:

TABLE 8.—*Filtering of water by the gills*

EXPERIMENT A, AUGUST 11, 1926. TEMPERATURE OF WATER 22°; RATE OF FLOW OF WATER THROUGH THE GILLS 1.01 LITERS PER HOUR

	Number of organisms in one liter of water		
	Before it passed through the gills	After it passed through the gills	Per cent of organisms passed through the gills
Diatoms	703,000	50,000	7.1
Dinoflagellates	312,000	12,500	4.0
Total	1,015,000	62,500	6.2

EXPERIMENT B, SEPTEMBER 19, 1926. TEMPERATURE OF WATER 19.1°; RATE OF FLOW OF WATER THROUGH THE GILLS, 1.9 LITERS PER HOUR

Diatoms	194,000	24,300	12.6
Dinoflagellates	259,000	49,000	18.9
Total	453,000	73,300	16.2

In experiment B the plankton was formed mostly by minute Naviculæ and Glenodinium, while in experiment A such large forms as Coscinodiscus, Rhizosolenia, and Ceratium were present. In both experiments the water discharged by the gills contained a considerable amount of mucus.

Because of the practical importance of the bacteriological examination of the oyster, it is interesting to determine how many bacteria can be retained by the gills. Three experiments were performed with oysters kept in water to which varying amounts of fresh 24-hour-old cultures of *Bacterium coli* were added. The experiments were carried out in October, 1925, at Doctor Pease's laboratory in New York. The water in the tank to which *B. coli* was added was well stirred and the oyster was allowed to filter it for 30 minutes. During this period the small vessel of the tank (fig. 2) was twice emptied and refilled with the water passed by the gills. For counting the number of *B. coli* 1 centimeter of water was planted on Endo's plates, and for the total number of bacteria the same amount was planted on beef agar. The plates were kept for 48 hours at 37°. The results of the experiments are as follows:

TABLE 9.—*Filtering of water by the gills*

Experiment No.	Temperature of water (°C.)	Rate of flow (liters per hour	Number of bacteria in 1 centimeter of water				Per cent of bacteria passed through gills	
			Before it passed through gills		After it passed through gills			
			B. coli	Total	B. coli	Total	B. coli	Total
A	22.8	0.6	200	----------	100	----------	50	----------
B	22.8	.6	16,000	23,000	11,200	12,600	70	54.8
C	23.2	.8	14,000	16,600	12,400	14,800	88.6	89.2

As can be noticed from this table, the water, after it passed the gills, always contained less bacteria than it had before but the difference was not constant. Apparently only a small number of bacteria are retained by the gills; the microorganisms are so small that they can pass easily between the lateral cilia and escape back into the surrounding water.

OPENING AND CLOSING OF THE SHELL

Feeding and respiration in the oyster is dependent on two distinct functions—the ciliary activity of the gill epithelium and the opening and closing of the shell. The movement of the shell is controlled by the adductor muscle, the relaxation of which causes the opening of the valves, while its contraction brings the valves together and keeps them tightly closed. Because the oyster has no power of locomotion, the contraction and relaxation of the adductor muscle is the only noticeable reaction by which the organism responds to the external and internal stimuli. One should anticipate, therefore, that the opening and closing of the shell is a complex phenomenon that is controlled by a great variety of factors. No attempts were made in the present paper to study the physiology of the adductor muscle, but it seemed desirable to obtain some data regarding the duration of time the oysters keep the shell open.

The oyster was immobilized by placing it on a brick and embedding its left shell in a mixture made of 1 part of cement and 3 parts of plaster of Paris. A glass rod, attached by means of the same mixture to the right valve of the oyster, was connected to the lever of a recording apparatus (fig. 9) and the oyster was kept in a large aqua-

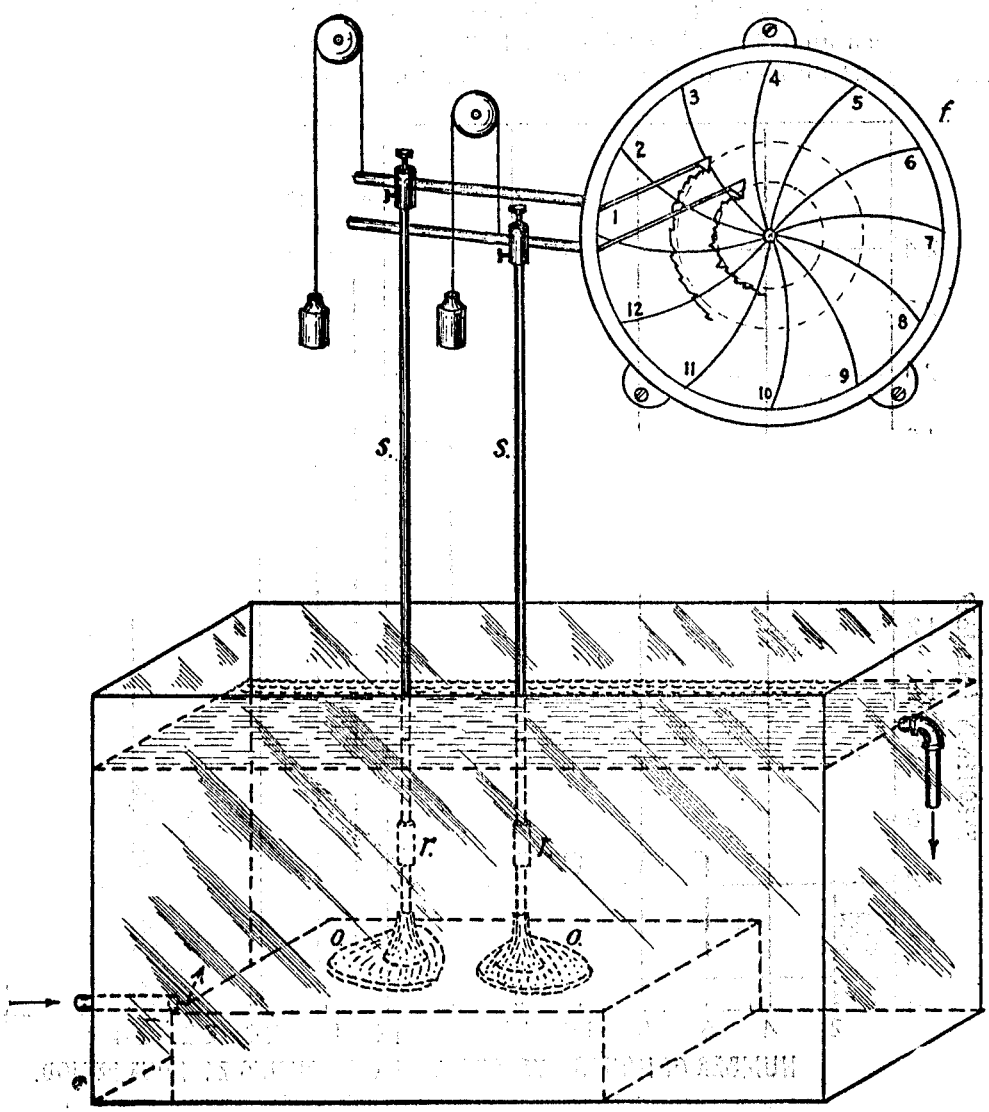

FIG. 9.—Method employed to study the shell movements of oysters. *o.*—oyster immobilized in plaster of Paris; *r.*—rubber connections; *s.*—glass rods attached to the levers (*l*) of the recording apparatus; *f.*—Foxboro time recorder; *w.*—weight

rium tank with running sea water. The records of the movement of the shells were made with a Foxboro or Bristol two-pen time recorder. The weight of the cement, glass rod, and lever was counterbalanced in such a way that the shell bore no additional pressure. (Fig. 9.) In all the experiments the records of two oysters were taken simultaneously and the temperature of the water was recorded on the thermo-

graph. For the purpose of the present experiments the use of a time recorder has several advantages over the ordinary kymograph—it eliminates the necessity of having a special time signal, and after the apparatus has been set it can be left for 24 hours without any further attention. The oysters were kept attached to the apparatus for varying periods of time ranging from one to eight days. Altogether, during the time between June 15 and October 15, 1926, there were obtained 132 daily records written by 34 different oysters. The temperature of the water varied from 13° to

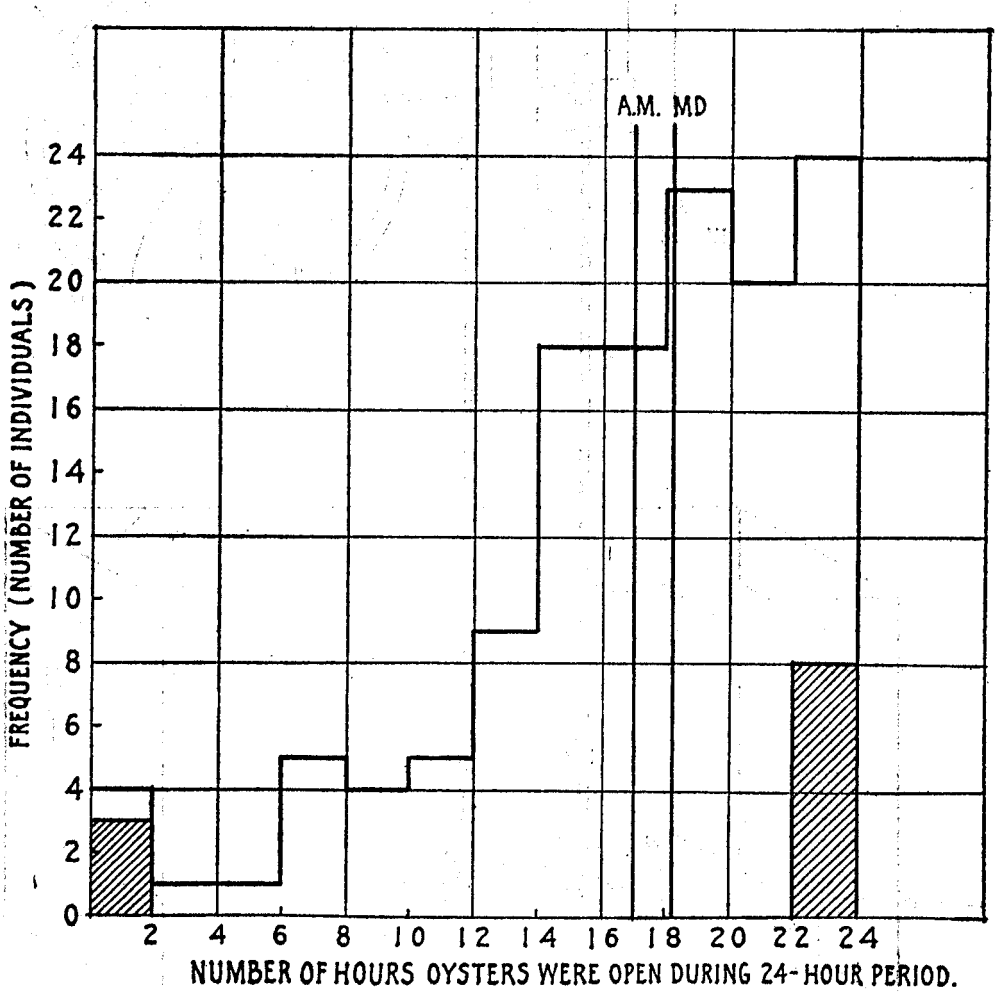

FIG. 10.—Frequency distribution of the duration of periods of shell opening

22° C. Within this range there was no definite correlation between temperature and the opening and closing of the shells. The results of all the observations are given in Figure 10. They are grouped in 12 classes, each having two-hour intervals and the frequencies are plotted as the ordinates. The number of oysters that were either closed or open for a 24-hour period are shown in cross-hatched areas. An examination of Figure 10 shows that the oyster has a tendency to keep its shell open as long as possible. The arithmetic mean of the number of hours the average oyster keeps its

shell open during a day is 17 hours 7 minutes; the median is 18 hours 5 minutes. In a preliminary paper published in 1926 (Galtsoff, 1926) it was stated that the average period of time the shells of an oyster are open during a day is 20 hours. Nelson (1921), analyzing the records of 3 oysters kept under observation for 21 days, also states that on the average the oysters were open for 20 hours. The present investigation, based on more numerous observations, shows that the average period of time when the shells are open is smaller. The decrease of the average from 20 to 17 hours and 7 minutes is due to a few instances where the oysters failed to open during the 24-hour period.

An analysis of the records shows that when the shells are open the adductor muscle contracts and relaxes periodically. The contraction is often so slight that it does not result in a complete closing of the shell (fig. 11) and is of brief duration, the muscle beginning to relax immediately after the maximum contraction is reached. It has been shown by several investigators that by periodical contractions the

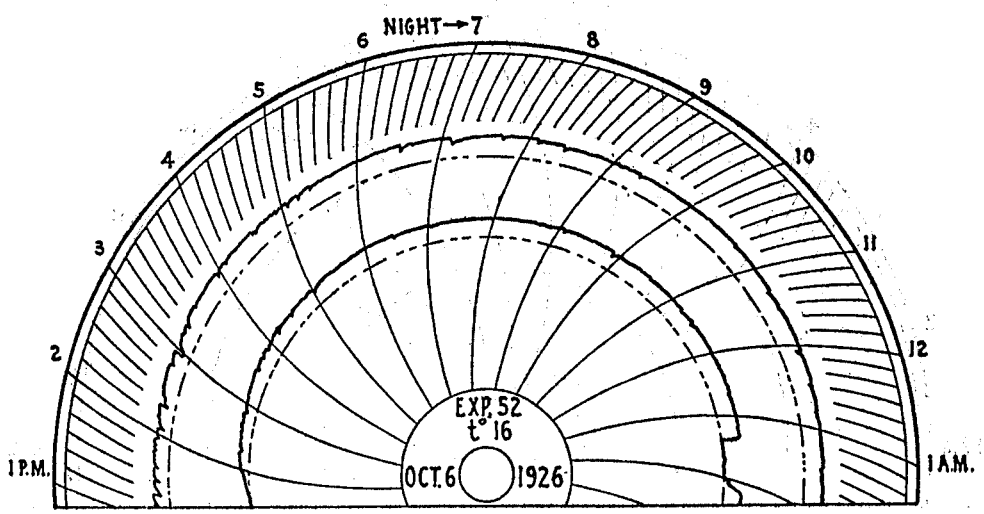

FIG. 11.—Part of the record of shell movements of two oysters made at 16° C. Dotted lines indicate the position of the pens when shells are closed

oysters cleanse themselves and discharge the material that had accumulated in the pallial cavity. Although by this reaction the organism is able to get rid of the material accumulated by the gills, the inference that every contraction of the muscle is an ejection reaction is incorrect. Nelson (1921, p. 343) states that from observation of the extent and frequency of the down strokes made by the oysters on the recording apparatus and representing the contraction of the adductor muscle, together with a knowledge of the turbidity of the water, it is possible to determine the rate of feeding. Employing this method he arrives at the erroneous conclusion (1921, p. 339) that "temperature within the limits observed during the experiment (69° to 90° F.) apparently did not operate as an independent factor in controlling the intake of food." It has been shown in this paper that the ciliary motion, which is responsible for the intake of food by the oyster, is a function of temperature. The number of contractions of the adductor muscle can not be regarded as an index of the rate of feeding, because the oyster may respond to any external or internal

stimulus by closing its shell. My observations on the oysters attached to the recording apparatus and kept in a glass tank show that ejection of the material accumulated in the pallial cavity takes place at irregular intervals and that rhythmic contractions of the adductor muscle (figs. 11 and 12) were not accompanied by a discharge of any material. Such different factors as changes in illumination, mechanical stimulation, changes in the pH or gas content in sea water, presence of certain chemicals, and so on, may cause the contraction of the muscle and temporary closing of the shell. The frequency of the contractions depends also on the physiological condition of the oyster. It has been found in the present investigation that after spawning the female oyster makes many less contractions than it does before spawning. The kymograph tracings represented in Figure 13 show this very plainly. During this experiment, in both cases the shell of the oyster was wide open and the temperature of the water and other external factors were

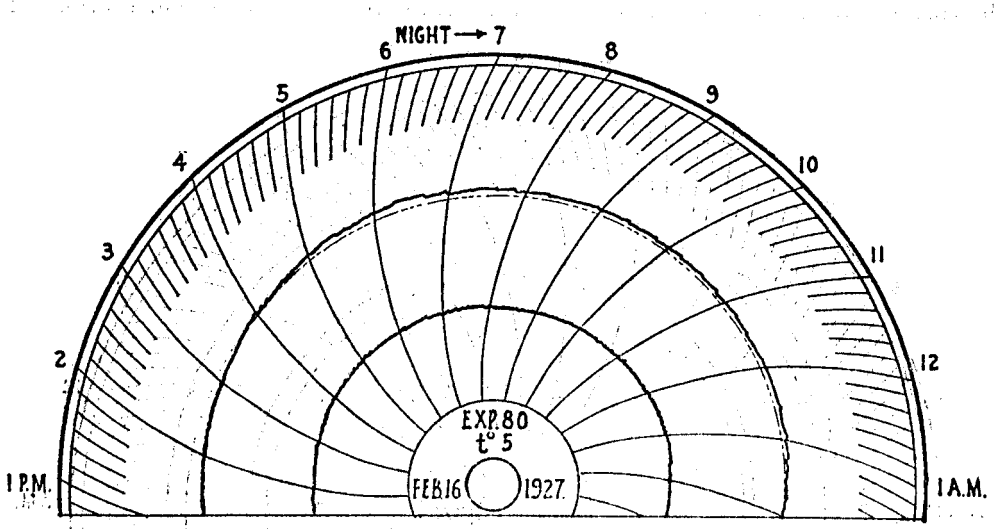

FIG. 12.—Part of the record of shell movements of two oysters made at 5° C. Dotted line indicates the position of the pen when shell is closed. In lower line the oyster was nearly closed and showed very slight motion

alike. At present we understand very little the conditions that control the periodical contractions of the adductor muscle, but it appears obvious that they can not be correlated directly with the rate of feeding, and the estimation of the latter can not be based on the frequency of the contractions.

It has been suggested by Nelson (1921) that there may be a certain amount of correlation between the times of opening and closing and the hour of the day and night. Nelson divides a day into four arbitrary periods, from 11.01 p. m. to 4.30 a. m., from 4.31 to 11 a. m., from 11.01 a. m. to 7.30 p. m., and from 7.30 to 11 p. m. Then he counts on the kymograph records the number of closures and openings that occur during each period. According to his data 50 per cent of closures take place in the 5½ hours between 11 p. m. and 4.30 a. m. (dawn). Nelson makes two somewhat contradictory conclusions—first, that "the period from 11 p. m. to dawn may almost be looked upon as a time of rest, or at least of greatly lessened activity", and second, that "the hours of inactivity on 50 per cent of all the days were confined

to periods 1 and 2" (i. e., from 11.01 p. m. to 11 a. m.). In another paper (Nelson, 1923) he states that from 60 to 70 per cent of the hours of inactivity (closure) occur during darkness. The examination of the number of closures and openings occurring during a given period of time does not convey a true idea of the activity or inactivity of the oyster. A better understanding can be gained by counting the number of hours the oyster was closed or open during a given period of a day. These observations should be made under controllable conditions, inasmuch as it has been shown by Nelson for Barnegat Bay (1921) and confirmed by Prytherch for Milford Harbor (unpublished report) that in these bays the oysters close their shells at ebb tide. We know that every change in the environment may cause the oyster to close its shell, and therefore the problem of whether oysters exhibit daily periodicity in

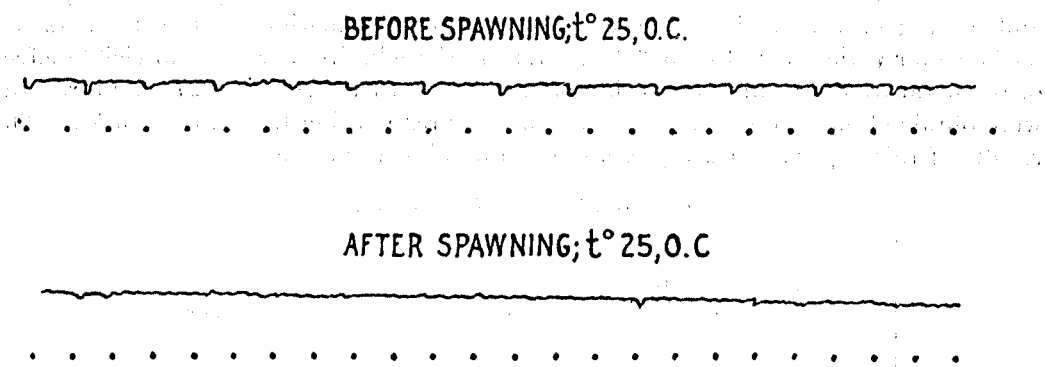

FIG. 13.—Kymograph records of the movement of the shell one hour before spawning (upper line) and one hour and a half after spawning. Oyster was open all the time. The marks under the line indicate one-minute intervals.

behavior should be studied without any possible interference of other factors that may produce the same reaction. The examination of the material obtained by the author during July–September, 1926, fails to disclose any correlation between the periods of inactivity (closure) and darkness. Analyzing the data, all incomplete records (i. e., those covering less than 24-hours periods) and all those showing that the oyster was either closed or open continuously for 24 hours were excluded, so that in each of 103 records taken into consideration the oyster was closed for a part of a day. The period of darkness was determined as beginning half an hour after sunset and ending half an hour before sunrise. The results of the examination are given in the following table:

TABLE 10.—*Opening and closing of the shell in relation to the time of day*

	Number of hours		Number of days
Total number of hours oysters were under observation	2,472	Number of days when shells were closed during day hours only	43
Number of hours oysters were closed during daytime	565	Number of days when shells were closed during night hours only	7
Number of hours oysters were closed during nighttime	266	Number of days when shells were closed during night and day hours	53

The only inference that can be drawn from an examination of this table is that there is no correlation between the closures of the shell and darkness. Out of 103 days there were only 7 during which the oysters were closed only at night. There were 43 days when the closures occurred during the daytime, and in 53 cases it took place both during day and night hours. The number of hours of night closure is 266, or 32 per cent of the total number of hours of inactivity (831). Inasmuch as the period of darkness is approximately 8 hours, or one-third of the 24-hour period, it is quite natural that one-third of the time of inactivity should fall in the night hours. Examination of these records forces us to come to the conclusion that under laboratory conditions the periods of opening and closing of the shell of the oyster are not correlated with time of day or night.

There arises the question as to whether the temperature has any effect on opening and closing of the shells. In the above-mentioned experiments the temperature of the water varied from 13° to 22° C. Within these limits there was no visible effect of temperature on opening or closing of the shell. In February, 1927, eight records were obtained on two oysters kept at temperatures varying from 4.5° to 5.5°. The results of this experiment are presented in the following table:

TABLE 11.—*Opening of shells at low temperatures*

Date	Temperature (C°)	Length of time oysters were open	
		Oyster No. 1	Oyster No. 2
Feb. 12 (half day)	5.0–5.5	12 hours	12 hours.
Feb. 13	4.5–5.5	19 hours	14 hours 50 minutes.
Feb. 14	5.0–5.5	19 hours 50 minutes	12 hours 20 minutes.
Feb. 15	2.0–5.5	13 hours 40 minutes	13 hours 50 minutes.

The shells were open very slightly, less than 1 millimeter apart (fig. 12), but the oysters exhibited typical periodical contractions. As has been shown above, no current is produced at this temperature, and several tests with carmine suspension failed to disclose any current in the oysters attached to the recording apparatus. On February 15 one oyster was attached to the kymograph and left 67 hours in cold water; during this time the temperature varied from 0.5° to 1.6° and the oyster remained tightly closed.

DISCUSSION AND CONCLUSIONS

The experimental data presented in this paper show that the functioning of the gills of the oyster is controlled by temperature. In spite of wide individual variations in the activity of the ciliary epithelium, it has been found that in all cases the ciliary motion follows strictly the changes in temperature, slowing down with its fall and increasing with its rise. Because of anatomical peculiarities, the normal functioning of the gills ceases at a temperature of 5° C., when the ciliary motion becomes irregular and is not able to maintain the head pressure necessary for the production of an outgoing current. The inhibiting effect of low temperature upon the activity of the oyster was suspected many years ago. Bashford Dean (1887) was the first to suggest that "in winter the oyster, with decreased movements of branchial cilia and reduced

heart action, may almost be said to hibernate." An indirect evidence of hibernation was supplied by Gorham (1912), Pease (1912), and Gage and Gorham (1925), who based their conclusions on the study of seasonal fluctuations in *B. coli* content in oysters taken from polluted bottoms. Physiological study of the problem was impossible, however, as no method was offered whereby the ciliary activity of the gills could be measured. The present paper, based on a quantitative study of the activity of the gills, supports fully the ideas advanced by Gorham, Pease, and Gage. However, the facts described in it contradict the conclusions reached by Nelson (1923) that "the rate of filtration of water during any given period of time, as deduced from the rapidity and extent of ejections of accumulated sediment from the mantle cavity, may vary widely, independently of the temperature and turbidity of the water." No attempts were made in the present investigation to study the effect of turbidity of the water, but the rôle of temperature in the ciliary activity of the gill epithelium was established and is shown in Figures 5, 6, 7, and 8.

Knowledge of the effect of temperature on the activity of the gill epithelium of the oyster is essential in many practical problems of the oyster industry. From the sanitary point of view, the fact that at a temperature of 5° C. and below the oyster does not take in any water and ceases feeding, supplies an additional safeguard, which can be applied in the sanitary control of oyster bottoms. In the purification of oysters by chlorination an understanding of the rôle temperature plays in the functioning of the gills is of great importance. The method of chlorination introduced in 1914 by Johnstone (1915) is based on self-purification of oysters, which are allowed to filter sterile sea water; and knowledge of the rate of filtration at a given temperature is necessary for an intelligent operation of the chlorination plant.

It is a common practice in certain areas to take oysters from slightly polluted beds and to relay them on clean, unpolluted bottoms. Sometimes this operation is carried out during the cold season when the temperature is below 5° and the oysters have no possible chance to cleanse themselves. It is obvious that the determination of the minimum period of time oysters should be left on new bottoms should be based on the rate of filtration of water at a given temperature.

For a study of the physiology of the oyster a knowledge of the rate of filtration of water is of fundamental importance. Fattening, growth, and ripening of the gonads are probably directly dependent on the amount of food consumed. At present we know almost nothing regarding these activities of the oyster, and the author is convinced that the present investigation may facilitate, to a certain extent, the attack of other problems that are of great importance for an understanding of the factors responsible for the fluctuations in the oyster crops in our waters.

RÉSUMÉ

1. Two methods are described whereby the rate of flow of water produced by the ciliary epithelium and the pressure inside the gill cavity of the oyster can be measured accurately.

2. The mechanical work performed by the oyster gills in producing a current of water can be expressed by the following formula: $W=2\pi l\mu S^2$, where W = work in ergs per second; l = length in centimeters of the glass tube through which the

current is running; μ = viscosity of water in poises; and S = speed at the axis of the tube in centimeters per second.

3. The rate of flow of water produced by the gills is controlled by the temperature. The optimum temperature lies between 25° and 30° C. No current is produced at 5° and below, although the cilia continue to beat. Absence of current at low temperature is due to the lack of coordination of the ciliary motion along the surface of the gill.

4. Hibernating oysters do not exhibit any adaptation to low temperature; they begin to produce a current as soon as the temperature rises above the critical point. In the majority of the oysters the current begins to flow when the temperature reaches 8° C.

5. There exists considerable individual variation in the rate of flow of water produced by different oysters. The maximum rate of flow observed during the present investigations is 3.9 liters per hour at 25° C.

6. The ciliary motion may continue at temperatures below 0° but becomes very slow and irregular. There is a noticeable difference in the efficiency of the frontal and lateral cells; the first ones are able to transport the particles along the surface of the gill at 3° C., while the lateral cilia can produce a current only above 5° C.

7. In straining water through the gills the oyster catches a considerable number of plankton organisms, but a certain per cent of them (from 1 to 18.9) escapes. The number of organisms that passes through the gills depends on their shape and size; small, elongated forms, devoid of any appendages, pass easily between the lateral cilia and escape. Bacteriological examination shows that from 50 to 89.2 per cent of bacteria present in the sea water pass through the gills.

8. The analysis of 132 daily records shows that the oyster has a tendency to keep its shell open as long as possible. On the average, the shell of an oyster remains open for 17 hours and 7 minutes during every 24-hour period. There is no correlation between the opening and closing of the shell and the time of day.

9. The results of the present investigation have many bearings on various problems of oyster industry. (*a*) They confirm the theory of hibernation and show that at a temperature of 5° and below oysters cease to feed. (*b*) the knowledge of the rate of filtration of water at various temperatures is essential for a successful application of methods of self-purification, consisting either in relaying the oysters on unpolluted bottoms or in purifying them with chlorinated water. (*c*) The knowledge of the rate of filtration of water is of fundamental importance for a study of growth, fattening, and ripening of the oyster.

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STATISTICAL REVIEW OF THE ALASKA SALMON FISHERIES. PART I: BRISTOL BAY AND THE ALASKA PENINSULA

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INTRODUCTION

The exploitation of the Alaska salmon fishery resources may be said to have begun in 1878, 11 years after the purchase of the Territory from Russia, when the first cannery was established at Klawak, on Prince of Wales Island. Previously there had been some salting of salmon by both Americans and Russians and, of course, the salmon had formed one of the important food supplies for the natives from prehistoric times. Previous to the spectacular development of the canning industry, however, the inroads made on this natural resource must have been inconsequential. For the first few years after the establishment of the first cannery there was no great production of canned salmon, but about 1885 or 1886 the development started, which, with minor fluctuations, increased steadily, culminating in 1918 with a total pack of 6,605,835 cases, valued at $51,041,949. Few of the world's fishery resources exceed this one in productivity and value, and none has shown such remarkable growth in little more than 30 years. With 1918, however, the general upward trend ceased, and production dropped over 2,000,000 cases in 1919 and again in 1921. In the latter year the total pack was only a little over 2,500,000 cases, the lowest since 1910. It rose gradually again to a new peak of 6,652,882 cases, valued at $46,080,004, in 1926, only to fall disastrously once more in 1927. This brief history of the Alaska salmon fishery is shown graphically in Figure 2.

The development of the industry was marked by the gradual opening of new fishing grounds and by the extension of operations to include species formerly unused. The sharp rise that came between 1899 and 1902 was due largely to rapid development in the red-salmon fishery in Bristol Bay. Following this, for nine years the general level did not change materially, but then, between 1910 and 1918, the pack more than doubled, due mainly to the development of the fishery for pinks and

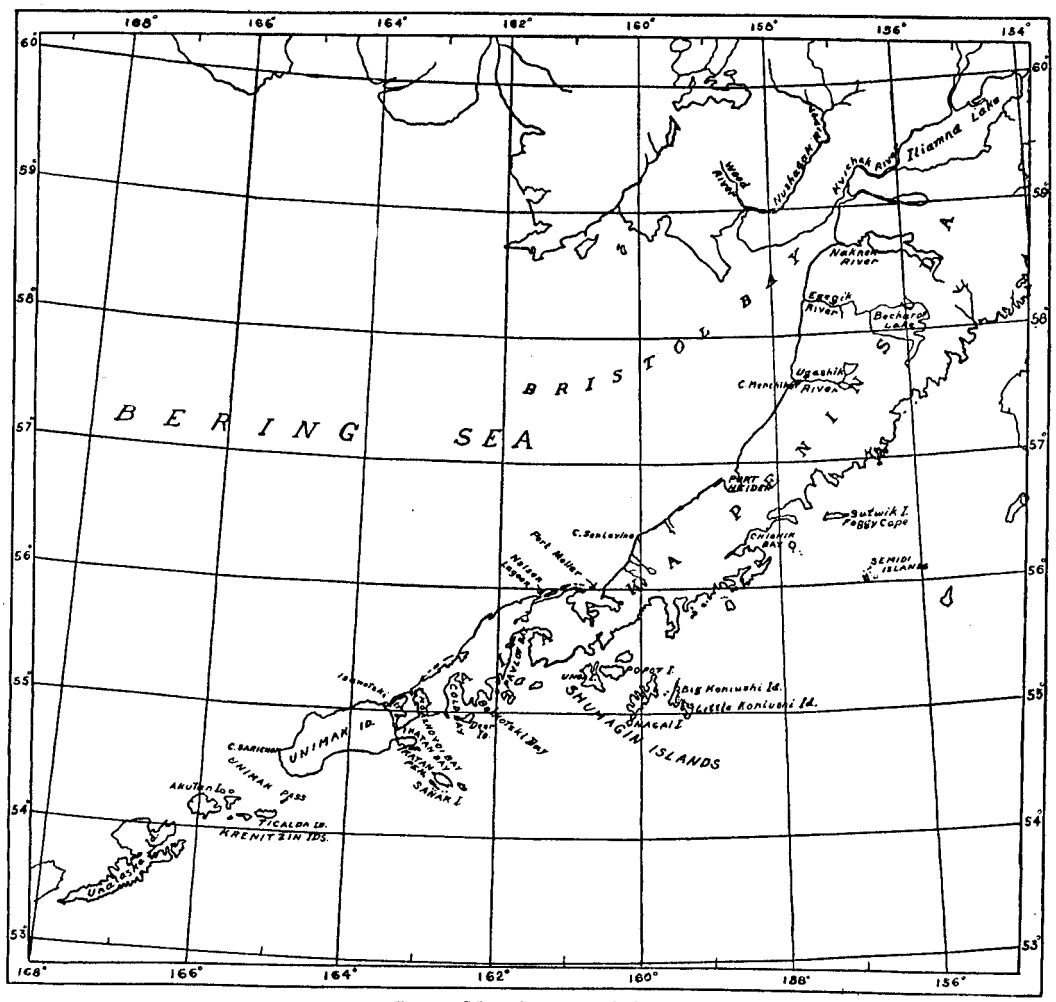

FIG. 1.—Map of western Alaska

chums in southeastern Alaska. The sudden drop in 1919 from over 6,500,000 cases to only a few over 4,500,000 was due to some extent to the postwar economic conditions; but it can not be ascribed entirely to that cause, as the red-salmon pack of western Alaska was poor in spite of intensive fishing, as indicated by the presence there of more gear than in any other year save one and a corresponding drop in the catch per unit of gear. Furthermore, a distinct drop in the pack of pinks took place in southeastern Alaska, while at the same time the pack of chum salmon maintained itself fairly well.

The striking drop in 1921 was an entirely different matter, however. The market was glutted with the cheaper grades held over from the previous two or three years, and in consequence no serious effort was made to pack pinks and chums in southeastern Alaska; the small total pack of 1921 was due almost entirely to this cause. In the following year the market recovered and operations were resumed in southeastern Alaska. For four years the pack fluctuated slightly around 4,500,000 and 5,000,000, rising sharply to a new maximum in 1926, followed by the remarkable drop in 1927. This rise and fall were shown, in general, by all species and in all districts; there was no marked change in the intensity of fishing, and the conclusion seems warranted that these fluctuations were caused primarily by biological factors.

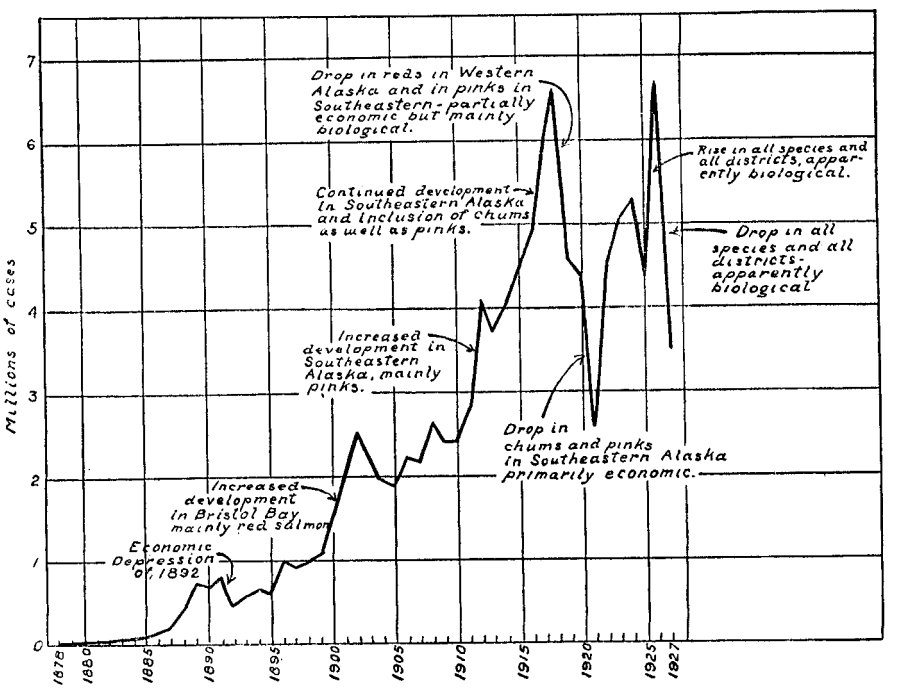

FIG. 2.—Total pack of canned salmon in Alaska

Our knowledge of these factors is too meager at present to warrant speculation as to their nature, but it seems safe to say that the wide fluctuations that have taken place since 1918 (although in part economic) are associated with the onset of depletion, or at least with the development of the fishery to the point of maximum productivity. This hypothetical point of maximum productivity may be defined as the number of fish that may be taken from the resource without impairing it. It will vary from year to year and can never be defined sharply, although it seems probable that ultimately we may be able to define it rather broadly. Any development of the fishery beyond the point of maximum productivity must lead inevitably to depletion and must be guarded against carefully. The conclusion that such wide fluctuations indicate that the fishery has reached its limit seems warranted from the following considerations: Under natural conditions, unaffected by exploitation, the abundance of fish in any fishery resource is certain to fluctuate rather widely, due to varying

natural conditions. The maximum productivity also will fluctuate widely, though not necessarily in proportion to the actual abundance of fish, as it would seem probable that a larger percentage could be taken in times of relative abundance than in times of relative scarcity. This available surplus, which can be taken for commercial use, will, then, on a percentage basis, fluctuate even more widely than will the general abundance. In the early stages of the development of a fishery the number of fish taken remains so far below the available supply that it is affected less seriously by the fluctuations in abundance. In times of scarcity the fishing effort may be adjusted readily, so that the annual catches will not show nearly as violent fluctuations as those of real abundance. When, however, the fishery has developed to the point where the actual take of fish exceeds the available surplus and approaches the total supply, it will be impossible to adjust the fishing effort so that in times of scarcity the annual catch may be maintained and wider fluctuations in productivity will appear. If, for instance, the annual catch of a fishery over a period of time is only one-tenth of the total supply, the great preponderance of the total supply will act as a buffer, so to speak, between the fluctuations in total abundance and the actual catch, and adjustments of the fishing effort will serve to maintain the catch at a fairly constant level. However, as the annual catch approaches closer and closer to the total abundance, until, for example, 75 per cent of the total supply is taken annually, it will become increasingly difficult to maintain the catch at a constant level and it will reflect more and more the inequalities in abundance. When this stage of development has been reached, therefore, it is logical to expect that the fluctuations in annual catches will become more violent, and we may assume that a fishery that shows such violent fluctuations has at least reached a point where more intensive exploitation will cut into the reserve necessary for the maintenance of the resource.

The Alaska salmon fisheries apparently had reached this stage at least by 1918, when the relatively smooth curve of development was replaced by the wide fluctuations of the succeeding years. The general level for the past 10 or 12 years has been around 4,500,000 or 5,000,000 cases, but if the hypothesis given above is correct it would seem that this is more than the resource can stand without injury. Perhaps the general level should be maintained at 3,500,000 or 4,000,000, but any such statement in reference to the total pack is necessarily very indefinite, as the total pack includes five species of salmon and an indefinitely large number of races taken throughout the vast extent of the Territory. In the more detailed analyses of separate species and localities, which follow, we shall attempt to show the fluctuations in the numerous components that together make up the total pack.

The studies of Alaska salmon statistics upon which this report is based were begun in 1925. The passage of the act of June 6, 1924, had placed full responsibility for the care and preservation of the Alaska fisheries upon the Department of Commerce. To fulfill this responsibility adequately, a knowledge of the trends and fluctuations in the fishery was imperative, and this report is the result of an effort to collect and analyze the available data on the salmon fisheries of Alaska. Fortunately, the bureau possessed detailed yearly statistics in the form of sworn annual reports submitted since 1904 by each firm or individual packing salmon in the Territory. These reports give, among other things, the number of salmon of each species caught, the locality where the capture was made, and the kind and amount of gear

used. Similar data bearing on the yield have been compiled and published in various publications of the Bureau of Fisheries, but the only segregation has been as to species and into three general districts—southeastern, central, and western Alaska. Although this arrangement has some value and is of long standing, having been originated when the collection of data pertaining to the Alaska fisheries was conducted by the Treasury Department, it masks the details of the fluctuations quite effectually, so that critical analysis is impossible. It has been necessary, therefore, to go to the original records for most of the data presented in this report, and this has been an arduous and time-consuming task. Certain data have been secured from published reports; those for the years previous to 1904 were taken mainly from the various reports of special agents of the Treasury Department and various others from the annual reports on the Alaska fisheries and fur industries published by the Bureau of Fisheries. It has not seemed desirable, in such a report as this, to give citations of the sources of data in any but certain special cases. Data of the sort presented in this report are subject to some inexactness, of course, but it is felt that they are as accurate as such data can well be and certainly are as accurate as is necessary for any practical purposes to which they may be put.

In the treatment of these data we have attempted to segregate them into the smallest possible geographical units. The ideal thing to have would be separate data for each stream, but this has been possible only in a few cases. As a rule, it has been necessary to combine the data for several streams or for an entire bay, inlet, channel, or larger geographical district. It has happened frequently that some companies gave detailed information as to the localities where the fish were captured, while others, operating in the same district, would assign the fish only to a general region; as, for instance, Prince William Sound, Bristol Bay, or southeastern Alaska. In such cases we have attempted first to complete the records for at least the larger items by correspondence with the companies that submitted the incomplete records. With the fullest available data at hand, it has then been necessary to decide whether to retain the smaller units (and if so, which ones) or to give the data for the larger unit only. Our procedure in such cases has not been uniform, as it was felt that each case presented a separate problem that must be decided on its own merits. In some instances the unapportioned fish formed so small a percentage of the whole that they could not possibly affect the general results, in which case they were merely included in the total for the district. For example, 194,045 red salmon and a few kings and chums were taken in Bristol Bay in 1922 and were unapportioned between the four districts. These are included in the table giving the totals for Bristol Bay but are not to be found in the tables for either of the four districts, so that, as given in these tables, the total catch for Bristol Bay for 1922 is greater than the sum of the catches in the four districts. Such discrepancies are more conspicuous in some of the other tables.

In other cases we found that the data for some of the minor localities within a larger unit were reliable and significant while many were not. In such cases it has seemed best to give the detailed data in so far as they were reliable, even though they aggregated but a small percentage of the catch in the larger district. As an instance of this, in the Shumagin Island district we have given separate data for Acheredin Bay, Orzinski Bay, Ivanof Bay, and Red Cove and have combined all the other

data into a single table for the remainder of the Shumagin Island district, finally giving a table of totals for the entire district.

Still other cases were even more confusing, and our decision to present separate data for a given locality or to include them with those of the next larger including unit has had to rest upon a consideration of such matters as the relative importance of the catches under consideration, the nature of the data supplied, and to a very considerable extent upon our personal local knowledge of the geography and fishing.

A study of this sort is primarily a study of abundance. We are concerned to know what changes in the abundance of salmon have taken place, and, so far as they may be discovered, the causes of these changes. We must decide immediately, therefore, what we are to use as a measure of abundance. The best measure undoubtedly would be one based on the yield per unit of fishing effort, but the introduction of new forms of gear, the enlargement and improvement of old forms, the replacement of sailing boats by motor boats, the impossibility of separating in our available data the catch made by different forms of gear, and other similar factors have made it impossible to define a sensible unit of fishing effort. We are forced, therefore, to use the total yield as our chief measure of abundance, although we recognize the unsatisfactory features of this procedure. Wherever possible we have given data showing the amount of gear as given in the available records, but we consider the records of gear to be only moderately reliable. The number of traps recorded in many instances includes "dummy" traps, which are driven primarily for the purpose of preempting a trap location and are never really fished. The gill-net records frequently include all the gill nets on hand during the season and so give no accurate idea of the actual number fished; and the aggregate length of the gill nets reported by a single company are given only in certain years.

In any carefully considered plan for the conservation of a fishery the most important thing is to determine, as accurately as may be, the condition of the resource. At any time we may wish to know the present condition of the fishery and the prospects for the future, and knowledge of this sort is dependent upon a knowledge of the changes the fishery has undergone in past years. Without a knowledge of the past and present conditions it is impossible to determine whether depletion has occurred or is imminent or what effect regulatory measures that may have been imposed have had. This last is an especially important function of such data, as it is necessary adequately to protect the resources and yet in the interest of true conservation the regulations must not be made so stringent as to reduce the commercial yield below what the resource can provide safely. And, if we can look into the future far enough so that the industry can be advised as to the prospects for the next season, a measure of efficiency and stability can be given which will make for the saving of millions of dollars now wasted in outfitting for runs that fail to materialize. Any appreciation of the present situation or any prophecy for a future year must be based upon consideration of the general trend of the fishery, the cyclic fluctuations about that trend (if present), the spawning escapements in preceding years, the conditions on the spawning grounds and in the streams and lakes that may have affected the mortality of the broods during their life in fresh water, and such information as may be available on the relative abundance in the preceding year or years of fish of younger age groups derived from the same brood years.

While other matters are involved, it is quite apparent that any knowledge of the state of a fishery will depend primarily upon the statistical records that are available. The importance of accurate, reliable, and adequate statistical data can not be stressed too strongly. They are, without doubt, the foundation stones of scientific fishery conservation. The better the statistical records the more accurate our knowledge will be and the better we can adjust our control to the requirements of rational conservation. It is especially important that the continuity of the statistical data be preserved, as we will want perpetually, as long as we have any interest whatsoever in maintaining our fishery resources, to know their immediate condition and future possibilities.

We have pointed out above various weaknesses in the available data on the Alaska salmon fisheries, and it is our belief that a more adequate system should be devised and adopted at the earliest possible moment. The past records, which form the basis of this report, are extremely valuable, but at best can answer our many problems in a general way only. The proper care of these fisheries, for which the Secretary of Commerce is now responsible, will depend in no small measure upon such knowledge as statistics alone can supply, and these should be made adequate at once to the demands of the future.

It is pertinent to inquire what effect legal restrictions may have had throughout the history of the fishery in modifying the catch, and we give herewith a brief chronological summary of the laws and regulations up to and including the act of June 6, 1924.

FEDERAL FISHERY LAWS AND RFGULATIONS AFFECTING THE SALMON FISHERIES IN ALASKA

Act of March 2, 1889.

Section 1. Prohibits erection of dams or other obstructions in salmon streams.

Section 2. Directs Commissioner of Fisheries to investigate salmon and salmon fisheries of Alaska.

Presidential proclamation, December 24, 1892.

Establishes Afognak Reservation.

Act of June 9, 1896, amended and reenacted by act of March 3, 1899. Treasury Department Circular No. 8, 1902, division of special agents.

Section 179. Prohibits erection of dams, barricades, fish wheels, etc., in salmon streams.

Section 180. Prohibits fishing above tidewater in streams less than 500 feet in width, except with rod or spear; setting gear across tidewaters of streams for more than one-third the width or within 100 yards of another net or seine in such streams or channels; fishing from midnight Friday to 6 a. m. Sunday, except in Cook Inlet, Prince William Sound, and Bering Sea; fishing between 6 p. m. and 6 a. m., except by rod or spear, in streams less than 100 yards in width.

Section 181. Authorizes setting aside streams for spawning grounds, close seasons, and limitation of fishing season, but only after giving a hearing to interested parties.

Section 182. Provides penalties.

Regulations promulgated May 2, 1900, under authority of act of March 3, 1899. Treasury Department Circular No. 57, 1900, division of special agents. Repeated in Circular No. 8, 1902.

Paragraph 2. Prohibits movable traps, etc.

Paragraph 3. Prohibits nets, etc., within 100 yards of stream mouths.

Paragraph 4. Prohibits wanton destruction.

Paragraph 5. Requires reports of operations.

Paragraph 6. Requires information to be given as required.

Paragraph 7. Requires establishment of hatcheries.

Regulations promulgated January 5, 1903. Treasury Department Circular No. 3, 1903.

Prohibits fishing until after June 30 in southeastern Alaska.

Act of February 14, 1903, Department of Commerce and Labor Circular No. 42, May 10, 1904.

Repeats act of March 3, 1899, changing authority to Department of Commerce and Labor.

Department of Commerce and Labor. Department Circular No. 34, April 18, 1904.

Rescinds regulation promulgated January 5, 1903, prohibiting fishing in southeastern Alaska until after June 30.

Executive order, February 1, 1906.

Establishes Yes Bay hatchery reservation and limits fishing therein.

Act of June 14, 1906, Department of Commerce and Labor Circular No. 136.

Prohibits aliens from fishing in the waters of Alaska.

Act of June 26, 1906, Department of Commerce and Labor, Circular No. 136, supersedes act of March 3, 1899.

Section 1. Provides license taxes as follows: Canned salmon, 4 cents per case; pickled, 10 cents per barrel; salt salmon, 5 cents per 100 pounds; fish oil, 10 cents per barrel; fertilizer, 20 cents per ton.

Section 2. Provides tax rebates on account of hatcheries at rate of 10 cases of salmon to every 1,000 red or king salmon fry liberated; provides for inspection and approval of hatcheries, submission of reports, and certification of reports.

Section 3. Prohibits maintenance of dams and other obstructions to passage of salmon in any waters where the distance from shore to shore is less than 500 feet, or within 500 yards of the mouth of any red-salmon stream less than 500 feet in width.

Section 4. Prohibits setting gear across or above the tidewater of any stream, estuary, or lagoon for more than one-third its width, or within 100 yards outside the mouth of any red-salmon stream less than 500 feet in width, or within 100 yards of another fishing appliance, or to construct a trap or other fixed appliance within 600 yards laterally or within 100 yards endwise of another trap.

Section 5. Prohibits fishing between 6 p. m. Saturday and 6 a. m. Monday except in Cook Inlet, Copper River Delta, and Bering Sea, and between 6 p. m. and 6 a. m. in any stream less than 100 yards in width. Provides for closing of trap and opening of heart walls of traps during weekly closed season.

Section 6. Authorizes reservations for spawning and limitation or restriction of fishing after giving hearing and in case those engaged in catching do not maintain adequate hatcheries.

Section 7. Prohibits canning or salting for sale for food any salmon more than 48 hours after it has been killed.

Section 8. Prohibits wanton waste.

Section 9. Prohibits misrepresentation on labels.

Section 10. Requires reports of operations.

Section 11. Authorizes regulations consistent with this act by Secretary of Commerce and Labor.

Section 12. Authorizes expenditures to enforce.

Section 13. Provides penalties.

Section 14. Method of enforcing act.

Section 15. Inconsistent acts repealed.

Section 16. Act effective June 26, 1906.

Order of Secretary of Commerce and Labor, December 19, 1907.

Closed to all commercial fishing Wood River and the area within 500 yards of its mouth.

Notice to packers by Commissioner of Fisheries, April 18, 1908.

Prohibits use of salmon bellies only without utilizing remaining edible portions of fish.

Department of Commerce and Labor Circular No. 192, April 24, 1909. Regulations of Bureau of Fisheries, Alaska Fisheries Service Circular No. 2, March 10, 1911.

Provides for numbering of fixed fishing appliances.

Department of Commerce and Labor Circular No. 238, March 21, 1912.

Regulates fishing in Afognak Reservation; restricts fishing rights to natives; gear and seasons subject to restrictions. (Presidential proclamation of December 24, 1892.)

Order of Secretary of Commerce and Labor, November 18, 1912.

Closes to all commercial fishing for salmon, streams flowing into Cook Inlet; Eyak Lake and its tributaries; Anan or Humpback Creek, its lagoon, lakes, and tributaries, and the region within 500 yards of its mouth; Naha stream and its tributary waters above a line from Loring Point to House Point.

Department of Commerce and Labor notice, February 6, 1913.

Extends privileges of fishing in Afognak Reservation to certain other natives and white men married to native women.

Department of Commerce Circular No. 251, August 19, 1913.

Repeats acts of June 14 and June 26, 1906, and regulations of April 24, 1909, changing authority to Department of Commerce.

Announcement, Department of Agriculture, Bureau of Biological Survey, April 13, 1914.

Permits to fish required in Aleutian Islands Reservation.

Department of Commerce Circular No. 251, second edition, May 4, 1915.

Gives acts of June 14 and 26, 1906; general regulations providing for (1) inspection, (2) numbering of fixed appliances, (3) filing of labels, and (4) waste of backs. Regulations in Afognak Reservation. Regulations in Aleutian Islands Reservation.

Closing orders:

1. Promulgated December 19, 1907. Closes fishing in Wood and Nushagak Rivers and within 500 yards of the mouth of Wood River.
2. Promulgated November 18, 1912. Closes fishing in (1) all streams of Cook Inlet, (2) Eyak Lake, (3) Anan Creek and for 500 yards outside, and (4) Naha River above Loring Point and House Point.

Order of Secretary of Commerce, October 25, 1915.

Closes to all fishing for salmon all waters tributary to Barnes Lake; Hetta Creek, its tributary waters, and the region within 500 yards of its mouth; and Sockeye Creek, its tributary Boca de Quadra waters, and the region within 500 yards of its mouth.

Department of Commerce Circular No. 251, third edition, March 20, 1916.

Includes, in addition to contents of second edition:

1. Executive order of February 1, 1906, establishing Yes Bay Reservation.
2. Closing order promulgated October 25, 1915, closing fishing in Barnes Lake, Hetta Creek and for 500 yards outside, and Sockeye Creek (Boca de Quadra) and for 500 yards outside.

Department of Commerce Circular No. 251, fourth edition, March 12, 1918.

Includes, in addition to contents of third edition:

1. Proclamation of April 28, 1916, establishing Annette Island Fishery Reserve.
2. Closing order promulgated November 30, 1917, closing Karluk River and Lagoon.
3. Closing order promulgated November 30, 1917, closing Bering River.
4. Closing order promulgated December 29, 1917, restricting fishing in Copper River, as follows:
   (1) Copper River Delta closed between January 1 and June 1 each year and at Miles Lake and Abercrombie Canyon between January 1 and June 5.
   (2) Weekly closed season.

(3) Gear in delta limited to gill nets excepting four traps at Cape Whitshed; no net over 1,000 feet in length, only one net to a location, no offshore nets, lateral distance between nets not less than 1,800 feet.
(4) Fishing prohibited between delta and Miles Lake.
(5) Fishing in Miles Lake only by stake and set nets not over 600 feet in length and only one net to a location, lateral distance between not less than 600 feet.
(6) Fishing in canyon by dip nets only, not greater than 16 inches in diameter and at least 300 feet between nets.
(7) Prohibits fishing above canyon.
(8) Set nets to be in straight line.
(9 to 12) Defines areas and certain forms of gear.

Department of Commerce Circular No. 251, fifth edition, January 14, 1919.

Includes, in addition to contents of fourth edition:

1. Closing order promulgated December 14, 1918, restricting fishing in Yukon River, as follows:
   (1) Pack restricted to not over 30,000 cases, 1,000 barrels, and 200 tierces. Pack to be apportioned among established plants. Weekly reports of pack required.
   (2) No packing for shipment out of Alaska above mouth of the Clear River near Andreafski.
   (3) Commercial fishing in the delta only in Kwikluak Pass.
   (4) Traps and pound nets prohibited.
   (5) Length of gill nets not to exceed 700 feet.
   (6) No fishing after August 31, except for local requirements.
2. Closing order promulgated December 20, 1918, restricting fishing in Copper River; revises closing order of December 29, 1917, as follows:
   (1) Closed season extended to June 10 (instead of June 1) in the delta and to June 15 (instead of June 5) in Miles Lake and Abercrombie Canyon.
   (2) Omits weekly closed season as required by section 2 of order of December 29, 1917; excludes all traps and limits length of gill nets to 800 feet (instead of 1,000 feet); lateral distance between set nets to be not over 600 feet (instead of 1,800 feet).
   (4) Excludes stake nets from Miles Lake. No set net to exceed 800 feet in length (instead of 600 feet); shore of lake to be considered throughout season as it was on June 15; fishing prohibited along west and north shores of Miles Lake and along islands between the bridge and head of lake.
   (5) No fishing permitted on east side of canyon.
   (8 to 11) Define areas more clearly and certain forms of gear; essentially the same as sections 9 to 12 in the order of December 29, 1917.

Department of Commerce Circular No. 251, sixth edition, January 2, 1920.

Revised as to closing orders, which are as follows:

1. Yukon River, December 14, 1918.
2. Copper River, December 20, 1918.
3. Southeastern Alaska and between Capes Spencer and Newenham (all of Alaska south of Cape Newenham), Dcember 23, 1919. This combines the orders for (1) Wood and Nushagak, (2) Cook Inlet, Eyak Lake, Anan, and Naha, (3) Barnes Lake, Hetta, and Sockeye Creek, (4) Karluk, and (5) Bering River and Southeastern Alaska, making general provisions as follows:
   (1) East of Cape Spencer—
      (*a*) Prohibits all fishing in salmon streams, their tributaries and lakes.
      (*b*) Prohibits all fishing except by gill nets and purse seines within 500 yards of the mouths of streams.
      (*c*) Prohibits fishing by gill nets and purse seines within 200 yards of the mouths of all salmon streams; all appliances prohibited within 500 yards of the mouths of the Chilkat, Chilkoot, Anan, Hetta, Sockeye, and Naha streams.

(2) West of Cape Spencer. Prohibits fishing within 500 yards of stream mouths except—
  (*a*) Bering River. Fishing permitted below a point 800 feet northwest of the mouth of Gandil River.
  (*b*) Copper River. Same as in order promulgated December 29, 1917.
  (*c*) Karluk River. Fishing permitted up to within 100 yards of the mouth.
  (*d*) Ugashik River. Fishing permitted below a line 500 yards below mouth of King Salmon River.
(3) Prohibits driving salmon downstream or outside the protected areas.
(4) Permits taking salmon with rod, hand line, or spear for family use.
(5) Afognak Reservation regulations remain as before (presidential proclamation of December 24, 1892).
(6) Previous orders by Secretary of Commerce over waters herein are suspended.
(7) Order effective January 1, 1920.

Announcement, Department of Agriculture, Bureau of Biological Survey, June 25, 1921.

Renews requirements for permits in Aleutian Islands Reservation.

Department of Commerce Circular No. 251, seventh edition, January 4, 1921.

Closing orders revised.
Fishing in Bering River prohibited.
Fishing in Copper River prohibited after September 1, 1921.
Fishing in Kuskokwim River prohibited after September 1, 1921.

Department of Commerce Circular No. 251, eighth edition, April 22, 1922.

Alaska Peninsula Fisheries Reservation established by Executive order February 17, 1922. Regulations therefor issued on April 18, 1922:

Districts defined.
Permits to operate required; will be issued only to present operators; pack will be limited.
Transportation of fresh salmon from one district to another prohibited.
Taking of salmon for fox food permitted.
Closing orders simplified, as follows:
1, 2, and 3. Prohibit fishing in streams and within 500 yards of stream mouths except in Karluk and Ugashik Rivers, which remain as before.
4. Driving salmon downstream prohibited.
5. Permits taking salmon for local requirements.
6. Afognak reservation remains as covered by presidential proclamation of December 24, 1892.
7. Previous orders of Secretary of Commerce over waters herein specified are suspended.
8. Order effective January 1, 1922.

Department of Commerce Circular No. 251, ninth edition, January 9, 1923.

Alaska Peninsula Reservation regulations include limitation of gear and fishing operations, otherwise essentially the same as for 1922.

Southwestern Alaska Fisheries Reservation established by Executive order, November 3, 1922; regulations therefor promulgated on December 16, 1922.

Districts and zones defined; permits to operate required; pack, gear, and operations to be limited; taking of salmon for fox food permitted; purse seines prohibited; transportation of salmon between districts or zones outside the reservation prohibited; transfer of salmon from one plant to another prohibited in Cook Inlet and Kodiak districts.

Buying from natives permitted, but salmon so bought come under pack limitations; fishing prohibited in Chinik Inlet; special regulations for Bristol Bay:

1. Transportation between Nushagak and Kvichak-Naknek-Egegik district prohibited.
2. Fishing restricted to gill nets except that traps operated in 1922 may be used in 1923.
3. Limits size of nets and mesh.
4. Use of motor boats used in 1922 permitted in 1923, after which they are prohibited.
5. Fishing season for reds, June 26 to July 25.
6. Fishing for king salmon may begin before June 26.

Executive Orders Nos. 4020 and 4021, June 7, 1924.

Revoke orders establishing Alaska Peninsula and Southwestern Alaska Fishery Reservations.

Act of June 6, 1924. Department of Commerce Circular No. 251, tenth edition, June 21, 1924.

Section 1. Gives broad authority to Secretary of Commerce for conserving fisheries of Alaska; authority given to establish areas in which fishing may be prohibited or limited by (*a*) limitation of size and character of gear, (*b*) limitation of catch, and (*c*) limitation of time, means, methods, and extent of fishing. Such regulations must be of general application and exclusive rights to fish shall not be granted; act does not affect specified closed areas; prohibits importation of salmon taken during closed periods.

Section 2. Not less than 50 per cent escapement required in streams where counting weirs are maintained.

Section 3. Amends section 3 of the act of June 26, 1906; prohibits erection of dams, traps, etc., in waters less than 1,000 feet in width or within 500 yards of salmon stream mouths except at Karluk and Ugashik; prohibits setting of gear within 100 yards of other gear or to drive a trap within 600 yards laterally or 100 yards endwise of another trap.

Section 4. Amends section 4 of the act of June 26, 1906; prohibits commercial fishing in streams or within 500 yards of stream mouths, except at Karluk and Ugashik.

Section 5. Amends section 5 of the act of June 26, 1906; provides for a weekly closed season from 6 p. m. Saturday to 6 a. m. Monday and for the proper closing of traps during closed seasons.

Section 6. Provides penalties for violations of regulations.

Section 7. Repeals sections 6 and 13 of the act of June 26, 1906, authorizing reservations and providing penalties.

The acts of June 14, 1906 (prohibiting fishing by aliens), and section 2 (providing tax rebates for hatcheries operated), section 7 (prohibiting use of salmon after 48 hours), section 8 (prohibiting waste), section 9 (prohibiting false labeling), section 10 (requiring reports), section 11 (authorizing regulations), section 12 (authorizing expenditures to enforce), and sections 14, 15, and 16 (formal) of the act of June 26, 1906, are still in force.

The acts of June 14, 1906, and of June 6, 1924, and the given sections of the act of June 26, 1906, remain (February 14, 1928) unmodified, except for the act of June 18, 1926, which modifies section 1 of the act of June 6, 1924, and permits the taking of fish and shellfish for bait purposes at any time. Numerous regulations have been promulgated under the authority given by these acts, the details of which may be found in the various editions of circular No. 251 and in the various annual reports of the Alaska fishery and fur-seal industries. Most of the current regulations are in the fourteenth edition of this circular, issued December 12, 1927.

It is apparent from this summary that there were no drastic restrictions on the fishery up to the time of the establishment of the Alaska Peninsula and the Southwestern Alaska Fishery Reservations, and even such mild restrictions as were imposed by the two acts of 1906 were not really effective because of lack of funds for adequate enforcement. A few dozen stream guards and a few small patrol boats could do comparatively little along such an extended coast line as that of Alaska. Up to 1922, then, it is safe to say that the catch of salmon had not been affected materially by legal restrictions. It remains to be seen whether the restrictions imposed in the central and western districts under the authority of the reservations or those imposed so far under the authority of the act of 1924 are adequate to protect the salmon resources. If the theory we have expressed above is correct and the Alaska salmon fisheries have reached a point beyond the safe limit of exploitation, it is obvious that

effective conservation must result in a general lowering of the yield. It is but blinding our eyes to an obvious if unwelcome fact to expect a resource that is being conserved adequately and intelligently to yield as much as it would yield, *for a very limited period,* under conditions of unrestricted and intensive fishing. So far as the data for the entire pack serve to indicate, it does not appear that the present restrictions have reduced the strain on the resource materially. There was a gradual recovery after the depression of 1921, and the total pack of 1926 was the largest in the history of the industry. The drop in 1927 may have been due, in part, to an increased effectiveness in the regulations and their enforcement, but there was an unquestionable scarcity of fish in that year, so that the effect of the regulations would seem, at best, to have had a relatively small influence in reducing the catch. It may safely be predicted that effective conservation will mean, on the one hand, an increased stringency in the regulations and, on the other hand, a generally reduced level of the yield when compared with the general level that has been maintained for the past 10 years. This statement applies to the salmon resources of Alaska as a whole. The conditions as found in separate localities will be discussed below.

The analyses of data presented in this report have been limited by lack of time, but the data themselves are presented in full, so that it will be possible to make any additional analyses in the future that may seem desirable. A careful rechecking of the work has been impossible, and no doubt various errors have crept in. It is our hope, however, that none of these is great enough to affect our general conclusions seriously.

BRISTOL BAY

The available statistics for the early years of the salmon fishery in Bristol Bay are unsatisfactory in that they give records of the pack only, not of the catch, and in these all species are combined. Beginning with 1893, however, the reports of the special agents of the Treasury Department give the number of fish taken in the various localities. This was continued until 1904, when the collection of statistics by the Bureau of Fisheries began. Moser [1] gives the best available record of the pack during the years preceding 1893. Pracht [2] gives a record, substantially the same as that of Moser, of the pack for 1892, but does not allocate all of the pack to a definite district. Moser gives the pack for each cannery and the location of the cannery, so that it has been possible to rearrange his data for these early years into the form given in Table 1.

TABLE 1.—*Salmon pack in Bristol Bay, 1884 to 1892, by cases*

Year	Nushagak	Ugashik	Year	Nushagak	Ugashik
1884	400		1889	115,985	
1885	14,000		1890	118,390	
1886	48,822		1891	129,423	3,995
1887	72,700		1892	63,499	
1888	89,886				

[1] "Alaska salmon investigations in 1900 and 1901," by Jefferson F. Moser. Bulletin, United States Fish Commission, Vol. XXI, 1901 (1902), pp. 173-398. Washington.

[2] See report of special agent Max Pracht, dated Jan. 19, 1893, in Seal and Salmon Fisheries and General Resources of Alaska, Vol. II (1898), p. 385. Washington.

Table 2 gives, in detail, the catch of each species of salmon in each region of Bristol Bay and the total of each species for the whole of Bristol Bay. Four quite distinct districts are recognized in the Bristol Bay region, known by the name of the chief river in each district. The Nushagak district includes several important streams flowing into Nushagak Bay—the Nushagak, Igushik, Wood, and Snake Rivers. The Kvichak district includes, besides the Kvichak, the Naknek River and several smaller streams, which are virtually tributary to the Kvichak. The Egegik and Ugashik Rivers are distinct. The data for the years 1893 to 1903, taken from the reports of special agents of the Treasury Department, do not give the locality of capture but only the location of the cannery where the fish were packed. Although doubtless there is some danger of confusion in assuming that the fish canned in any one of the four districts of Bristol Bay were captured in that same district, we believe that the confusion is not likely to be serious and, therefore, have included the figures in our tables.

It is quite apparent, from a comparison of the catch figures with those for the pack, that in many cases the figures for the catch have been derived from those of the pack by multiplying the number of cases by a factor assumed to represent the number of fish per case. This is a source of some error, especially in the earlier data; but as most of the companies keep fairly reliable records of the number of fish per case the data are considered adequate for such analysis as we have made.

No records of the amount of gear used are available until 1904. Without doubt these records are much less satisfactory than are the records of the catch of fish and must be used with the greatest care. The records of gill nets in Bristol Bay seems especially unsatisfactory, as the records indicate a decided change in the average length of gill net during the history of the fishery. For several years the standard length has been 200 fathoms, but in former years the standard length was only about 100 fathoms. Again, in most instances the number of gill nets recorded in the statements submitted by the companies is apparently a record of the total number of gill nets on hand for the season and does not state the number of nets actually fished. No doubt the number of gill nets on hand bears a fairly definite and constant ratio to the number fished, but this is certainly a possible source of serious error. Furthermore, there are two kinds of gill nets in common use—a large-meshed net used for king salmon and a small-meshed net used primarily for reds. Some of the companies show the number of nets of each kind, while others do not segregate them, although there is no reason to suppose that they have not operated the same sort of gear. In spite of these and other weaknesses we have thought best to include in these tables the number of nets and traps operated, although we have not given the number of fathoms of nets used, as in some of the later tables. These data will serve to give some measure, however roughly, of the gross changes in the intensity of fishing, and even a rough measure of this is better than none.

TABLE 2.—*Salmon caught and fishing appliances used in Bristol Bay, 1893 to 1927, by districts*

Year	Coho	Chum	Pink	King	Red	Gill nets	Traps
Nushagak:							
1893	74,000			44,000	640,000		
1894	47,000			10,500	860,000		
1895	28,050			18,473	938,946		
1896	117,530			14,777	1,262,690		
1897	150,000		35,348	18,134	1,240,080		
1898	55,744		59,786	16,736	1,890,092		
1899	100,396		16,758	37,011	2,517,436		
1900			7,803	55,146	4,234,533		
1901	2,893		218,188	86,431	5,401,051		
1902	193,838		447,433	98,216	4,725,715		
1903	60,073		238,804	81,640	6,319,189		
1904	123,661	34,570	340,139	85,787	5,345,659	760	10
1905	65,568	34,933	183,153	96,929	7,387,935	496	9
1906	207,257	169,541	1,545,585	105,058	5,427,512	518	13
1907	129,065	415,372	344,148	104,157	2,627,351	421	12
1908	103,013	415,369	392,797	69,175	6,092,031	495	10
1909	80,513	356,621	94,119	108,311	4,906,635	394	11
1910	139,200	206,220	430,369	86,433	4,469,755	431	8
1911	129,971	245,795	79,764	103,806	2,957,073	492	10
1912	195,083	341,059	1,516,039	87,489	3,993,428	758	8
1913	66,640	265,184	418,015	67,656	5,409,933	871	8
1914	81,434	541,690	390,776	88,693	6,457,815	977	8
1915	117,172	444,146		116,387	5,904,862	1,163	8
1916	293,210	1,173,914	638,607	81,921	3,744,551	1,078	8
1917	62,260	303,620		74,316	5,847,239	1,263	7
1918	108,576	638,537	583,981	46,386	6,296,702	1,224	7
1919	46,687	170,501	13	93,778	1,477,336	1,096	7
1920	145,510	208,601	1,095,318	97,937	2,682,056	1,172	3
1921	84,564	235,763	15	71,048	3,717,284	1,057	
1922	159,783	425,572	222,100	60,924	3,408,358	952	3
1923	9,274	152,161		56,397	1,921,874	760	
1924	39,787	152,235	101,031	53,532	2,168,154	405	
1925	16,591	96,266	18	68,596	3,903,125	625	
1926	12,947	175,295	283,876	54,856	4,022,328	450	
1927	137	137,525	3	68,044	657,467	444	
Kvichak:							
1893					100,000		
1894					262,550		
1895				1,452	413,651		
1896	127,538			2,524	487,630		
1897				1,247	1,410,287		
1898				1,845	2,241,113		
1899				1,248	1,649,127		
1900				2,342	3,208,263		
1901	1,286		13,000	15,245	3,622,638		
1902			46,752	6,755	6,038,386		
1903				3,032	7,516,329		
1904	5,250	1,138	35,593	11,406	5,856,442	351	5
1905	7,000	4,946	32,200	17,470	6,773,275	317	5
1906		24,000	319,563	33,574	4,954,905	123	4
1907		45,458		28,495	6,782,072	307	3
1908		5,024	2,570	17,565	9,088,285	327	3
1909		1,872	28	17,084	9,533,337	357	4
1910		93,840	219,330	13,629	6,336,382	395	3
1911		89,688	12,000	7,951	4,587,344	525	4
1912	10	11,149	145,536	9,570	13,821,905	584	2
1913	2	5,830	4,524	5,648	13,691,550	655	2
1914	17,508	9,662	167,423	10,657	12,584,809	652	
1915	13,271	129,130	124,385	29,392	7,156,488	638	
1916	288	259,013	45,164	20,934	11,551,086	792	
1917	3	45,997	37,082	16,155	15,762,582	1,076	
1918		94,036	35,322	39,540	14,219,530	1,233	
1919		25,251	439	106,705	4,929,761	1,305	
1920	3,900	188,469	950,098	27,791	5,275,140	1,146	
1921		102,157	924	19,540	9,690,857	984	
1922	180	57,309	38,766	11,225	15,636,907	853	
1923		17,319	3	9,681	14,361,488	1,066	
1924	152	113,731	2,025	17,715	6,813,083	1,080	
1925	5	110,396		26,149	3,355,293	1,228	
1926	350	130,644	4,165	18,933	12,717,504	1,001	
1927	8	44,489		14,298	8,917,893	910	

TABLE 2.—*Salmon caught and fishing appliances used in Bristol Bay, 1893 to 1927, by districts*—Con.

Year	Coho	Chum	Pink	King	Red	Gill nets	Traps
Egegik:							
1893							
1894							
1895					54,321		
1896					20,400		
1897				257	203,458		
1898				537	247,842		
1899					284,650		
1900				41	307,574		
1901				616	427,886		
1902					403,444		
1903			2,700	264	781,038		
1904			2,691		136,759	45	
1905			49,000		140,000	15	
1906			14,000	400	238,000	15	
1907		20,925		1,410	481,578	41	
1908		29,197		1,213	781,131	44	
1909		8,917	7,132	2,891	840,674	47	
1910		3,002	2,430	801	619,001	50	
1911		3,416		460	1,158,176	67	
1912		2,419	4,900	202	1,455,247	57	
1913	165		2,954	254	902,728	56	
1914		1,064	6,717	405	897,767	52	
1915		1,591	10,413	510	1,217,252	62	
1916		7,500		365	1,578,862	71	
1917		5,726		143	1,856,600	89	
1918		6,663		427	1,818,217	82	
1919		2,627		198	607,688	109	
1920	264	5,503	21	441	498,949	67	
1921		8,634		566	1,136,670	103	
1922	21	27,631	28,929	936	2,529,129	115	
1923		7,169		394	1,116,057	100	
1924	440	6,042		126	874,019	94	
1925		9,321		833	212,987	98	
1926		1,017		331	1,522,721	72	
1927	1	5,413		735	1,285,059	84	
Ugashik:							
1893					200,000		
1894					112,850		
1895					65,219		
1896					229,020		
1897				259	463,698		
1898				142	548,793		
1899					661,524		
1900				778	796,965		
1901				3,755	769,002		
1902			8,080	4,118	1,640,973		
1903				1,570	1,703,536		
1904	558	1,600	19,723	760	564,492	105	
1905	5,733	19,105	26,662	2,456	532,779	75	
1906		60,000	22,797	4,162	203,014	57	
1907		26,972		3,615	302,402	26	
1908		10,309	3,890	2,056	272,355	46	
1909		10,728		2,203	218,237	27	1
1910		7,156		892	168,471	27	1
1911		8,967		946	112,521	47	
1912			14,167	467	425,763	48	
1913		13,704		691	577,615	79	
1914		14,531	82	1,209	254,716	65	
1915		18,212		1,739	509,076	70	
1916		49,196		1,904	647,422	60	
1917		879		531	1,047,111	66	
1918		6,588		695	756,206	64	
1919		6,095		1,273	146,590	52	
1920	3,630	31,765		1,181	441,770	86	
1921		8,777		828	1,135,265	62	
1922		4,883		623	1,863,638	84	
1923		8,253		541	782,545	130	
1924		13,455		290	446,810	77	
1925		15,825		1,870	438,103	118	
1926		19,062		484	1,151,541	81	
1927		8,376		769	211,409	78	

TABLE 2.—*Salmon caught and fishing appliances used in Bristol Bay, 1893 to 1927, by districts*—Con.

Year	Coho	Chum	Pink	King	Red	Gill nets	Traps
Total:							
1893	74,000			44,000	940,000		
1894	47,000			10,500	1,235,400		
1895	28,050			19,925	1,472,137		
1896	245,068			17,301	2,099,740		
1897	150,000		35,348	19,897	3,317,523		
1898	55,744		59,786	19,260	4,927,840		
1899	100,396		16,758	38,259	5,112,737		
1900			7,803	58,307	8,547,335		
1901	4,179		231,188	106,047	10,220,577		
1902	193,838		502,265	109,089	12,808,518		
1903	60,073		241,504	86,506	16,320,092		
1904	129,469	37,308	398,146	97,953	11,903,352	1,261	15
1905	78,301	58,984	291,015	116,855	14,833,989	903	14
1906	207,257	253,541	1,901,945	143,194	10,823,431	713	17
1907	129,065	508,727	344,148	137,677	10,193,403	795	15
1908	103,013	459,899	399,257	90,009	16,233,802	912	13
1909	80,513	378,138	101,279	130,489	15,497,883	825	16
1910	139,200	310,218	652,129	101,755	11,593,609	903	12
1911	129,971	347,866	91,764	113,163	8,815,114	1,131	14
1912	195,093	354,627	1,680,652	97,728	19,696,343	1,447	10
1913	66,807	284,718	425,493	74,249	20,581,826	1,661	10
1914	98,942	566,947	564,998	100,964	20,195,107	1,746	8
1915	130,443	593,079	134,798	148,028	14,787,678	1,933	8
1916	293,498	1,489,623	683,771	105,124	17,521,921	2,001	8
1917	62,263	356,222	37,082	91,145	24,513,532	2,494	7
1918	108,576	745,824	619,303	87,048	23,090,665	2,603	7
1919	46,687	204,474	452	201,954	7,161,375	2,562	7
1920	153,304	434,338	2,045,437	127,350	8,897,915	2,471	3
1921	84,564	355,331	939	91,982	15,680,076	2,206	
1922 [1]	159,984	515,915	289,795	74,020	23,632,077	2,004	3
1923	9,274	184,902	3	67,013	18,181,964	2,056	
1924	40,379	285,463	103,056	71,663	10,302,066	1,656	
1925	16,596	231,808	18	97,448	7,909,508	2,069	
1926	13,297	326,018	288,041	74,604	19,414,094	1,604	
1927	146	195,803	3	83,846	11,071,828	1,516	

[1] Includes 520 chums, 312 kings, and 194,045 reds not given above.

We may now examine these data in an attempt to answer several important and more or less interrelated questions: 1. Do the trends of the four districts vary independently or together? In other words, has the development of the fishery in the four districts been parallel? 2. Do the deviations from the trends, the yearly fluctuations in abundance, vary independently or together? 3. What is the present state of the fishery in each of the four districts? We shall consider the catches of the various species separately, and as the red salmon is by far the most important species in Bristol Bay we shall discuss it first.

RED SALMON

Figures 3 to 6 present graphically the data for red salmon given in Table 2 and in addition the trends of the catches. These trends are five-year moving averages and were calculated in the usual manner. The value of such a trend for any given year is determined as the average of the catch for that year, the two preceding years, and the two succeeding years.[3] The trends alone are shown in Figure 7 on a proportional (logarithmic) scale, so that the relative changes in the four districts may be more readily compared.

[3] Principles and Methods of Statistics. By R. E. Chaddock. Page 310 and following. Houghton Mifflin Co., 1925.

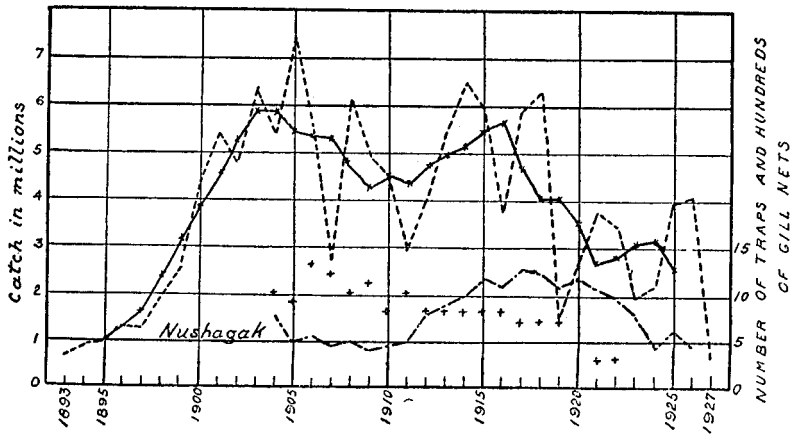

FIG. 3.—Catch of red salmon at Nushagak. Dotted line, catch; solid line, trend of catch; crosses, number of traps; dots and dashes, number of gill nets

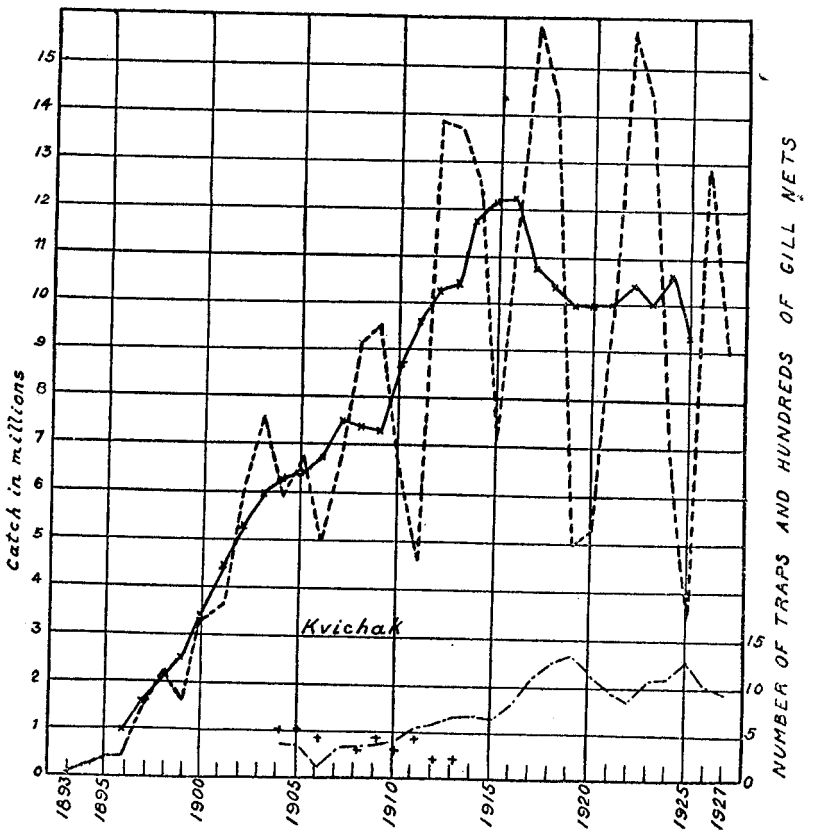

FIG. 4.—Catch of red salmon at Kvichak. Dotted line, catch; solid line, trend of catch; crosses, number of traps; dots and dashes, number of gill nets

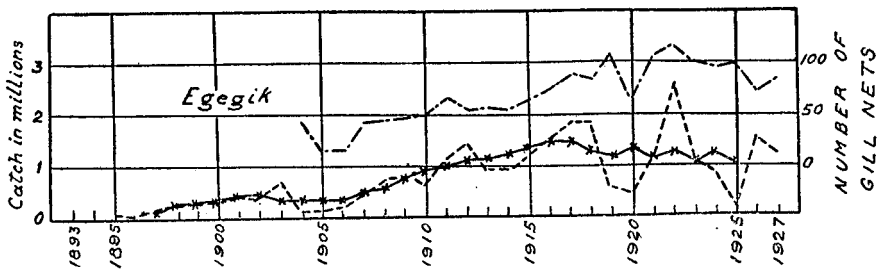

FIG. 5.—Catch of red salmon at Egegik. Dotted line, catch; solid line, trend of catch; crosses, number of traps; dots and dashes, number of gill nets

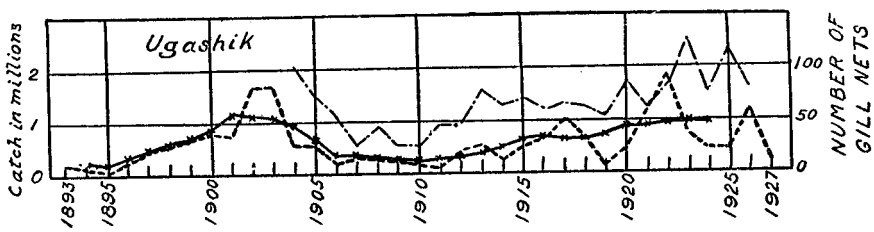

FIG. 6.—Catch of red salmon at Ugashik. Dotted line, catch; solid line, trend of catch; crosses, number of traps; dots and dashes, number of gill nets

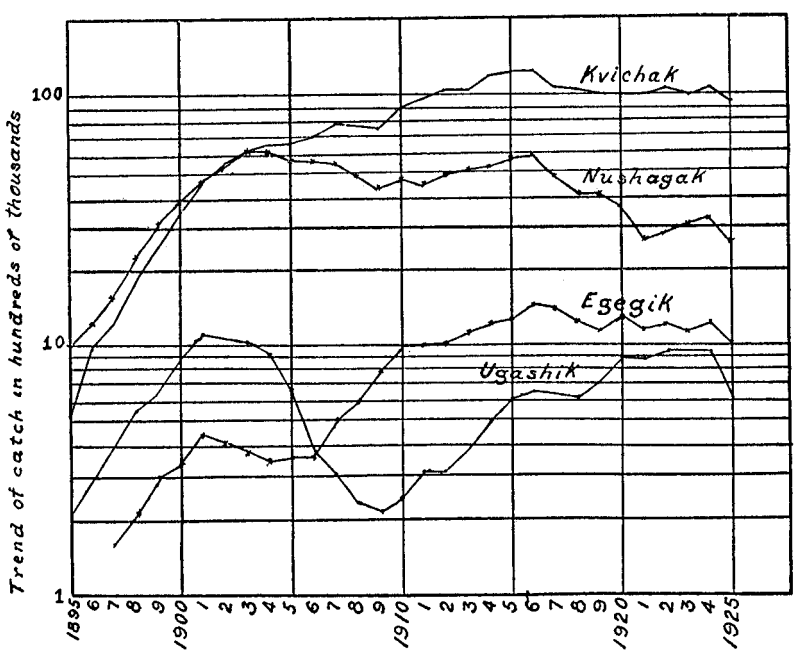

FIG. 7.—Trends of the catches of red salmon in the four districts of Bristol Bay on a logarithmic (proportional) scale

The trends in all four districts show a constant and fairly regular rise during the first 10 years or so (up to 1903 or 1904), which is indicative of the gradual development of the fishery during that period. In the Nushagak district the trend remained generally high (near the 5,000,000 level) for the next 15 years (1902 to 1916) then fell off sharply. Since 1920 it has remained at about the 3,000,000 level. This drop was even more sharply marked than shown by the trend, as may be seen by reference to Figure 3. This shows that the change to a lower level came very suddenly and without warning in 1919. In this case the process of smoothing, by which the trend was obtained, has obscured the very sharp drop in the general level. It is of the greatest importance to those interested in conservation to note the suddenness with which the catch sank to this lower level. It seems impossible to ascribe this phenomenon to any cause other than depletion—to overfishing in the 15 years or more that preceded the drop. This is exactly the sort of thing that biologists have warned could be expected, the logical explanation being that the catch was held up, in spite of real depletion, by an increased intensity in fishing, until finally the break came and severe depletion became apparent all at once. It is interesting to note, in accordance with the hypothesis advanced above that wide fluctuations are a mark of a too intensive fishery, the decade and more that preceded the year 1919 was marked by wide fluctuations in the total catch. The question immediately arises, is the present intensity of fishing on the Nushagak side too great for the lowered level of abundance that is now established? Unfortunately the problem is complicated by a number of factors, which it is impossible to evaluate with the available data. During the period of heavy catches (from 1902 to 1918) there was a considerable increase in the number of gill nets but a decrease in the number of traps, and to what extent one offset the effect of the other we can not know. Neither do we know how the intensity of fishing has been modified by changes in the length of gill nets and the length of time each gill net was actually in the water. It would appear that a reduction in gear from 8 traps and over 1,000 gill nets to no traps and about 500 gill nets was more of a change than that of a catch of approximately 5,000,000 to one of approximately 3,000,000, but this is by no means certain. Furthermore, the former intensity of fishing was unquestionably too great, but just how excessive it was we have no way of telling. With the greatly decreased abundance it may well be that the present intensity is still too great and that further depletion will result. The extremely poor catch of 1927 certainly would indicate that the intensity of fishing had not been reduced sufficiently in 1921, 1922, and 1923 to permit an adequate escapement, as the red salmon of Bristol Bay are largely 4, 5, and 6 years old; and even though the reduction in gear has been sufficient to permit the maintenance of the catch at the 3,000,000 level, should there not be a sufficient reduction in the catch to permit the runs to increase to something approaching their former abundance? Unquestionably the general tendency on the Nushagak has been downward, and if the depletion should continue at the present rate we may anticipate that within the next two or three decades the formerly magnificent runs here will be so reduced as to be worthless commercially.

None of the other districts of Bristol Bay show such sudden and serious depletion as does the Nushagak. While the Nushagak catch reached its maximum size about

1903, the Kvichak catch continued to increase, and the trend reached its peak in 1915 and 1916, since when there has been a material drop, although this is by no means as marked as in the case of the Nushagak catch. The trend at Egegik has been much the same as that in the Kvichak, with the exception of a drop in the years 1902 to 1906. The peak of the Egegik trend came in 1916, since which time the trend has slowly but unmistakably declined. The Ugashik trend is quite different, rising to its highest peak in 1901 and then falling gradually until 1909, since which time it showed a gradual but steady recovery, which was broken sharply in 1925. Without much doubt the early drops in the trends at Ugashik and Egegik were due to reduced intensity of fishing, as shown by corresponding decrease in the number of gill nets. For some reason the early development of the fishery in these two districts was arrested for a time but was resumed later.

It is apparent that there has been a certain amount of independence in the trend of the red salmon fisheries in the four districts. With the possible exception of the Ugashik, however, they all show a present tendency to drop. In the case of the Ugashik it would appear, from the raw data presented in Figure 6, that this stream, too, is entering a period of decreased productivity. While the depletion of the Nushagak is much more pronounced than in the other districts, it is quite evident that the red-salmon catch in the entire Bristol Bay region is distinctly on the decline.

We will now examine the short-time fluctuations, as distinguished from the long-time fluctuations, or "secular" changes indicated by the trends. We have discussed above the general importance of a knowledge of the character of these short-time fluctuations. To be more explicit, it is important that we know (1) whether or not there is any regularity in these short-time changes—whether they occur in cycles or not; (2) what the interval of the cycles is, if the changes are cyclic in character; (3) whether there are sudden or progressive changes in the nature of the fluctuations, and (4) whether there is any correlation in the fluctuations in different streams.

Our interpretation of the facts disclosed by an analysis of the fluctuations will depend, as in the case of any statistical analysis of such data, upon an understanding of the biological and economic factors that may affect them. We are concerned here chiefly with the discovery of the facts about the fluctuations in the catch of salmon and must leave the consideration of the true causative factors for future treatment.

The study of the short-time fluctuations has been based on the percentage deviation of the yearly catch from the trend or moving average by fives. In this method, adequately described by Chaddock (loc. cit.), the percentage deviation for any year is the algebraic value of the catch minus the trend, divided by the value of the trend. When the catch is greater than the trend, the deviations have a positive value and a negative value when less than the trend. Such treatment does two important things to our data—it removes the effect of the long-time, secular fluctuations, which might accentuate or destroy any correlation that might exist between two series of data, and it makes it possible to compare more fairly and more directly the fluctuations at very different levels of abundance, whether in different streams or in the same stream at different periods. For example, if the trend in one series of data was at 1,000,000 and in another series of data was at

10,000,000, a deviation of 100,000 in the first case would be just as significant as a deviation of 1,000,000 in the second case.

In our analysis of these fluctuations we have not made use of the data collected previous to 1904. The Bureau of Fisheries began the collection of statistics in that year and it seemed best to confine this analysis to data obtained by a single agency. Furthermore, as we pointed out above, the fishery apparently became fully developed about this time, and it is quite probable that the fluctuations during the period of rapid growth were largely obscured by great changes in the intensity of fishing.

The use of deviations from a moving average by fives has one disadvantage, in that two years are lost at each end of the series; thus, our series of data extends from 1904 to 1927, both inclusive, but our trend of moving averages extends only from 1906 to 1925. It would be possible, of course, to use some sort of a straight-line trend or to extend more or less arbitrarily the trend of moving averages so as to make use of the extreme values, but we have not thought it advisable to do either. The straight-line trend certainly does not fit some of the localities, and any extrapolation of the line of moving averages will introduce a personal element, which we have been anxious to avoid.

Figure 8 shows the deviations from the moving average for each of the four districts in Bristol Bay, and in Table 3 we present various coefficients of correlation (Pearsonian), which we have calculated and which measure the degree of association in the fluctuations at 4, 5, and 6 year intervals. We have made some estimates of the correlation between fluctuations at 3 and 7 year intervals, also, but these were invariably without significance, and we have therefore omitted them from consideration.

TABLE 3.—*Coefficients of correlation between catches of red salmon at intervals of 4, 5, and 6 years for the four districts in Bristol Bay and Karluk River*

Locality	Interval		
	4 years	5 years	6 years
Nushagak	+0.624±0.103	−0.090±0.159	−0.538±0.133
Kvichak	+.468± .131	+.786± .067	−.066± .172
Egegik	+.383± .143	+.466± .136	+.289± .165
Ugashik	+.466± .132	+.716± .085	−.290± .164
Karluk	+.297± .108	+.581± .080	+.028± .122

Examination of Figure 8 shows that in all of the districts of Bristol Bay there is a strong tendency toward a repetition of conditions at intervals of four or five years. The extent to which the catches are correlated with the catches of 4, 5, and 6 years earlier or later is shown in Table 3. For purposes of comparison we have added to this table a similar series of correlation coefficients for the run of red salmon in the Karluk River. While the exact significance of an association between catches at four or five year intervals can not be stated definitely, it seems more than probable that it is indicative of the prevailing age groups in the run in question. In the case of the Karluk River we know definitely that a large percentage of the fish are in their fifth year when they return to spawn. This is reflected in the relatively high coefficient of correlation between catches at five-year intervals—over seven times its probable error—and

statisticians generally agree that a coefficient that is three times its probable error is significant of some degree of association. It is possible, of course, that some factors other than a predominance of five-year fish has caused this high correlation between catches at five-year intervals, but we have no suggestion to make as to what these factors may be.

In the Nushagak district there is an undoubtedly significant correlation between the size of the catches at four-year intervals; the coefficient is over six times its probable error. It is apparent from the graph, however, and also from the work sheets made in the process of calculating the correlation coefficients, that the correlation between the catches at four-year intervals is due mainly to an exceptionally close association, which has been maintained in comparatively recent years since about 1914. Previous to this time there was much more of a tendency toward correlation in catches at five-year intervals, but the strong tendency toward correlation at four years, which has prevailed recently, has, in considering the entire series, entirely outweighed the earlier condition. The correlation between catches at five-year intervals in the Nushagak district is not significant, the coefficient being less than its probable error and, as would necessarily be the case with a strong correlation at the four-year interval, the correlation at the six-year interval is significantly negative. Such a negative coefficient of correlation means that in general a good catch in a

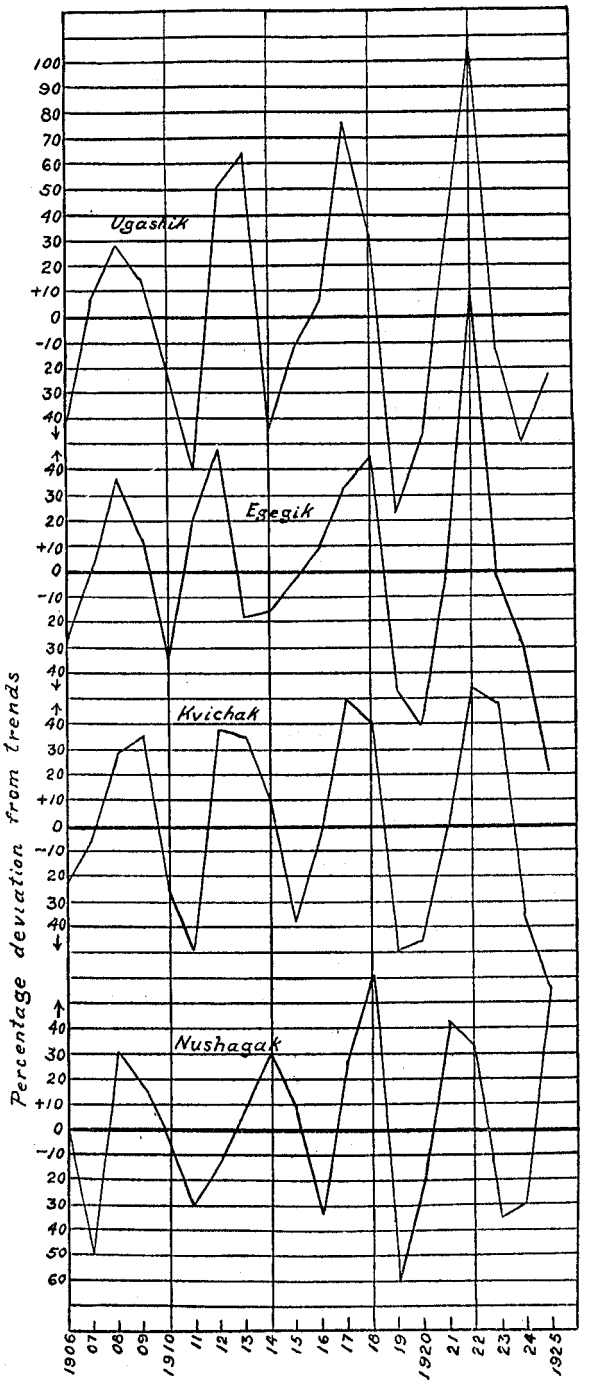

FIG. 8.—Percentage fluctuations from the trends of the catches of red salmon in the four districts of Bristol Bay

given year will be followed by a poor catch six years later, and vice versa. If, as we have indicated, there has actually been a change in the Nushagak district from an association between catches at five-year intervals to an association at four-year intervals it is most interesting, and certain possible explanations may be suggested. Most of the fishing in the entire Bristol Bay region has been carried on by gill nets, and it is generally supposed that this type of gear has a tendency to select the larger individuals in a run. With such a selective agency at work it is possible that a race or several races of predominantly large, five-year fish might be so reduced in numbers as to disappear almost entirely from the commercial catch. It may have been that this occurred in the Nushagak district quite suddenly in 1919, when the run at Nushagak was abnormally low. It is possible, though hardly probable, that the selection of the larger and older fish by the gill nets has operated to change the predominant ages of all the races that make up the Nushagak catch from five to four years. In any event it does not seem likely that this high degree of correlation between the catches at four-year intervals is due merely to the operation of chance fluctuations.

In the case of the other three districts in Bristol Bay the highest correlation occurs between catches at five-year intervals. In the Kvichak and Ugashik catches there is also a low but probably significant correlation at four-year intervals but there is no significant correlation at six-year intervals. In the discussion of the cycles at Nushagak we pointed out that a significant correlation between catches at any given interval of years was strong indication that the prevailing age of the fish was of the same number of years. If this be true, the data herewith presented would indicate that a considerable percentage of the Kvichak, Egegik, and Ugashik red salmon are in their fifth year. We find a similar degree of correlation between catches at five-year intervals at Karluk, where the fish are known to be chiefly 5 years old; and the maintenance for many years of a four-year cycle on the Frazer River, where the fish were predominantly 4 years old, is well known. We wish to emphasize again the fact that no correlation of this sort can be expected to be very high, not only on account of inaccuracies in the data but because of the presence of more than one age group in the catches, fluctuations in the relation of escapement to catch, possible fluctuations in the percentage of fish of different ages coming from different broods, fluctuations in the efficiency of spawning and the rate of mortality at different stages in the life history, and various other factors.

TABLE 4.—*Coefficients of correlation (r) between catches of red salmon in the four districts of Bristol Bay*

Localities	r	Localities	r
Nushagak and Kvichak	+0.305±0.137	Kvichak and Egegik	+0.738±0.069
Nushagak and Egegik	+.209± .144	Kvichak and Ugashik	+.822± .049
Nushagak and Ugashik	+.453± .120	Egegik and Ugashik	+.720± .073

Figure 8 shows clearly that there is a distinct tendency for the catches in the four districts to vary together, although at times, and especially in certain districts, the catches vary independently to a considerable degree. The extent of the correlation

between all possible pairs of districts is presented in Table 4. It is apparent from a consideration of these values that there is a high degree of association between the catches in the three districts on the eastern shore of Bristol Bay at Kvichak, Egegik, and Ugashik, but the correlation between any of these districts and Nushagak is distinctly lower; in fact, so low that the correlation of Nushagak with Kvichak and Egegik is without significance. The correlation between Nushagak and Ugashik is significant of some slight degree of association but is less than four times its probable error. On the whole, it appears that the fluctuations at Nushagak are independent of those on the eastern side of the bay. The correlation between the catches at Kvichak, Egegik, and Ugashik is so marked, however, as to indicate some causal relationship, and it seems more than probable that it is due to the catching in the Egegik and Ugashik districts of fish bound for the Kvichak district. This possibility was pointed out by Gilbert and O'Malley in their report on the salmon fishery in central and western Alaska.[4] It may also be due, in part at least, to fish being reported as taken in one district when actually they were caught in another and were brought into the district from which reported for canning; or it is possible that there is enough "straying" from the parent stream to cause the catch in near-by streams to fluctuate together. This last possibility does not seem likely, however, as one would suppose that any such straying might affect the correlation between the catches at Nushagak and the other streams as well as between the other three streams.

We have mentioned above that an increase in the size of the fluctuations may be an indication that the fishery has been developed to the danger point or that depletion has occurred already. This hypothesis has also been advanced by Gilbert and O'Malley (loc. cit.), who, in discussing the situation in the Kvichak region of Bristol Bay, say: "Other river basins have been watched during the progress of depletion. The sequence of events is always the same. Decreased production is [accompanied] by increase of gear. Fluctuations in the seasons become more pronounced. Good seasons still appear in which nearly maximum packs are made. But the poor seasons become more numerous. When poor seasons appear, no attempt is made to compensate by fishing less closely. On the contrary, efforts are redoubled to put up the full pack. The poorer years strike constantly lower levels, until it is apparent to all that serious depletion has occurred." Figure 8 shows, with great clearness, that the amplitude of the fluctuations in all districts of Bristol Bay has been increasing with considerable regularity, thus corroborating the evidence given by the trends of general depletion throughout Bristol Bay.

Such cyclic fluctuations in the abundance of salmon are extremely interesting biological phenomena, and a knowledge of them is of great practical importance to the industry and to an adequate conservation program. It may not be out of place here, therefore, to speculate briefly upon some of the characteristics of such fluctuations. It seems safe to assume that in a state of nature the abundance of any race of salmon would be constant from year to year, except as modified by environmental conditions, and that the level of abundance will be at the maximum capacity of the waters occupied by the race. If under these conditions unusually favorable circum-

[4] Special Investigation of Salmon Fishery in Central and Western Alaska. By C. H. Gilbert and Henry O'Malley. *In* Alaska Fisheries and Fur Industries in 1919, by Ward T. Bower. Appendix IX. Report, U. S. Commissioner of Fisheries for 1919 (1921). Bureau of Fisheries Document No. 891, pp. 143-160. Washington.

stances should operate to increase the survival (and therefore the spawning run) in any year, the effect of such an increased run would not necessarily be felt in future years, as the area occupied by the race will not, in general, accommodate a population greater than the normal maximum capacity. On the other hand, if the general level of abundance be reduced materially by fishing, this level will be below the potential capacity of the area, and then an increase in abundance in one year can have a very definite effect upon the future generations and would start a series of years marked by good runs separated by years of ordinary runs. The interval between the good years would be determined by the prevailing age at maturity of the race in question—more particularly, perhaps, by the prevailing age of the females. Somewhat similar results would follow the occurrence of a year in which survival was reduced. Under natural conditions the abundance of fish resulting from a poor year would be below the normal capacity of the area, and we may suppose that the race would react by an increased survival of the progeny of the reduced spawning run, so that the size of the resultant spawning runs would tend to approach the normal level. It seems possible that the effect of a very poor year might be felt for one or two generations while building up to the normal level, in contrast to the effect of an unusually good year, which, on account of the limitation imposed by the capacity of the occupied area, could not greatly affect the future runs. Under conditions of exploitation, however, a poor year will tend to be perpetuated, just as in the case of a good year, but for a different reason. The perpetuation of a good year is dependent upon what we may term the elasticity of the race—the tendency to approach the normal level of abundance; but the perpetuation of a poor year will depend mainly upon the continuous application of a fishing effort sufficient to keep the spawning escapement down to a low level. There is no doubt that fishing operations ordinarily operate so that the spawning escapement in good years is better in proportion than in poor years, which is just the reverse of what sensible conservation would call for. On the other hand, it seems probable that the lower the actual level of abundance the stronger the tendency of the race to resist further lowering and the greater the tendency to return toward the normal level of abundance. In other words, as the level of abundance drops there is a tendency toward an increased survival rate. This is well illustrated by the present situation on the Karluk River. It has been shown [5] that the present production from the spawning escapements is approximately 300 per cent; that is, for each spawning fish three adults may be expected to return in future years. Under natural conditions the production in general is 100 per cent, of course. This increased percentage of production is exactly what we would expect in the case of a depleted run such as that in the Karluk; but however strong this tendency toward an increased percentage productiveness at the lower levels of abundance may be, it is impotent in the face of intensive fishing. It may operate to retard the depletion of the poor years, but without some relief from intensive fishing it can not rebuild poor years into good ones or even average ones.

The chief contention in the above argument is to the effect that cyclic fluctuations are associated especially with the exploitation of a fishery, and that under natural conditions such fluctuations would not be so conspicuous. However, there

[5] Investigations Concerning the Red-Salmon Runs to the Karluk River, Alaska. By Charles H. Gilbert and Willis H. Rich. Bulletin, U. S. Bureau of Fisheries, Vol. XLIII, 1927, Part II, pp. 1–69, 34 figs. Washington, 1927.

is the possibility that cyclic fluctuations in the abundance of fish might follow cyclic changes in environmental conditions, such as those that have been shown to accompany the periodicity of sun spots;[6] but it does not seem likely that such a factor could cause such cycles as we observe in the salmon. We have also the remarkable four-year cycles of the Frazer River sockeyes, which existed for an unknown number of years before the white man came and recorded the phenomenon. In this case, as is well known, the tremendous runs that came every fourth year consisted of two races (or groups of races), one spawning in the lakes tributary to the lower course of the Frazer and the other in the higher lakes above the Frazer River Canyon. The first race entered the river yearly, but it was only every fourth year that the second and much more important race entered the river. The latter was a race in which 4-year fish (especially among the females) predominated to a remarkable extent.[7] The last "big" year was in 1913, and in that year a slide in the Frazer River Canyon prevented the ascent of the fish to the upper spawning grounds, the race died out, and the four-year cycle became virtually obliterated. One can hardly doubt that originally the runs of salmon in the Frazer were "big" every year; that every year saw the upper spawning grounds as well covered with spawning fish as they were in the "big" years that we have known. At some more or less remote prehistoric time, however, a slide probably blocked the river for a period of three years and destroyed the race that spawned in the upper lakes. In the fourth year the obstruction was removed and the fish were able to proceed as usual to the spawning grounds. On account of the great predominance of 4-year fish in this race this one year was perpetuated, perhaps for centuries, until the disaster of 1913. In this case the most remarkable cycle known developed under natural conditions, quite unaffected by exploitation, but we have a sufficient understanding of the circumstances so that an adequate explanation can be given. Under ordinary circumstances it seems probable that marked cycles occur most commonly under the conditions resulting from exploitation.

Cycles may become established by the occurrence of various unusual conditions, such as an expecially large or small spawning escapement or the effect of environmental conditions that make for a high or low rate of mortality during the life of a brood. Such conditions may be expected to occur only occasionally and at irregular intervals, and the effect will tend to be perpetuated more or less strongly in future generations by the dominance of certain age groups in the race in question. If a single age group is dominant the effect may last indefinitely, but if two or more age groups occur in fairly large percentages the effect will be spread out gradually and the cycles will lose their sharpness and become obscured, or they may be destroyed entirely or modified by the incidence of another set of unusual conditions, which in turn may give rise to an entirely different cycle. Overfishing, especially at critical times, may be an important determinant of such cycles, although undoubtedly they are frequently caused by natural conditions about which we know very little at present.

[6] Climatic Cycles and Tree Growth. By A. E. Douglass. Carnegie Institution of Washington, Publication No. 289. Washington.

[7] Contributions to the Life History of the Sockeye Salmon. Nos. 1 to 9. By Charles H. Gilbert. Reports of the Commissioner of Fisheries for British Columbia, 1912 to 1923.

In our Bristol Bay data we can see occasional evidence of sudden, unexplained fluctuations, which apparently have been reflected in later years. Perhaps the best example of this is the sudden drop of 1919, which affected all the districts. The fourth and fifth years before 1919 had been exceptionally good on the Nushagak. On the Kvichak the fourth preceding year had been below average but the fifth had been excellent, and we have shown above that the highest correlation between catches in this district is at five-year intervals. So far as the evidence of previous catches goes, therefore, there was no reason to anticipate a poor catch in 1919. Whatever the factors that caused this sudden fluctuation, the effect has been reflected in a poor catch on the Nushagak in 1923 and again in 1927 and on the Kvichak in 1924. It seems probable that we have witnessed here the operation of just such factors as we have been discussing, and that for some unknown reason one or more of the spawning runs that were the parents of the run of 1919 failed to produce the usual number of adult fish, and that this sudden fluctuation has tended toward the production of cycles. The situation is extremely complex, of course, and we have no way of telling how long these fluctuations (which appear to have been fixed by the poor run of 1919) will persist. They may be distinguishable for several cycles, or they may have been obliterated already by factors about which we know nothing and the effect of which we will not see until it becomes apparent in a modified run.

With the data at hand we do not feel that it is possible to make any reliable prophecy as to future runs. The probable errors of all our measures are large, and there is always the chance that unusual circumstances may intervene to upset any estimate that may be made. At present we know virtually nothing about these unusual circumstances in the Bristol Bay region. Apparently they have operated in former years to modify the runs very materially, and there is no reason to suppose that they may not operate again and just as unexpectedly as they have in the past. In spite of all this it seems desirable to review what evidence we have and to point out certain indications as to the future.

In the Nushagak region we have had a general decline in abundance, as indicated by the trend. It has been shown also that the short-time fluctuations here are at four-year intervals at present. The run of the coming season (that of 1928) should bear a general relationship to the run of 1924, therefore, which was one of the poorest in recent years. The run of 1923 on the Nushagak River was exceedingly poor also, so that we can expect no marked effect in 1928 due to five-year fish derived from that year. On the other hand, we have some evidence that in spite of a poor catch the spawning escapement of 1924 was better than usual. The report of observers on the spawning grounds in Wood River states that the escapement to that river was "the most satisfactory for the last several years." [8] Nothing is known, however, of the escapement to the other spawning regions in the Nushagak district. Except for this meager evidence of a good spawning escapement, then, all indications point toward an unfavorable year at Nushagak, possibly as bad as 1927. Knowing the present depleted condition of this district, it would seem to be the part of wisdom to reduce the intensity of fishing as far as possible. Even if a fairly good run should develop, it does not seem at all likely that it will approach the magnitude of the runs

[8] Alaska Fishery and Fur-Seal Industries in 1924. By Ward T. Bower. Appendix IV, Report, U. S. Commissioner of Fisheries for 1925 (1926), p. 99. Washington.

previous to 1919, and a distinctly larger spawning escapement certainly is called for if further depletion of this region is to be prevented.

On the eastern side of Bristol Bay the situation does not appear to be so serious. It seems useless to try to give separate consideration to the Kvichak, Egegik, and Ugashik districts on account of the high degree of correlation, which we have shown exists between the catches in these three localities. If the correlation in catches at five-year intervals holds for 1928, we would expect the run of the coming season to be correlated largely with that of 1923, which was a very good year in the Kvichak district and about average in both Egegik and Ugashik. The year 1922, from the runs of which the 6-year fish of 1928 will come, was also an excellent year, but 1924 was relatively poor. So far as this evidence goes, then, it would appear that the coming season on the eastern shore of Bristol Bay ought to be good. The trend of the catches here has been slightly downward, but it would not appear from this that a serious deficiency would occur in 1928. The escapment to the Kvichak in 1923, as indicated by observations on the spawning grounds, was exceptionally poor, however, in spite of the good commercial catches.[9] The escapement of 1922 was excellent, and if we had discovered a correlation between catches at six-year intervals it would seem a favorable indication. As it stands, the evidence for the Kvichak is conflicting, although on the whole it would appear to indicate a somewhat less favorable year than 1927.[10]

In this general connection there is one other matter that seems worthy of mention, and that is the remarkable association between climatic conditions and catches in 1926 and 1927. The winter of 1925–1926 was one of the warmest on record in Alaska, as was also the summer of 1926. The winter of 1926–1927, on the contrary, was exceptionally cold, and the summer of 1927 proved correspondingly cold and rainy. It seems not beyond the bounds of possibility that there was some causal connection between these conditions and the exceptionally heavy run of 1926 and the exceptionally light run of 1927. We know nothing of the factors, other than age and size, that affect the sexual maturing of salmon, and it may be that temperature or conditions associated with temperature during the winter months may affect materially the percentage of fish of a given age group that matures in a given year. A high temperature may result in the maturing of a larger than normal percentage of the fish in the ocean, while a low temperature may retard maturation. On some such basis as this we might explain the large run of 1926 as due in part to the maturing of a large number of fish that under normal conditions would not have matured for another year; and the poor run of 1927 as due in part to the reduction of the stock by the unusual maturing of fish in 1926 and in part to the retardation of maturation in a large number of fish that normally would have matured in 1927. If this were so, we might expect a rather better run than otherwise in 1928, due to the maturing of fish retarded in 1927. This seems to be a rather remote possibility, it being more likely that the fluctuations in salmon catch and weather conditions in 1926 and 1927 were

[9] Alaska Fishery and Fur-Seal Industries in 1923. By Ward T. Bower. Appendix III, Report, U. S. Commissioner of Fisheries for 1924 (1925), pp. 80 and 81. Washington.

[10] Since this report went to press, the 1928 salmon runs in Bristol Bay have proved to be of considerably greater proportions than our data indicated. We have discussed above some of the possible causes that may upset any prophecy based on such data. With such large probable errors as we have to deal with, close estimates of the size of salmon runs are impossible, but it is our belief that carefully considered estimates of this kind will, in the long run, be justified.—W. H. R., July 17, 1928.

merely chance coincidences. Certainly such considerations could not be made the basis for any prophecy, but they have seemed worthy of recording.

OTHER SPECIES

For several reasons we have not thought it desirable at this time to attempt a detailed analysis of the data pertaining to the catches of pinks, chums, cohos, and king salmon in Bristol Bay. These species are all of minor importance in this region, and we have some reason to suppose that the records are less reliable. We will confine ourselves, therefore, to the brief mention of a few interesting points that

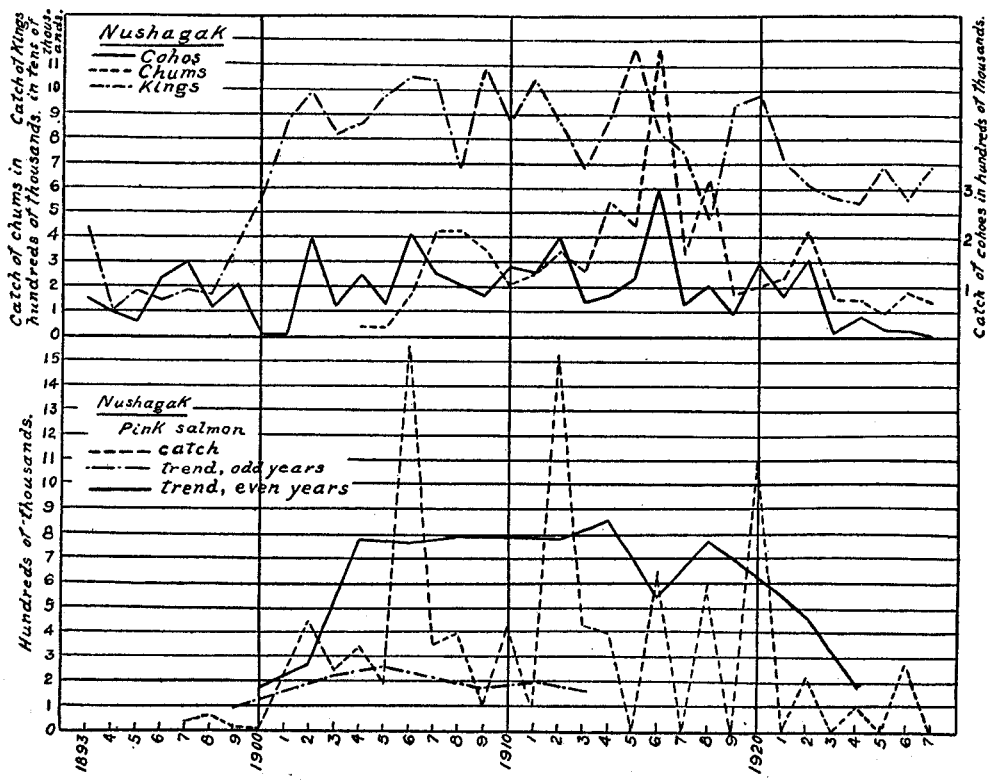

FIG. 9.—Catch of pinks, cohos, chums, and kings at Nushagak

have developed from the limited study we have made. The data for the Nushagak district are presented graphically in Figure 9 and for Kvichak in Figure 10. The catches of all these species at Egegik and Ugaskik and the catch of cohos at Kvichak have been so small and irregular that the data do not lend themselves to analysis, and therefore they have not been included.

Our procedure in the analysis of the catch of pink salmon has been affected by the fact that, to the best of our knowledge, these are always 2-year fish; that is to say, they always return to spawn at the end of their second year. On this account the fish running in the odd years are quite independent of those running in the even years, and vice versa. The two-year cycle in the pink salmon is so well known that this subject need not be enlarged upon here. We have calculated separate trends

for the series of odd and even years, therefore, and have shown these two distinct trends on the graphs. These trends represent a moving average of three years instead of five, as used in the case of the red salmon, as the use of a five-year average would have shortened our trend unduly.

In general, throughout western and central Alaska the pink salmon run much more heavily in the even years than in the odd. This is shown clearly in the graphs for both Nushagak and Kvichak by the conspicuous "peaks" that occur, with very few exceptions, in the even years. The size of the catches, especially in the even years, varies tremendously, as is exemplified particularly well by the catch of over

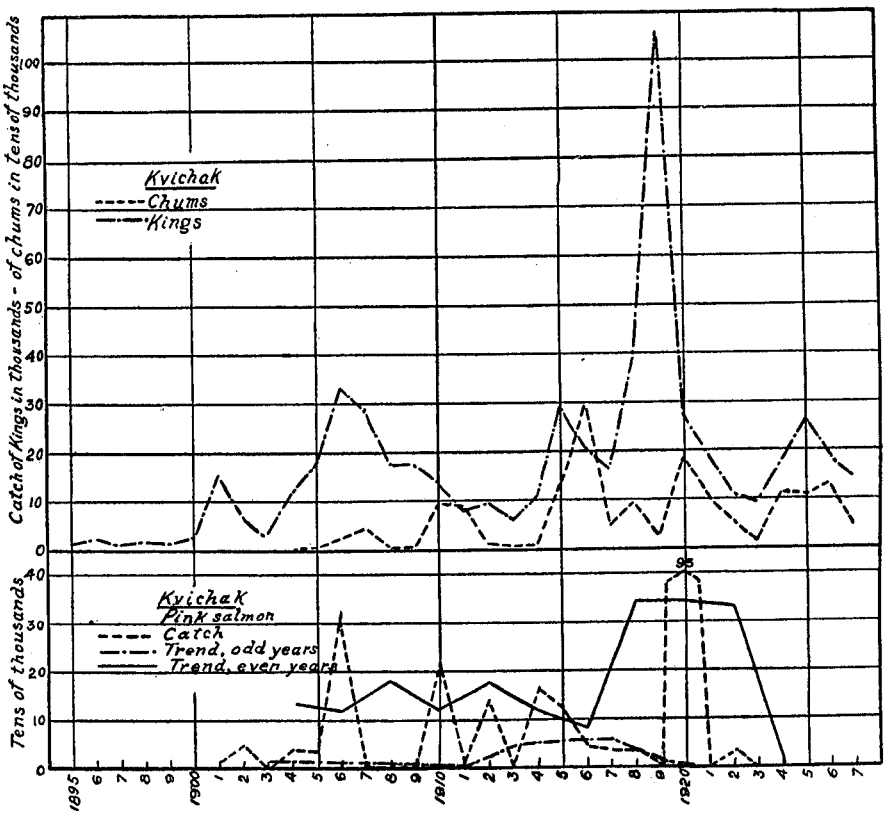

FIG. 10.—Catch of pinks, chums, and kings at Kvichak

950,000 pinks at Kvichak in 1920—approximately three times the next largest catch. The catch of pink salmon in Bristol Bay has been largely affected by the regulations that have been in effect since 1922. These regulations have closed the fishing season on July 25, and as the pink-salmon run occurs mainly after this date the catch of this species has been reduced materially.

The trends of the catches of pink salmon in the odd and even years show some interesting variations, both at Nushagak and Kvichak. In both localities the trend for the odd years is distinctly below that for the even years, as would be expected. The odd year trend at Nushagak rises gradually to a peak in 1905, then declines gradually to an abrupt termination in 1913. After that date no pink salmon have

been reported from this district in the odd years. Whether this is due to the complete failure of the run or whether there is some economic explanation we have no way of knowing. Inquiries have been made of some of the companies operating at Nushagak, but they have been unable to offer any acceptable explanation of the phenomenon. The trend of the even-year catches at Nushagak rose rapidly to the level of 800,000 in 1904, where it remained remarkably constant for over a decade. In this case, however, the level of the trend is determined very largely by the two exceptionally large catches of 1906 and 1912, and the method of determining the trend has so spread these large catches that the constancy of the level is especially marked. The catch during the even years from 1914 to 1920 remained fairly constant and at a level above that of the preceding years, with the exception of 1906 and 1912. The trend for these years (1914 to 1920) is somewhat lower, however, but this is due to the influence of the two exceptional catches. Since 1920 the even-year catches have been poor, but those for 1924 to 1926 were influenced by the regulations, as mentioned above, and that for 1922 possibly was influenced by the economic factors that operated to reduce the pack of 1921 throughout Alaska. It does not appear from these data that the pink-salmon run of the even years has been depleted. In this connection it should be noted that if the parent-stream theory holds as rigidly in the case of the pink salmon as in the case of the reds, the pinks would be expected to show the effects of over fishing very promptly.

The catch of pink salmon at Kvichak is much smaller than at Nushagak but shows similar extreme fluctuations and the same two-year cycle with good catches in the even years and poor catches in the odd. In only two of the odd years were any significant catches of pink salmon recorded—1915 and 1917. The general trend of the catches in the even years was approximately level until 1918; then came the remarkable catch of 1920, and since then the catch has been insignificant; but the catch of the years since 1922, as at Nushagak, has been affected by the regulations, and it seems possible that the catch of 1922 was reduced by economic causes. So here, again, we have no evidence of depletion in the pink-salmon run.

We have not calculated the trends for the other three species, believing that the graphs are sufficiently clear. The catch of cohos at Nushagak shows a gradual increase up to about 1916. Subsequently a somewhat lower level was maintained until 1922, since which year the catch has been lower than at any time since 1901. The cohos as well as the pinks run late in the season, and there is no doubt that the closing of the season on July 25 has been responsible for the reduced catch of cohos in the years following 1922. It is possible that some depletion is shown by the reduced catches in the years 1917 to 1922, inclusive, but this is by no means certain.

In the case of the king salmon there appears to have been a slight reduction in the catch at Nushagak since 1916, but the catch at Kvichak does not seem to have been affected similarly. The catch of kings has not been affected so much by the regulations, however, as provision is made for the use of king-salmon nets not less than 8½ inches stretched mesh previous to June 25, when the season begins in which red salmon may be taken.

The catch of chum salmon at Nushagak reached a maximum in the years from 1914 to 1918 and since then has maintained a decidedly lower level. On the Kvichak side no general change has occurred. The effect of the regulations is apparent again

in the Nushagak catch of chums by the very much reduced catches since 1922. It seems doubtful that any serious depletion is indicated by these data.

One very striking phenomenon for which we have no adequate explanation is apparent from the graphs. This is the distinct correlation between the catches of pink salmon and those of cohos and chums. This is especially well marked on the Nushagak side, where all these species show a distinct two-year cycle, the catches being higher in general in the even years than in the odd. This is what we expect of the pinks, of course, but there seems to be no reason why the cohos and chums should follow the same fluctuations. It seems probable that there is some association between the intensity of fishing for pinks and that for the other two species, but we have not been able to assure ourselves that this is the case. We are unable to suggest any reasonable biological explanation, and it seems more probable that the phenomenon is due to the operation of some economic factor at present unknown.

ALASKA PENINSULA

PORT HEIDEN

The salmon fishery at Port Heiden is of minor importance but is quite isolated from other districts, either north or south. A small commercial saltery has been maintained here at various times, and reports of operations are at hand for four years. Some fishing undoubtedly has been carried on here in other years but apparently mainly for local use, as no records have been submitted to the bureau. Cobb states [11] that a saltery was operated here in 1918, but of this we have no record. The available data are given in Table 5 but are obviously too few to permit of any analysis.

TABLE 5.—*Salmon caught and fishing appliances used at Port Heiden, 1912 to 1917*

Year	Coho	King	Red	Beach seines		Purse seines		Gill nets		Pile traps
				Number	*Fathoms*	*Number*	*Fathoms*	*Number*	*Fathoms*	*Number*
1912	11,029	20	7,280			1	175	2	200	1
1913	18,720		19,410			1	75	8	400	1
1914			10,450			1	75			
1917	6,800	108	13,140	2	150			9	450	

NOTE.—No catches reported in 1915 and 1916.

PORT MOLLER

The data for Port Moller are presented in Table 6, and graphically in Figure 11. It is well known that the red-salmon run in this district is seriously depleted, and this is distinctly shown by the trend (five-year moving average), which has been constantly downward since 1916. It is true there have been material reductions in the amount of gear used and the weekly closed season was extended (in 1924) from 36 to 84 hours; but this can not entirely account for the reduction in catch, although the low level maintained since 1921 probably is due in part to the regulations. The fishery at Port Moller was discussed in 1920 by Gilbert and O'Malley (loc. cit.), who concluded that the run already was showing depletion at that time. The fish

[11] Pacific Salmon Fisheries. Third edition. By John N. Cobb. Appendix I, Report, U. S. Commissioner of Fisheries for 1921 (1922). Bureau of Fisheries Document No. 902, 268 pp., 48 figs. Washington, 1921.

taken in the Port Moller fishery are produced mainly in two small rivers—the Bear and the Sandy, a few miles east of Port Moller proper. Gilbert and O'Malley gave cogent reasons for believing this to be the case, in spite of the opinion held by some that the Port Moller fishery drew upon the Bristol Bay runs to a greater or less extent. It was believed by some of the men in the industry that in certain years, if not in all, the salmon bound for Bristol Bay approached the coast in the region of Port Moller and thus were taken in the fishery at that point. The tagging experiments carried out in 1922 and 1925 [12] proved conclusively that this was not true, and that the red salmon taken in this region did not belong in any appreciable measure to the Bristol Bay runs. Additional evidence of the independence of the Port Moller runs is given by a comparison of the data presented in Table 6 with those for Bristol Bay. It is obvious from such a comparison that there is no significant correlation between the fluctuations in the catches in the two regions, as would be expected if they drew to any great extent upon the same body of fish. These additional lines of evidence, therefore, support the conclusion of Gilbert and O'Malley that the red-salmon fishery at Port Moller is dependent primarily upon the runs supported by the Bear and Sandy Rivers, and we can have no doubt that these are very seriously depleted. The very limited supply has been greatly overexploited, and it seems probable that the process of depletion is continuing even with the reduced intensity of fishing that now prevails. Even under present conditions the intensity of fishing is high, as is shown by the fact that, in the tagging experiments of 1925, 47.5 per cent of the tagged fish were recovered.

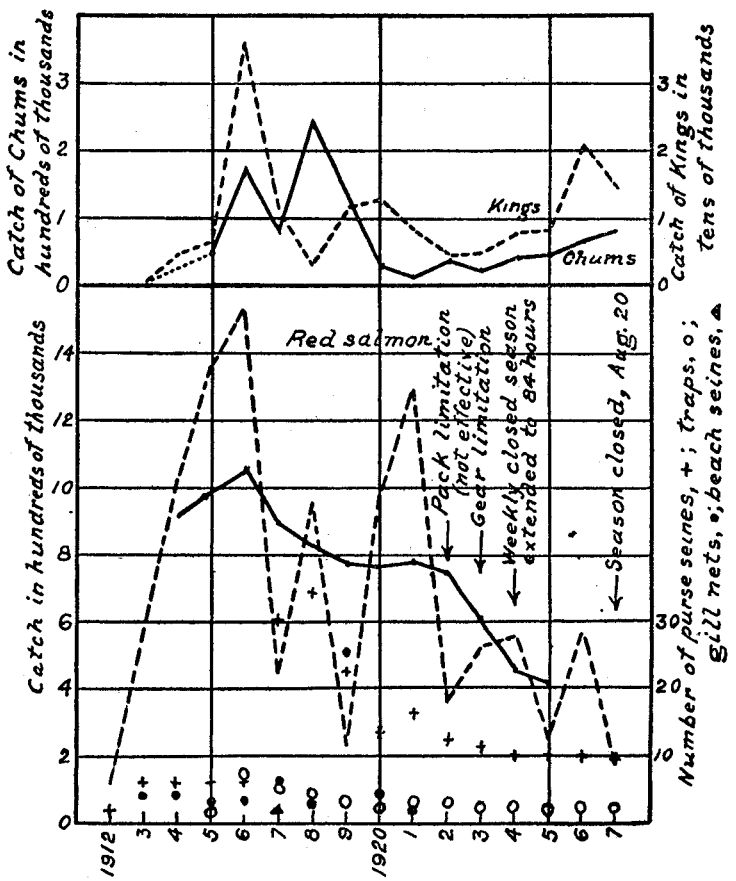

FIG. 11.—Catch of salmon at Port Moller

[12] Experiments in Tagging Adult Red Salmon, Alaska Peninsula Fisheries Reservation, summer of 1922. By Charles H. Gilbert. Bulletin, U. S. Bureau of Fisheries, Vol. XXXIX, 1923-24 (1924), pp. 39-50, Washington, 1923. Salmon-Tagging Experiments in Alaska, 1924 and 1925. By Willis H. Rich. Bulletin, U. S. Bureau of Fisheries, Vol. XLII, 1926 (1927), pp. 109-146, Washington, 1926.

TABLE 6.—*Salmon caught and fishing appliances used in the Port Moller district, 1912 to 1927*

Year	Coho	Chum	Pink	King	Red	Beach seines		Purse seines		Gill nets		Pile traps
						Number	*Fathoms*	*Number*	*Fathoms*	*Number*	*Fathoms*	*Number*
1912					101,606			2	440			
1913	17	1,964		258	571,713			6	1,440	4	600	
1914				4,655	1,012,713			6	960	4	600	
1915		50,701		6,361	1,349,030			6	1,500	3	450	2
1916		175,620	2,567	35,859	1,532,942			6	1,500	3	450	7
1917		82,604	560	11,164	436,450	2	120	30	8,120	6	375	5
1918		243,231	1,211	3,172	953,015	11	745	34	9,150	3	225	4
1919		138,905	12,041	11,578	221,738			22	5,800	25	1,780	3
1920		29,285		12,806	971,090			13	3,400	4	100	2
1921		11,444		8,452	1,314,069			16	4,630	2	150	3
1922		34,906		4,891	357,751			12	2,900			3
1923	61	21,542		5,043	523,933			11	2,675			2
1924		41,509		7,751	562,006			10	2,375			2
1925		49,373		8,598	247,934			10	2,500			2
1926		68,931		20,986	567,190			10	2,500			2
1927		81,781		14,109	172,934			9	2,175			2

NOTE.—According to Cobb (loc. cit.), a saltery was operated on the Bear River in the years 1902 to 1906, but we have no record of the catch or pack during those years.

The fluctuations in the catch of red salmon are somewhat peculiar in that the "peaks" and the "valleys" come at two and three year intervals. Without much doubt this is to be explained by the predominance of 5-year fish in the runs and the existence of two maxima and two minima in each cycle of five years. Thus, referring to Figure 11, the peak coming in 1916 probably is associated with the peak of 1921, and that again with the peak of 1926, while the peak of 1918 is associated with those of 1923 and 1924. On account of the few data available for study, we have not thought it worth while to calculate the correlation of catches at different intervals (as was done for Bristol Bay), but the fluctuations are sufficiently well marked to warrant such a tentative interpretation.

The catch of king salmon has fluctuated considerably, up to a maximum of over 35,000 fish. There was a slight reduction in the average annual catch during the interval from 1921 to 1925, inclusive, but the catches of 1926 and 1927 were among the best on record, being exceeded only by the catch of 1916. There seems to be no evidence here of depletion nor of any reduction in the catch due to the regulations.

The catch of chums dropped suddenly in 1920 from an average of over 100,000 to the relatively low level of less than 30,000. The catch has been increasing gradually since that time and by 1927 was over 80,000. The sudden drop may have been due to depletion, but it seems more likely that it was due to economic causes, inasmuch as the catch has increased during the past seven years in spite of the reduced intensity of fishing brought about by the decrease in gear and the extension of the weekly closed season.

NELSON LAGOON

Salmon fishing in Nelson Lagoon always has been a closely restricted one conducted almost entirely with traps and drawing solely upon the run of fish entering Nelson River to spawn. The catch of species other than red salmon never has been of great importance, but the catch of reds has been remarkably large considering the size of the stream. The data are presented in Table 7 and Figure 12.

The catch of red salmon shows a fairly steady rise from the early years of the fishery to a maximum in 1915 and 1916. The catch for the next three years was

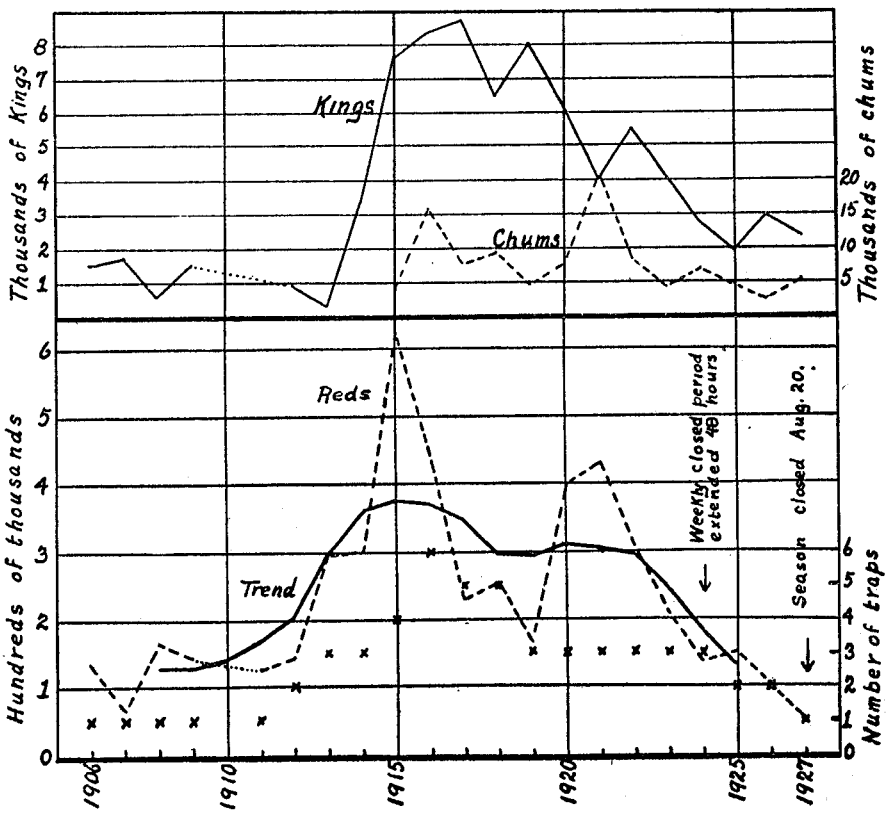

FIG. 12.—Catch of salmon at Nelson Lagoon

relatively poor, but it rose again in 1920 and 1921. Since that time the catch has dropped off consistently, that of 1927 being the poorest on record. These records of the total catch show quite clearly the usual story of excessive exploitation, accompanied by large catches and followed by wide fluctuations and an ultimate decrease due to depletion. In this case depletion appears to have been more rapid and more severe than in Bristol Bay, and in this respect the situation resembles that at Port Moller. A five-year cycle is indicated clearly by the peaks in 1915 and 1916 and 1920 and 1921, and the fact that no maximum appeared in 1925 and 1926 is further indication of the serious extent of the depletion. We have mentioned above the

disadvantages of using the total catch as a measure of abundance and have suggested that some measure of the yield per unit of gear or per unit of fishing effort would be more satisfactory. Such measures of abundance have been used with marked success in various recent fishery investigations, notably those conducted by W. F. Thompson and his associates for the California Fish and Game Commission and the International Fisheries Commission.

TABLE 7.—*Salmon caught and fishing appliances used in Nelson Lagoon, 1906 to 1927*

Year	Coho	Chum	Pink	King	Red	Gill nets		Pile traps
						Number	*Fathoms*	*Number*
1906				1,530	135,000	2		1
1907	3,150		1,500	1,725	66,500			1
1908				600	166,870			1
1909		1,000	15	1,500	143,000			1
1911					129,600			1
1912		2,448		920	143,860			2
1913				342	297,693			3
1914				3,435	301,918			3
1915		4,088		7,592	625,240			4
1916		15,784		8,385	441,776	2	120	6
1917		7,697		8,734	230,002	2	120	5
1918		9,056		6,507	255,530	1	120	5
1919		4,559		8,054	167,438			3
1920		7,669		6,195	400,849			3
1921		21,306		4,022	432,396			3
1922		8,006		5,540	310,139			3
1923		4,213		4,035	207,735			3
1924		6,880		2,742	139,706	2	140	3
1925		4,501		1,952	152,300			2
1926		2,602		2,939	105,670	3	225	2
1927	104	5,182		2,386	57,660			1

NOTE.—No catch reported in 1910. Cobb (loc. cit.) states that a saltery was operated also in 1902 and 1903 but of this we have no record.

As fishing in Nelson Lagoon has been conducted so largely with traps, it has been possible to analyze the data, and while the results are not entirely satisfactory they have proved suggestive enough to warrant inclusion in this report.

It is apparent from Figure 12 that the rise in the catch, which culminated in 1915 and 1916, was accompanied by an increase in gear from one to six traps, and similarly the later reduction in the catch accompanied a decrease in gear. Furthermore, the intensity of fishing has been affected by the increase in the weekly closed period, which has been in effect from 1924 to 1927, inclusive. This has reduced the weekly open period from 132 to 84 hours. In other words, the present time available for fishing is only seven-elevenths (63.6 per cent) of the time available previous to 1924. It is pertinent to inquire how much of the reduction in the total catch is due to the decreased intensity of fishing and how much to depletion.

In order to answer this question, it is essential to have some measure of the fishing effort maintained from year to year, and this is by no means simple, as there are various complicating factors. In the first place, we have to consider the fact that the multiplication of gear, beyond a certain point at least, will, even with a constant supply of fish, tend to reduce the catch per unit of gear solely as a result of what may be called competition between the units of gear. Thus, in the case of Nelson Lagoon an increase in the number of traps in all probability would tend to

reduce the catch per trap simply because of the competition between traps. Supposing that a single trap were operated and caught 25 per cent of the run, then if another trap were placed in an equally advantageous position, but beyond the first trap, so that the only fish to reach the second trap would have to pass the first trap, we would expect the second trap to catch less than the first. If the second trap were equal in efficiency to the first, it would catch 25 per cent of the fish that passed the first one—that is, 25 per cent of 75 per cent, or approximately 19 per cent of the run. In the same manner a third trap, equally efficient but located beyond the second, would catch only 25 per cent of the fish that evaded the second trap, or 14 per cent of the run. Undoubtedly there is some such competition between units of gear, and undoubtedly this will tend to reduce the catch per unit as the number of units is increased, regardless of any depletion due to overfishing. The situation is complicated further by the fact that the fish do not always pass directly through a given fishing area but move back and forth, often on the tides, and thus repeatedly run the gantlet of the fishing gear. In this way the effect of the competition between gear is reduced and under certain circumstances might be entirely nullified, so that any change in the amount of gear would cause a corresponding change in the size of the catch.

In the second place, it is quite possible that a given fishing effort will take a different percentage of a small run than of a large run. To make use again of the example given above it is possible that while a single trap would take 25 per cent of an average run it might take only 20 per cent of a large run but would take 30 per cent of a small run, or vice versa. So far as we know, there is no evidence that such is the case, but it is a possibility that should be kept in mind.

Again, it is very probable that a present-day trap is, in effect, entirely different from those used in 1906; that the two are by no means comparable units. The one trap fished in 1927 or the two fished in 1925 and 1926 were planned and driven in the light of all the experience gained in nearly two decades of fishing in these waters and undoubtedly were driven in the localities and in the manner which have proved most effective. Certainly, as the number of traps has been reduced since 1916 it was the less productive ones that were eliminated.

A fourth complicating factor is the reduction in the intensity of fishing due to the increase in the weekly closed period from 36 to 84 hours, which has been effective for the past four years. This undoubtedly has tended to reduce the annual catch per trap, and it may be assumed that the reduction in catch has been approximately in proportion to the reduction in the time during which fishing is permitted. Such an effect necessarily must be taken into account in any analysis of catch per unit of gear and an adjustment made therefor.

In spite of the difficulties in the way of getting an accurate measure of the catch per unit of effort, we have felt that it was worth while to make the attempt in the case of the Nelson Lagoon data, inasmuch as the conditions here for the analysis of the trap catches are about as ideal as they are likely to be anywhere in Alaska. The available data do not show the actual number of days or weeks fished per season, so that we could not calculate the number of fish caught per trap per day or per trap per week.

The best measure of the catch per unit of fishing effort that we have been able to devise is the catch per trap per days of fishing per week; that is to say, we have taken as our unit of fishing effort one trap fishing one day per week throughout the season, and to secure the catch per unit of effort have divided the total catch for the season by the product of the number of traps and the number of days of fishing per week. This makes the necessary adjustment for the effect of the decline in the number of days per week during which fishing is permitted but does not take into account any changes that may have occurred in the effectiveness of traps.

Figure 13 shows the changes this measure of the catch per unit of effort has undergone. Although there have been wide fluctuations the general trend has been downward, and there can be no doubt that the actual abundance of fish has decreased in much the same proportion. The present yield approximates two-thirds that obtained in the early years of this fishery. It will be noted that the greater number of traps employed between 1914 and 1919 is reflected in the smaller yield per unit of

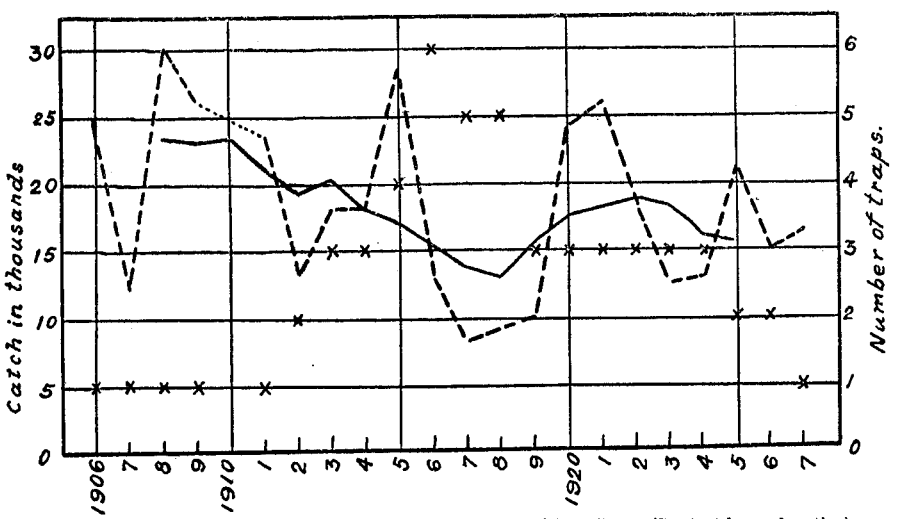

FIG. 13.—Catch of red salmon at Nelson Lagoon per unit of fishing effort. (See text for explanation)

fishing effort, an effect that may be ascribed (in part, at least) to competition between the units of gear. The decreased abundance indicated by the yield per unit of effort does not appear to be so marked as that indicated by the decline in total yield, although the two are of the same order of magnitude. Furthermore there is a general impression current that the fishery is even more seriously depleted than is indicated by either of these measures of abundance. It appears fairly clear that neither the total catch nor the catch on the basis of the unit of effort is entirely satisfactory as a measure of the actual abundance. However, both indicate serious depletion, and the future will show whether the present greatly reduced fishing effort will permit the recovery of the run into Nelson River to something like its original proportions.

ALEUTIAN ISLANDS

Table 8 presents the data on the salmon catch made in the numerous localities of the Aleutian Islands from which reports have been received. The data are so scattered that it is useless to try to determine whether the changes in catches have

been due to depletion, natural fluctuations, or shifts in the fishery. They are presented without any attempt at analysis.

TABLE 8.—*Salmon caught and fishing appliances used in the Aleutian Islands District, 1911 to 1927*

Year	Coho	Chum	Pink	King	Red	Beach seines		Gill nets	
						Number	*Fathoms*	*Number*	*Fathoms*
Akun Cove: 1918					3,250				
Beaver Inlet:									
1917	764	409	72		163				
1918	945								
Chernofski Harbor: 1917		100							
Kalekta Bay:									
1918	360				840				
1919					300				
Kashega Bay:									
1916	1		8,986	4	16,367				
1917					6,749				
1918					6,000				
1919	300								
1920					5,000				
1925					4,291				
Makushin Bay:									
1916	148	8	159,592		1,212				
1917	2,330		247		17,120				
1918	2,000		48,625		30,624				
1920					5,050				
1924		123	673,846		5,676				
1925			3,842		11,422				
1926		3,460	515,841		427				
1927	20		334,575		16,768				
Nikolski Creek:									
1917					17,343				
1922					14,000				
Swanson Lagoon:									
1924				8	19,200				
1925		9,136			2,501				
1926		4,337	5,883		908				
Unalaska Bay:									
1916			10,007						
1918	1,100		26,975		4,330				
1919	500		4,000						
1920	2,790								
Urilia Bay: 1927					491				
Volcano Bay:									
1916	1,025	129	1,679	43	58,915				
1917	675	22,636	293		27,125				
1918					10,200				
1919					3,600				
Winslow Bay:									
1911					9,252				
1917					1,934				
1925					420				
Total:									
1911					9,252	2	75		
1916	1,174	137	180,264	47	76,494	6	1,050		
1917	3,769	23,145	612		70,434	17	2,030		
1918	4,405		75,600		55,244	13	495	1	75
1919	800		4,000		3,900	7	300	1	75
1920	2,790				10,050	4	160		
1922					14,000	1	50		
1924		123	673,846	8	24,876	4	500		
1925		9,136	3,842		18,634	4	340		
1926		7,797	521,724		1,335	3	300		
1927	20		334,575		17,259	3	375		

NOTE.—No catches were reported in years not shown above.

IKATAN DISTRICT

This district includes the waters of Ikatan Bay, False Pass, and eastward as far as but not including the Shumagin Islands. There are a number of independent fisheries in this district that draw upon more or less local runs of salmon, and we have kept these separate so far as practicable. The following localities are not named on the map:

Arch Point, western shore of Pavlof Bay, north of Volcano Bay.

King Cove, mainland shore between Belkofski and Cold Bays.

Nicholaski Spit, western shore of Pavlof Bay, south of Volcano Bay.

Thin Point, western entrance to Cold Bay.

Volcano Bay, indentation on the western shore of Pavlof Bay just north of Belkofski Bay. Also known locally as Bear Bay.

Various regulations have been promulgated from time to time under the authority provided for the administration of the Alaska Peninsula Fisheries Reservation in 1922 and 1923 and that of the act of June 6, 1924. As the interpretation of our data for these years will depend to some extent upon the probable effect of the restrictions imposed, we shall review the regulations briefly.

The restrictions were intended to prevent undue expansion of the industry during the life of the reservation, and they had no material effect upon the then established intensity of fishing. Beginning with the season of 1924, however, effective restriction of the fishing intensity began. The regulations that presumably had the greatest effect upon the catch of salmon may be summarized as follows:

1. The weekly closed period was extended from 36 to 60 hours. In 1925 and subsequent years this order was modified and made effective only up to July 25, after which date the weekly closed period remained as before, 36 hours.

2. On August 20, 1927, the fishing season was closed for the remainder of the year.

3. The use of purse seines was prohibited in 1925 and subsequent years.

4. Beginning with 1926 all traps were prohibited in False Pass, and it was required that traps be spaced at least 1 mile apart in all waters.

5. In 1924 Thin Point Lagoon and the waters within 500 yards of the entrance were closed to fishing.

6. The east side of Morzhovoi Bay and all of Cold Bay were closed in 1925 and 1926, but in 1927 were opened to fishing after July 25.

The data for the various localities in the Ikatan district are given in Table 9.

TABLE 9.—*Salmon caught and fishing appliances used in the Ikatan district, 1908 to 1927*

Year	Coho	Chum	Pink	King	Red	Beach seines		Purse seines		Gill nets		Pile traps
						Number	*Fathoms*	*Number*	*Fathoms*	*Number*	*Fathoms*	*Number*
Arch Point: 1927	168	8,413	18,998		815							1
Belkofski Bay:												
1911	800	8,231										
1912		1,112										
1915		12,491	2,692									
1916		74,207	10,309									
1917	90	12,251	168		168							
1918		32,065	8,928									
1919		7,730										
1923	37	11,392	3,525		19							
1924	188	88,130	206,583		2,533							1
1925	4,203	124,881	34,503	6	8,758							1
1926	3,545	102,619	267,471		4,635							1
1927	1,554	104,313	97,529		24							1
Cold Bay:												
1911	3,500				33,167							
1912	2,200	5,976	3,856		20,525							
1914		15,710	1,187		3,316							
1915	336	38,690	20,852		17,605							1
1916	4,042	10,138	2,187		33,640							
1917	116	8,557	883		21,260							
1918		24,483	7,874		13,500							
1919	362	8,444	145		3,274							
1920	126	2,178	22,621		12,005							
1922		4,065	194		12,705							
1923	19	785	72		28,661							
1924		29,412	14,708		20,405							
1927	1,562	24,562	9,675		14,114							

TABLE 9.—*Salmon caught and fishing appliances used in the Ikatan district, 1908 to 1927*—Continued

Year	Coho	Chum	Pink	King	Red	Beach seines		Purse seines		Gill nets		Pile traps
						Number	*Fathoms*	*Number*	*Fathoms*	*Number*	*Fathoms*	*Number*
Deer Island:												
1916			51,088									
1918		18,084	96,232									
1925	6	9,720	19		48							
1927		4	50,841		1							
Ikatan Bay:												
1911					653							
1912		22,993	3,632		42,865							
1913		2,316		1,832	272,694							
1914		100,387	174,448	227	284,032							2
1915	3,005	107,715	44,352	1,873	109,378							4
1916	2,180	247,759	237,842	3,345	198,027							2
1917	722	149,218	42,224	3,047	670,680							14
1918	3,215	373,208	304,306	3,880	516,509							15
1919	15,018	524,501	60,954	7,384	422,344							22
1920	21,201	644,443	759,577	5,488	786,123							8
1921	1,457	81,712	44,685	678	783,246							6
1922	965	153,798	219,468	3,235	1,900,139							13
1923	16,416	184,247	52,953	3,574	1,084,797							12
1924	58,146	378,806	571,343	3,079	888,910							16
1925	33,037	254,745	73,183	6,930	309,305							12
1926	62,236	256,794	713,955	6,127	1,497,850							9
1927	44,588	420,322	266,093	7,213	430,989							10
King Cove:												
1914		10,312	1,988									
1915		41,450	6,130									
1916		27,227	5,568									
1917		4,041										
1918		12,235										
1919		3,622										
1920		8,965										
1922			3,014		1,442							
1923		2,499	127		5							
1925	3	28,192	892		9							
1927		22,938	5,799		3							
Morzhovoi Bay:												
1911	4,147	29,428			57,693							
1912	3,868	41,509	14,063		101,036							4
1913		4,634			141,648							3
1914	3,904	66,445	105,143	421	182,232							2
1915	8,859	48,217	45,014	2,880	141,773							4
1916	17,317	54,360	82,122	3,347	340,153							2
1917	3,184	101,591	26,702	2,377	651,603							14
1918	6,423	513,874	479,246	4,547	216,114							13
1919	11,477	119,693	10,494	1,039	122,588							14
1920	6,254	116,715	350,537	1,127	167,913							1
1921		2,915	2,635		47,420							5
1922	1,058	73,234	121,468	413	875,012							5
1923	2,988	28,091	6,141	61	255,017							4
1924	8,045	171,647	191,225		82,341							4
1925	7,878	58,533	9,182	120	47,745							4
1926	3,175	55,623	83,804	101	400,302							3
1927	2,234	114,816	33,920	27	24,490							3
Nicholaski Spit:												
1924	2,818	52,989	151,001		43,356							1
1925	4,763	62,711	12,778	42	17,214							1
1926	8,125	71,589	321,711	233	137,628							1
1927	1,318	57,314	77,002	101	20,955							1
Pavlof Bay:												
1912					4,425							
1916			162,188									
1917	130	11,675	130		1,650							
1918	494	91,829	854,219		30,590							2
1919	1,414	31,567	1,617	56	9,929							2
1920	6,943	49,891	319,017	14	4,484							2
1922		2,936	135,860	10	3,000							1
1923	1,103	21,988	2,075		1,074							2
1924	4,509	90,916	1,012,937		3,876							2
1925		30	60		315							2
1926	13,293	107,465	830,860		43,558							2
1927	22	61,155	30,319		356							6
Sanak Island:												
1911			25,232		46,067							
1912		1,854	10,700		23,592							
1914					46,004							
1915					30,677							
1917		3,147	319		22,626							

TABLE 9.—*Salmon caught and fishing appliances used in the Ikatan district, 1908 to 1927*—Continued

Year	Coho	Chum	Pink	King	Red	Beach seines		Purse seines		Gill nets		Pile traps
						Number	*Fathoms*	*Number*	*Fathoms*	*Number*	*Fathoms*	*Number*
Sanak Island—Contd.												
1920			132		8,283							
1922			99		19,857							
1923			2,209		10,012							
1924			1,854		5,427							
1927		44	18		736							
Thin Point:												
1908					46,942							
1909	7,200				92,075							
1910	5,500				45,000							
1911	4,000				78,200							
1912	20,914	24,360	8,158		58,309							
1913					43,028							
1914	342				68,265							
1915	4,037	2,938	1,095		44,383							
1916	10,406			70	77,482							
1917	106	722	344		37,349							
1918	1,579	5	639		134,563							
1919	18,535				21,553							
1920	9,156	44	6,563		90,410							
1922	50	133	284		76,310							
1923	1,449		175		82,463							
1924		27,127	54,031		34,703							
1925	9,997	16,060	2,595		45,456							
1926					20,000							
1927		13	52		19,363							
Volcano Bay:												
1911		31,755										
1912		97,213			556							
1914		28,211	28,211									
1915		81,640										
1916		95,029										
1917		98,674	300									
1918		324,217	90,275									2
1919	942	102,471	166		911							2
1920	142	66,675	115,624	526	182							2
1922	100	72,359	127,572	40	2,501							2
1923	2,840	132,165	4,607	46	7,286							2
1924	356	369,328	236,534		2,634							2
1925	762	178,696	15,182	45	5,453							2
1926	12,466	268,618	378,954	24	27,117							2
1927	1,051	129,201	83,460	8	8,140							4
Unallocated:												
1911		13,549			15,257							
1927	3	90	170		10							1
Total:												
1908					46,942	2	90	2	80			
1909	7,200				92,075	3	280					1
1910	5,500				45,000	2	75					
1911	12,447	82,963	25,232		234,632	7	400	2	400			
1912	26,982	195,017	40,409		251,308	6	600	4	800	1	150	4
1913		6,950		1,832	272,694	1	125	2	250			3
1914	4,246	221,065	310,977	648	583,849	4	350					4
1915	16,237	333,141	120,135	4,753	343,816	5	362					8
1916	33,945	508,720	551,304	6,762	649,902	8	980			1	40	4
1917	4,348	389,876	71,060	6,424	1,405,336	11	1,500					28
1918	11,711	1,390,000	1,841,719	8,427	911,276	12	1,550	4	875			32
1919	47,748	805,716	73,398	8,479	579,599	15	1,745	6	1,700			40
1920	43,822	888,911	1,578,421	7,155	1,069,400	15	1,745	6	1,700			17
1921	1,457	84,627	47,320	678	830,666							7
1922	2,173	296,936	603,691	3,698	2,890,966	5	510	2	600			21
1923	24,852	381,167	71,884	3,681	1,469,334	4	395	2	600			20
1924	74,062	1,208,355	2,440,216	3,079	1,084,185	3	375	6	1,055			26
1925	60,739	733,568	148,394	7,143	434,303	3	350					22
1926	102,840	862,708	2,596,755	6,485	2,131,135	5	550					18
1927	50,951	936,502	674,659	7,349	519,997	9	900					27

NOTE.—The years in which no catches were reported have been omitted. The catches at Volcano and Belkofski Bays in 1918 were not separated in the reports received from the packers for that year. They have been divided on the basis of the total production in both localities in 1917 and 1919, whereby 91 per cent was credited to Volcano Bay and 9 per cent to Belkofski Bay. In the same way an undivided catch taken at Deer Island and Cold Bay in 1918 was allocated 92 per cent to Deer Island and 8 per cent to ColdjBay. The number of traps has been determined in part from the company records, which show all traps driven, and in part from the records of the bureau's agents, which show the traps actually fished. Whenever possible the bureau's records have been used as providing a more accurate measure of the fishing effort.

The two most important localities, especially as regards the catch of red salmon, are Ikatan and Morzhovoi Bays. The tagging experiments of 1922 and 1923 [13] showed that the runs of red salmon in these two bays were intimately associated, not only with one another but with the runs of Bristol Bay. It was apparent that there was a considerable interchange of fish between Ikatan and Morzhovoi Bays, and that important percentages of the fish from both localities went ultimately to Bristol Bay. It was shown further that the traps located on the east side of Morzhovoi Bay caught a smaller percentage of Bristol Bay fish and a correspondingly larger percentage of red salmon derived from local spawning streams along the southern shore of the Alaska Peninsula than did the traps on the west side of the bay. On this account it would be desirable to separate the catches made on the east and west sides of this bay, but it has been impossible to do this with the data at hand. In view of the close association between the red-salmon runs in Ikatan and Morzhovoi Bays we have combined the catches for the purpose of analysis, and the data are presented graphically in Figure 14.

The trend of the total catch increased consistently up to 1922, but since that year has fluctuated rather widely, although the general tendency seems to be downward. We can not say whether this downward tendency is due to the restrictions imposed during the past four seasons or whether it is a reflection of the general downward trend that has been demonstrated in the Bristol Bay catches for the past few years. It seems probable that both factors may have had their effect.

It is quite clear from Figure 14 that the fluctuations in Morzhovoi Bay have been proportionally greater than those in Ikatan Bay, the poor years being relatively much poorer at Morzhovoi than at Ikatan. It has been suggested that in years marked by poor runs a smaller percentage of the fish enter Morzhovoi Bay. It is as though the mass of fish passing along the southern shore of the peninsula kept to the more direct routes for Ikatan Bay and False Pass in the poor years, while on the good years the relatively greater mass of fish tended to crowd large numbers off the direct route and into such side branches as Morzhovoi Bay. The available evidence lends some weight to such an hypothesis.

On account of the proved relationship between the red-salmon runs in Ikatan and Morzhovoi Bays and those of Bristol Bay we have been interested to learn to what extent the catches at Ikatan and Morzhovoi Bays are correlated with the catches in Bristol Bay. Figure 15 shows the percentage deviations of the red-salmon catches from the trend as compared with the similar data for Nushagak and Kvichak and for Bristol Bay as a whole. The Pearsonian coefficients of correlation for three combinations are as follows:

Ikatan–Morzhovoi and Nushagak	+0.163	±0.181
Ikatan–Morzhovoi and Kvichak	+.814	±.063
Ikatan–Morzhovoi and Bristol Bay	+.792	±.070

The high correlation between the Ikatan and Kvichak catches leaves little doubt that the Kvichak fish form by far the most important element in the catch at Ikatan. The lack of correlation with Nushagak is doubtless due to the dominating influence

[13] Gilbert, footnote 12, p. 74. Second Experiment in Tagging Salmon in the Alaska Peninsula Fisheries Reservation, Summer of 1923. By Charles H. Gilbert and Willis H. Rich. Bulletin, U. S. Bureau of Fisheries, Vol. XLII, 1926 (1927), pp. 27-75. Washington, 1925.

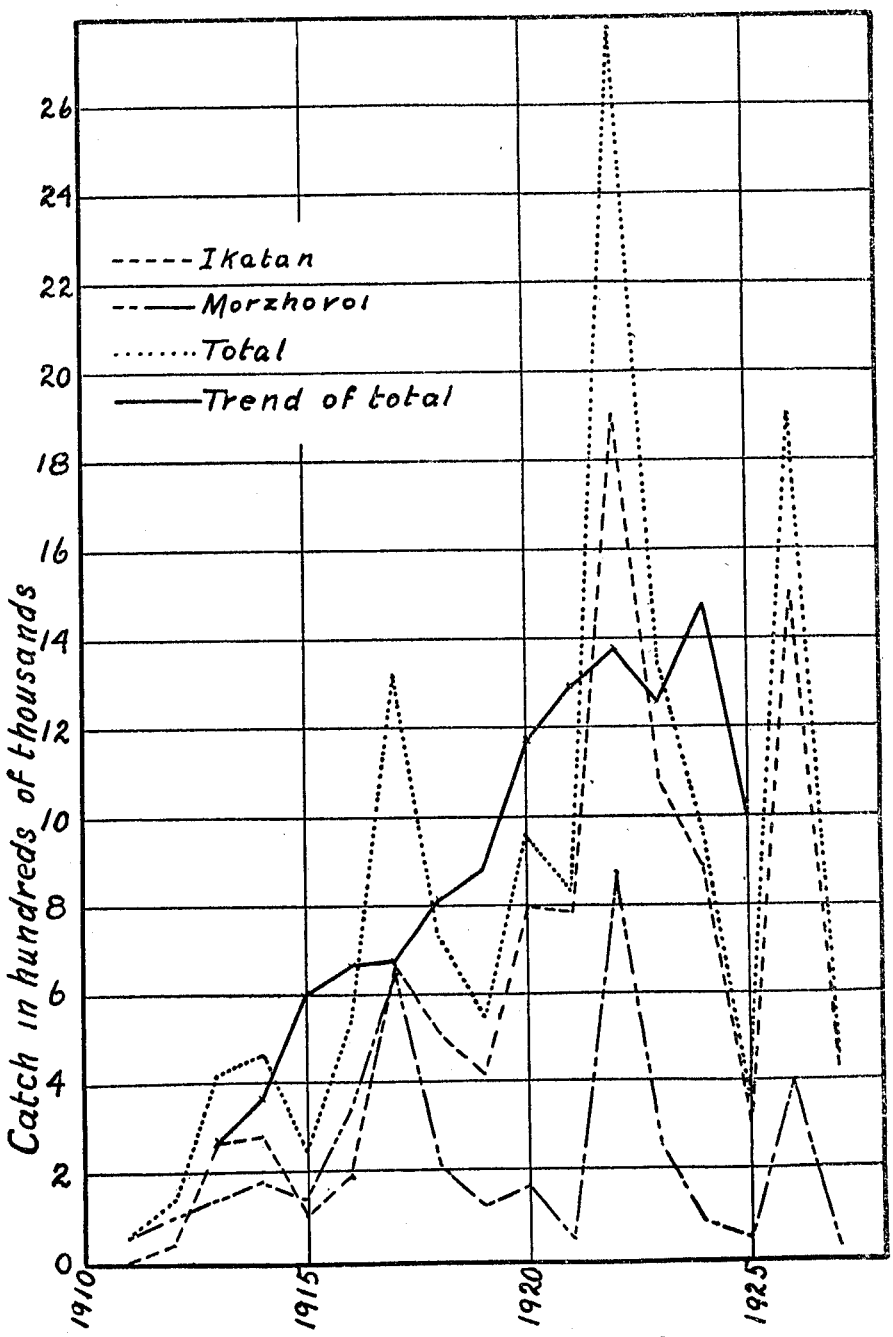

FIG. 14.—Catch of red salmon in Ikatan and Morzhovoi Bays

of the much larger run of Kvichak fish; in the period 1911 to 1927 the catch of salmon on the Nushagak side averaged only 23.8 per cent of the total for Bristol Bay. It does not appear probable that either the Kvichak or the Nushagak fish appear in the runs south of the peninsula in materially different proportions than in Bristol Bay. This is borne out by the results of the tagging experiments in 1923; 11.5 per cent of the tags recovered in Bristol Bay that year were taken on the Nushagak side, and the catch at Nushagak for the season was 10.5 per cent of the total for Bristol Bay. These facts indicate strongly that the red salmon of the Ikatan district are composed, in large part, of a mixture of Bristol Bay fish, in which each run is proportionally represented. One would anticipate, if this be true, that the correlation between Ikatan and Bristol Bay as a whole would be greater than the correlation between Ikatan and any one of the units. In fact, the correlation with Kvichak is slightly higher, but the difference is so small that it can have no possible significance.

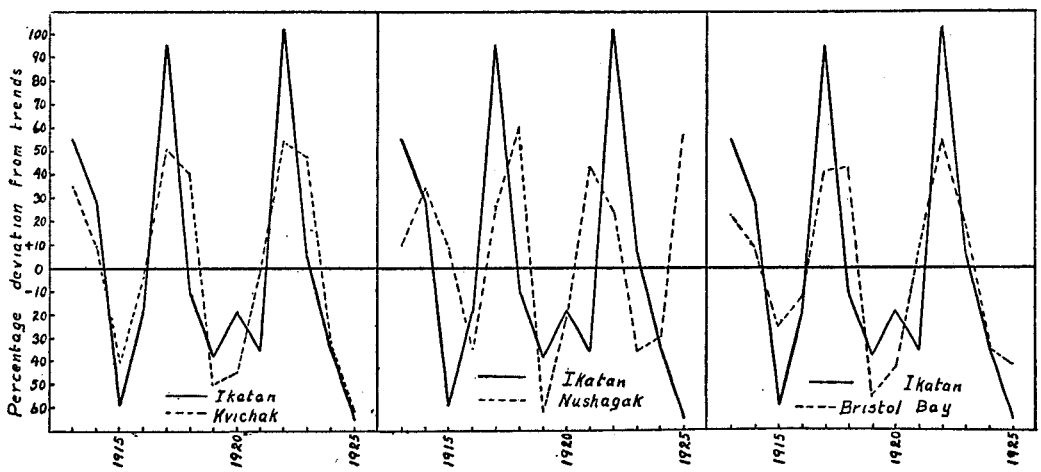

FIG. 15.—Percentage fluctuations in the catch of red salmon at Ikatan compared with those in Bristol Bay

An interesting possibility suggests itself as a result of this intimate correlation between the catches of red salmon at Ikatan and Bristol Bays and in view of the fact that the fish require about two weeks in which to make the journey between the two regions. It should be possible to determine from the run of fish at Ikatan what may be expected in Bristol Bay later in the season. To do this with any accuracy would involve a careful comparative study of the daily catches in both places, with particular reference to the reliability (as measured by the probable error) of determinations of the Bristol Bay run based on the accumulated totals of catches at Ikatan on various dates during the season. If such an analysis should prove accurate within reasonable limits, it might have some very interesting and practical applications.

Relative to the catches of other species of salmon, there does not seem to be any material correlation between the catches taken in Ikatan and Morzhovoi Bays except that due to the simultaneous development of the fisheries and other economic factors. Therefore, we shall consider them as separate units in the following discussions of the various localities in the Ikatan district.

ARCH POINT

This locality is at present of minor importance and was first fished in 1927, when a trap was driven. It seems probable that this locality will be included with the rest of Pavlof Bay ultimately, but on account of the possibility that the catch might prove to draw upon a different body of fish it was thought better to keep the data separate for the present.

BELKOFSKI BAY

The fishery here has been spasmodic and of little importance up to 1924, when a single trap was driven. Since then the catches of all species except kings have been much larger. Previous to the installation of the trap the catch had been chiefly of chums and pinks, but reds and cohos have appeared in noticeably larger numbers since 1924. The pinks, as usual in this region, are taken in much greater numbers in the even years. On account of the recent change in the character of the fishery no further analysis is possible.

COLD BAY

Beach seines were operated in Cold Bay in most years since 1911, and one trap was operated in 1915. The bay was closed to fishing in 1925 and 1926 but in 1927 was reopened to fishing after July 25. The most valuable element in the catch has been the red salmon. The catch of this species has been subject to wide fluctuations, which may have been caused by changes in the intensity of fishing. The data appear to indicate that some depletion occurred previous to 1925, but this is by no means certain on account of the irregularity in the fishery and the wide fluctuations in the catch that have prevailed from the beginning. Much the same thing may be said of the catch of pinks and chums. It is interesting to note, however, that the largest catch of pinks (over 38,000) was made in an odd year (1915), contrary to the usual rule in this region. As this was the year in which the one trap was operated, the large catch doubtless was due to this; but the fact that so large a catch could be made in an odd year would indicate the presence of a considerable run of this species.

DEER ISLAND

Catches have been reported from Deer Island in four years only and were confined virtually to pinks and chums. These fish are presumably though not certainly of local origin. The fishing has been carried on irregularly, and the data are too few to permit analysis.

IKATAN BAY

The red salmon of Ikatan Bay have been treated above. All four of the other species show a somewhat similar history. The catches in general increased up to 1920, then fell off sharply in 1921 due to the economic conditions that have been mentioned above frequently. Since 1921 all of these species have shown gradual recovery, until at present the level of the catches is approximately the same as it was in the years immediately preceding 1921, and in the case of cohos the level is noticeably higher. The data are shown graphically in Figure 16.

MORZHOVOI BAY

As in the case of Ikatan Bay the red-salmon catch of Morzhovoi Bay has been discussed above. The data relative to the other species are shown graphically in Figure 17. It will be apparent from a comparison of this figure with the similar one for Ikatan Bay that the recent history of the catches of pinks, chums, cohos, and kings has been somewhat different in the two localities. Up to 1921 the development in the two localities had been similar, but Morzhovoi Bay does not show the

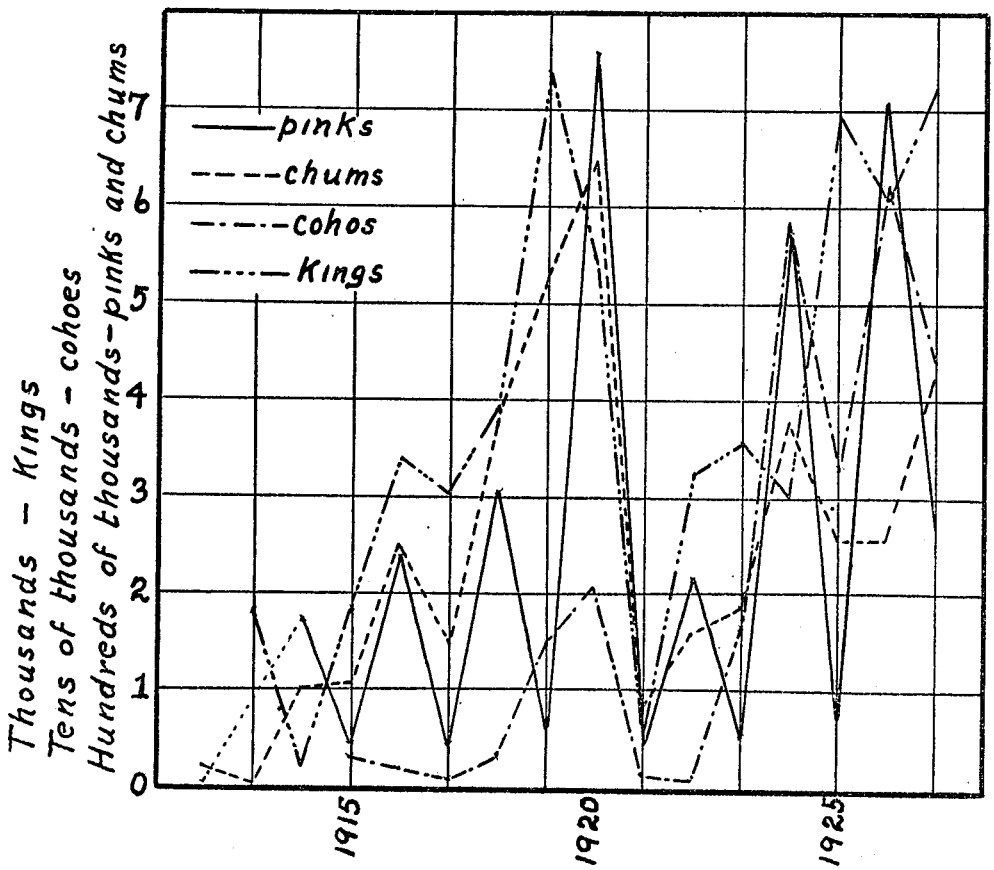

FIG. 16.—Catch of pinks, chums, cohos, and kings at Ikatan

same recovery from the depression of 1921 that is shown by Ikatan Bay. The tendency for the catches to return to the former level is evidenced by the pinks and chums, but neither the cohos nor kings have recovered to any marked degree. The cause of these differences is not apparent.

KING COVE

This small fishery, carried on chiefly in King Cove Lagoon, has produced chiefly chums and a few pinks. It has not been continuous, and the yield has been subject to wide fluctuations. No depletion is indicated by the available data.

NICHOLASKI SPIT

This particular locality has been fished only since 1924, when a trap was driven here. This trap has caught an unusually large number of red salmon, and Doctor Gilbert has stated, on the basis of scale studies, that these reds apparently were Bristol Bay fish (in part, at least) that were intercepted here as at Ikatan, Morzhovoi Bay, and Unga Island. A tagging experiment planned for the coming summer (1928) undoubtedly will settle this point, but it is interesting to note that our catch data lend considerable support to the theory even though only four years are available for study. If the catches of red salmon from 1924 to 1927 at Nicholaski be compared with the catches for the same years at Ikatan, it will be seen that, based on the size of the catch, the rank of each year is identical in the two localities. The largest catch was made in 1926, then came 1924, 1927, and 1925. While such a "rank" method of determining correlation is not especially reliable, particularly

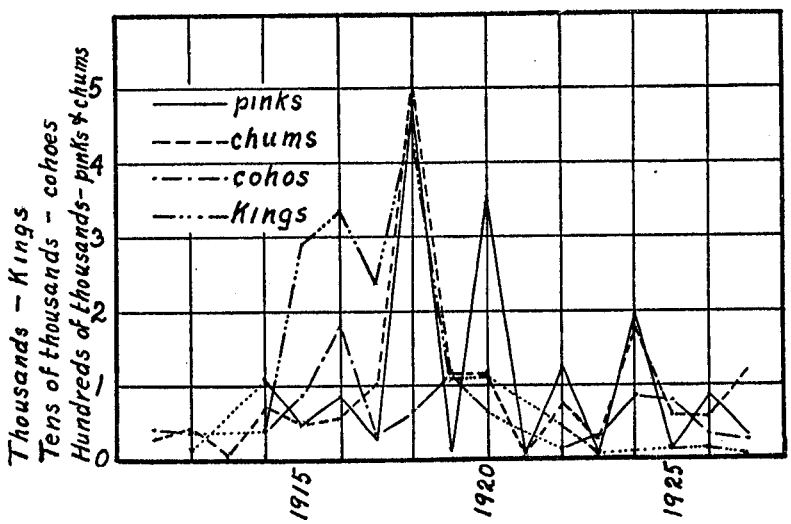

FIG. 17.—Catch of pinks, chums, cohos, and kings at Morzhovoi Bay

with so few data, in this case it is so marked as to lend considerable weight to the theory advanced by Doctor Gilbert. The data are too few to warrant any discussion of the other species.

PAVLOF BAY

The fishery in Pavlof Bay has been conducted with some intensity since 1918 (with the exception of 1921), when traps were first installed. The yield of red salmon has never been consistently large, although in 1918 the catch was over 30,000 and in 1926 exceeded 43,000. The catch of kings has been negligible and that of cohos has been very irregular and never large. The chief species taken in Pavlof Bay have been pinks and chums, and of these the catch of pinks has been by far the more important; but both species have shown such wide fluctuations that it is difficult to see any general trend. The pinks, of course, show the usual two-year cycle, abundant in the even years and scarce in the odd years; and the catch of both species shows the effect of the economic situation that prevailed in 1921. The poor catch of 1925 can

not be accounted for from the data at hand, but it appears reasonable to suppose that for some reason the traps were not actually fished. In general, the catches of all species appear to be as good now as they ever were.

VOLCANO BAY

In reality Volcano Bay is only an arm of Pavlof Bay and also was first fished intensively in 1918, when traps were driven. Previous to this time it had been fished regularly by seiners since 1911, except for 1913. Up to 1918 the yield had been almost exclusively chums, but after the traps were installed large catches of pinks were made and a few reds and cohos also were taken. As in Pavlof Bay, the catch of king salmon is negligible. The general trend of the catches of all four species is clearly upward. This rise is remarkably constant in the case of the even-year catches of pinks—each catch has been greater than the one preceding and the series does not even show the effect of the depression of 1921. As usual the catch of pinks in the odd years has been relatively small, although that, too, has been increasing, the catch of

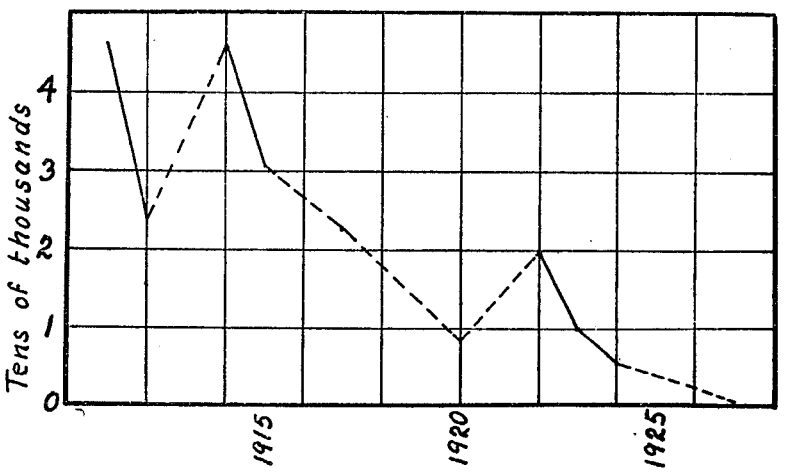

FIG. 18.—Catch of red salmon at Sanak

1927 being over 80,000. In the case of the chums the rise has been less regular, but the present level is distinctly higher than formerly. With the exception of 1918 there was no year previous to 1923 in which the catch equaled that of the poorest year since 1923; and the catches of both cohos and reds, while relatively small and subject to wide proportional fluctuations, show a constant tendency to increase. It is especially to be noted that the general tendency here is quite different from that shown by the fishery in Pavlof Bay. Our data are insufficient to show whether this is because the two localities draw upon fairly distinct stocks of salmon or because of fluctuation in the intensity of fishing. The general tendency for increased catches in Volcano Bay naturally would lead one to infer that the intensity of fishing has increased gradually, probably through improvements in the efficiency of the traps inasmuch as the number of traps remained constant until 1927.

SANAK ISLAND

The fishery at Sanak Island has always been a small one, conducted with beach seines, and has produced mainly red salmon. The data for the catch of reds are given graphically in Figure 18, and if our records of the total catch may be relied

upon to show abundance they tell a story of depletion to the point of practical extermination. The Sanak Islands are isolated and are visited rarely, and there can be little doubt that fishing has been mercilessly intense, with a result that might have been foreseen.

THIN POINT

The fishery at Thin Point is the oldest in the district, having been established in 1889, when a cannery was built and was operated for three seasons. A second cannery was built here in 1890 and was operated for two years only. In 1892 both canneries were closed, but salteries were operated during the period from 1892 to 1896, inclusive. Between the years 1896 and 1908, when our more detailed statistics begin, we have no record, and Cobb infers in his historical account of this fishery

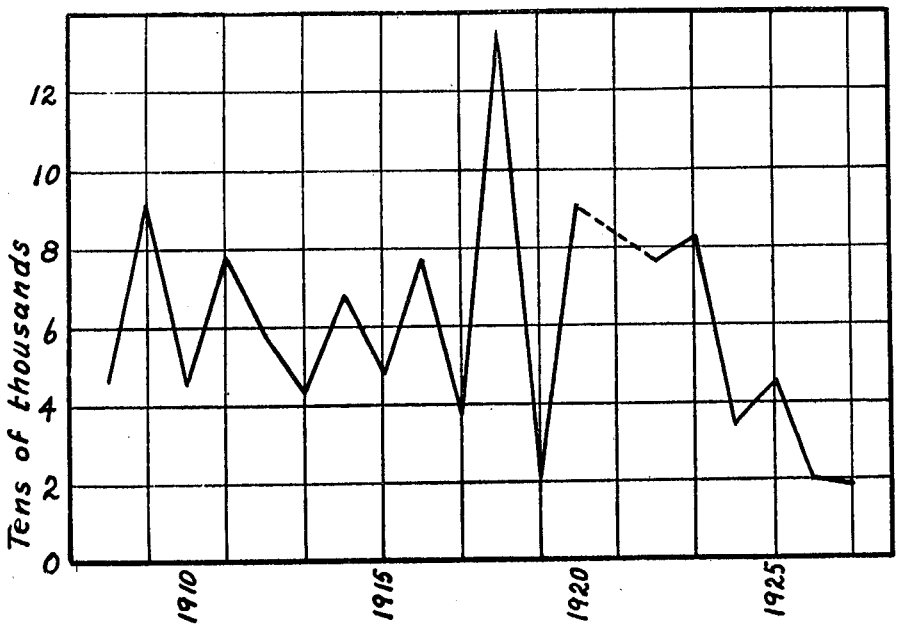

FIG. 19.—Catch of red salmon at Thin Point

that no commercial operations were carried on then at Thin Point. Most of the data we have for these early years has been taken from the reports of the special agents of the Treasury Department. For the three years in which the canneries were operated we have no record of the species canned, but it is fairly certain that they were all reds. The packs were as follows: 1889, 28,748 cases; 1890, 9,417 cases; and 1891, 11,000 cases. The pack of salted fish in 1892 amounted to 1,500 barrels. There is no record for this year of the species used nor of the number of fish caught, but it is probable that they were all red salmon and that approximately 75,000 fish were taken. The records for the years 1893 to 1896 state definitely that the fish were all red salmon, and the packs and catches were as follows: 1893, 1,232 barrels, 60,000 fish; 1894, 2,519 barrels, 125,950 fish; 1895, 375 barrels, 23,453 fish, and 1896, 611 barrels, 27,198 fish. The records for the recent years, beginning with 1908, are given in Table 9, and the catch of red salmon is shown graphically in Figure 19.

This fishery, like the one at Sanak Island, has been conducted solely with beach seines and has produced chiefly red salmon, although occasional good catches of pinks, chums, and cohos have been reported in recent years. It does not appear from our records that the catches of red salmon were, on the whole, greatly reduced previous to the closure of the lagoon to fishing in 1924. As a result of this closure the fishing has been restricted to the beach outside the entrance to the lagoon, and a marked reduction in the catch has resulted. This fishery has also been a very intense one, and it is rather surprising that the catches previous to 1924 did not show evidence of greater depletion.

SHUMAGIN DISTRICT

The following localities of the Shumagin district are not named on the map:

Acheridin Bay, southern shore of Unga Island.

Red Cove, southwest side of Popof Island.

Balboa Bay, Alaska Peninsula, directly north of Unga Island across Unga Strait.

Ivanof Bay, Alaska Peninsula, the first bay east of Kupreanof Point.

Stepovak Bay, Alaska Peninsula, the first bay west of Kupreanof Point.

Orzinski (Orzenoi) Bay, a small bay on the west side of Stepovak Bay.

The same general regulations have applied to the Shumagin district as were in force in the Ikatan district, and the following special regulations have been promulgated: Stepovak and Balboa Bays, with the exception of Orzinski Bay, were closed to fishing in 1925, and the catch at Orzinski was limited to 25,000 red salmon. In 1926 traps were prohibited on all islands except Unga, and beginning with 1928 the traps on Unga Island will be restricted to the east side (Popof Strait). Table 10 presents the data for this district.

TABLE 10.—*Salmon caught and fishing appliances used in the Shumagin Islands district, 1908 to 1927*

Year	Coho	Chum	Pink	King	Red	Beach seines		Purse seines		Gill nets		Pile traps
						Number	*Fathoms*	*Number*	*Fathoms*	*Number*	*Fathoms*	*Number*
Acheredin Bay:												
1912					30,925							
1922					11,227							
1923		11,989	2,766		293							
1924					5,316							
1925					6,285							
1926					6,500							
1927					4,498							
Balboa Bay:												
1918	66	85,967	121,046									
1919	100	36,100	750		192							
1920	620	21,130	129,498	5	4,600							
1922		10	50		40							
Ivanof Bay:												
1912		14,200										
1917		16,629			210							
1918		37,168	51,655									
1919		11,791										
1923		3,293	268									
1924			15,000									
Orzinski Bay:												
1908					22,500							
1909					16,362							
1910					1,324							
1911					3,593							
1912					45,000							
1913					27,000							
1914	5,650				25,800							
1915					20,400							
1916			5,600	30	20,000							

TABLE 10.—*Salmon caught and fishing appliances used in the Shumagin Islands district, 1908 to 1927*—Continued

Year	Coho	Chum	Pink	King	Red	Beach seines		Purse seines		Gill nets		Pile traps
						Number	*Fathoms*	*Number*	*Fathoms*	*Number*	*Fathoms*	*Number*
Orzinski Bay—Continued.												
1917					30,000							
1918		559	400		29,666							
1922					26,000							
1923					14,000							
1924					30,066							
1925			300		12,450							
1926					25,000							
1927	5,600		83,314		2,364							
Popof Strait:												
1916			9,000									
1917	300	23,400	1,000		14,339							
1918	4,557	24,511	172,851	255	33,687							
1919	6,239	39,118	5,462	1,147	31,650							6
1920	1,850	23,100	314,146	375	59,694							6
1922		52,358	153,000	3,241	513,890							3
1923	50,054	144,342	68,000	378	336,711							3
1924	53,250	122,370	1,491,092	839	226,494							3
1925	64,390	245,956	223,454	3,599	354,662							4
1926	83,735	292,244	986,294	2,711	483,426							2
1927	69,760	341,752	561,674	2,261	178,572							3
Red Cove:												
1911					2,597							
1917					19,161							
1918					10,506							
1922					24,688							
1923					6,097							
1924					5,931							
1925			10,000		12,780							
1926					1,261							
1927		190	190		5,598							
Stepovak Bay:												
1919	2,200	40,503	561		7,700							
1920	39	900	4,451	28	8,558							
Unallocated:												
1912					7,150							
1914					19,290							
1916	200	160	10,200		61,020							
1917		2,200			17,430							
1918			14,800		28,980							
1920	1,400		83,289									
1922					10,000							
1923	370	1,450	960		720							
1925	1,958	158										
1926	7,215	24,830	136,656	290	38,005							
1927	2,021	28,100	128,801		3,720							
Total:												
1908					22,500	1	40					
1909					16,362	1	40					
1910					1,324	1	40					
1911					6,192	2	100					
1912		14,200			83,075	7	550			2	100	
1913					27,000	1	100			2	200	
1914	5,650				45,090	1	100					
1915					24,072	4	265			6	125	
1916	200	160	24,800	30	81,020	3	305			3	125	
1917	300	42,229	1,000		80,930	10	680			3	125	
1918	4,623	148,205	360,752	255	102,839	5	575			3	220	
1919	8,339	127,512	6,773	1,147	39,542	4	205	2	210			6
1920	3,909	45,130	531,384	408	72,852	5	255	2	315			6
1922		52,368	153,050	3,241	485,846	2	135	4	475	2	100	3
1923	50,424	161,074	71,994	378	357,821	1	75	1	150			3
1924	53,250	122,370	1,506,092	859	267,807							3
1925	66,348	256,114	233,754	3,599	386,177	2	150	4	400	1	90	4
1926	90,950	317,074	1,122,950	3,001	940,369	5	395	1	100	4	200	3
1927	74,381	363,164	780,857	2,261	194,752	4	425	2	200	2	150	3

NOTE.—No catches were reported in the years not shown. The unallocated catches were taken wholly in the coastal waters of the Shumagin Islands, but the specific locality was not indicated in all cases. Among the places mentioned are the following: Barn Cove, Bay Point, Coal Harbor, Eagle Harbor, East Bight, Falmouth Harbor, Korovin Island, Little Harbor, Meno Creek, Nagai Island, Northeast Bight, Red Bluff, Sanborn Harbor, Unga Strait, and Wosnesenski Island.

ACHERIDIN BAY

So far as our records go, the fishery here has been very irregular. A catch of nearly 31,000 red salmon was made in 1912, but no other catch was recorded until 1922, although since then reports have been received yearly. It is very probable, however, that the fishery was fairly continuous between 1912 and 1922 and that for one reason or another records have not been submitted. The fishery is mainly for red salmon, but in 1923 a small catch of pinks and chums was made also. If our record be taken as it stands and the catch of 1912 be considered as a fair indication of the abundance at that time, it is clear that this locality has been seriously depleted. The available data are too few to warrant a definite conclusion to this effect, however.

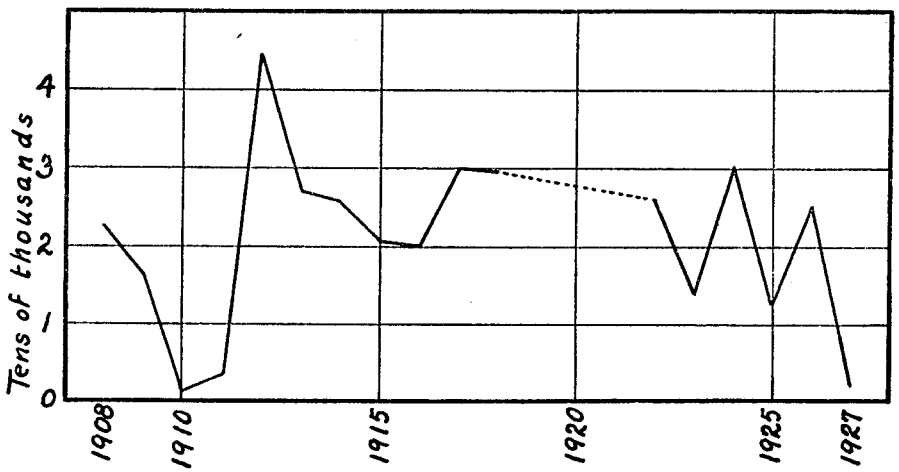

FIG. 20.—Catch of red salmon at Orzinski

BALBOA AND IVANOF BAYS

The fisheries in both these localities have been irregular so far as our reports show and no analysis is possible. They have produced chiefly pinks and chums caught by beach seines and presumably of local origin.

ORZINSKI BAY

This bay receives a small river that supports a run of red salmon that has formed the object of a fishery for many years. Cobb states that a cannery was started here in 1889 but operated only for two years. For these years we have no record of either the pack or the catch. Cobb states further that a saltery was established here about 1905, but the earliest records available to us begin with 1908. Very few fish other than red salmon had been taken here up to 1927, but in that year an unprecedented catch was made of over 83,000 pinks. It seems possible that this was due to some economic factor with which we are not acquainted. The catches of red salmon are shown graphically in Figure 20. It is not apparent that there has been much change in the yield, unless the poor catch recorded for 1927 is an indication of a fall. However, as this smaller yield of reds was accompanied by a greatly augmented yield of

pinks we are inclined to the opinion that there was some marked change in the conduct of the fishery. Leaving 1927 out of consideration, there would still appear to be some slight fall in the yield, which possibly may be referred to depletion. It is very interesting to note, however, that the discontinuance of the fishery during the years 1919 to 1921, inclusive (if, indeed, our records are reliable), had no appreciable effect in increasing the future runs.

POPOF STRAIT

The most important fishery in the Shumagin district is prosecuted in Popof Strait, where several extremely productive traps are situated. Our records show that traps were driven here first in 1919, but it was not until 1922 that the production increased markedly. Doubtless this was due to improvements made in the location and contruction of the traps. The tagging experiments of 1922 and 1923 showed that these traps caught large numbers of the fish bound for Ikatan and Morzhovoi Bays and thence for Bristol Bay. With this in mind we have investigated the correlation shown between the catches in Popof Strait and those at Ikatan and in Bristol Bay for the years 1922 to 1927, inclusive. For this purpose we have used Spearman's coefficient of correlation (ρ), which is recommended for cases in which the number of items is small. While this method is not as accurate as the better-known formula of Pearson (r) it is as reliable a method as is justified by the available data. The following values of ρ have been determined:

Popof Strait and Ikatan	+0.657 ±0.164
Popof Strait and Bristol Bay	+.600 ±.184

A high degree of correlation is indicated, as would be expected from our knowledge of the routes of migration.

On account of the marked change in the effectiveness of the fishery, which took place in 1922, and the short series of years since that event we do not feel justified in making any additional analyses of the data.

RED COVE

This fishery has drawn chiefly upon a small run of red salmon that enters a stream flowing into Red Cove. As is the case in most such small fisheries, doubtless it has been prosecuted intensely, and our data, although not extensive, indicate a general decline in the yield, which may safely be ascribed to depletion.

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ELECTRIC FISH SCREEN

By F. O. McMillan

Associate Professor of Electrical Engineering, Oregon State College

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FISH-PROTECTION PROBLEM

Every year millions of game fish and fry of anadromous food fish are carried out on the fields and left to die because they have followed some irrigation canal instead of the main stream channel. Many others are killed by mechanical injury or sudden pressure change incident to passing through hydraulic turbines. The problem of protecting fish from these dangers is not new but probably is as old as the knowledge of irrigation. However, as irrigation and power projects increase in size and number and the supply of fish is depleted, the problem commands greater attention. As early as 1895, Dr. C. H. Gilbert, of Stanford University, called the attention of Hollister D. McGuire (then fish and game protector of Oregon) to the destruction of blueback-salmon fry on the irrigation projects near Wallowa Lake (McGuire, 1896). This led to legislation in Oregon requiring the screening of waterways dangerous to

fish. Virtually without exception the biennial reports of the fish and game commissioners since that time have stressed the importance of fish screens.

Two classes of fish of quite different habits are involved in the problem of fish protection. They are those of anadromous habits, such as the salmon and steelhead trout, and those that confine their migration entirely to fresh water. Sportsmen are interested in both classes, while the commercial fishermen, especially in the West, are interested almost entirely in fish that mature at sea.

Of the anadromous fish, the various species of salmon are by far the most important on the Pacific coast. Their habits are such that they are particularly susceptible to destruction, due to unnatural waterway conditions. Artificial stream barriers prevent the mature fish, returning from the ocean, from reaching their spawning beds in the headwaters of the streams. This necessitates the construction of fishways around or over these barriers. The young salmon fingerlings, when impelled by instinct to migrate seaward, are confronted by the peril of destruction in large numbers by entering irrigation ditches, canals, mill races, and other dangerous watercourses. This danger can be eliminated only by the proper protection of the entrances to these waterways. This is not an easy task, especially if mechanical screens are used, because ¼-inch mesh is required to give protection to the very young fry in the yolk-sac stage. The largest salmon to which protection would have to be afforded during their seaward migration would probably be the yearling chinook salmon. Dr. Willis H. Rich has found that the average length of yearling chinook salmon is approximately 4 inches (100 millimeters), both in the Columbia and Sacramento Rivers (Rich, 1920). It is obvious, then, that if mechanical screens were constructed to protect only the yearling salmon, the mesh would be small and the accumulation of leaves and débris would be a constant menace to the flow of water through the screen. What is true of the screens for the protection of salmon is likewise true of screens for protecting the fish living exclusively in fresh water. Some of the larger sizes of these fresh-water fish could be protected by screens of larger mesh. This would make the screen slightly less susceptible to the accumulation of débris. However, such screens obviously would offer only partial protection.

PROTECTIVE LAWS

Adequate laws have been enacted by the legislatures in all of the States having this fish-protection problem. These laws give all legal authority necessary for the protection of the entrances to dangerous waterways if satisfactory devices are available with which to screen them. A typical example of such laws is found in section 61 of the game laws of Oregon, quoted here:

Any person owning, in whole or in part, or leasing, operating, or having in charge any irrigation ditch, or canal, mill race, or other artificial watercourse, taking or receiving its waters from any river, creek, or lake in which fish have been placed or may exist, shall, upon order of the State game commission, place or cause to be placed, and shall maintain, to the satisfaction of the State game commission, over the inlet of such ditch, canal, mill race, or watercourse, a grating, screen, or other device, either stationary or operated mechanically, of such construction, fineness, strength, and quality as shall prevent any fish from entering such ditch, canal, mill race, or watercourse, to the satisfaction of the State game commission. But before said State game commission shall adopt any permament plan for a screen or device to be placed in irrigating ditches, it shall be its duty to conduct a competitive examination, and at such examination all persons desiring to do so may

submit to said State game commission, for its approval or rejection, working models of its [their] respective screens or other devices for the protection of fish. Inadequate screening devices may be ordered removed and new screens ordered installed when, upon investigation by the State game commission or any of its representatives, it is determined that any screen, grating, or other device, either by construction, operation, or otherwise, is found to be inadequate by the State game commission. In the event the owner in whole or in part, or person leasing, operating, or having in charge such ditch, canal, mill race, or other artificial watercourse, shall fail or refuse to comply with the instructions of the State game commission with respect to the installation, maintenance, or repair of such screen, grating, or other device within such reasonable time as may be specified by the State game commission, he shall be guilty of a misdemeanor, and said State game commission or any of its representatives shall have power to close forthwith the head gates or place such other barrier or obstruction in such ditch, canal, mill race, or other artificial watercourse as said State game commission may deem necessary to prevent the flow of water through such ditch, canal, mill race, or other artificial watercourse until a screen, grating, or other device shall be placed therein to the satisfaction of the State game commission.

From the above law it is obvious that there is nothing lacking in the way of legal authority for the protection of fish from dangerous waterways. Unfortunately, however, the effectiveness of these laws has been impaired greatly because adequate screens have been expensive to install and very difficult to maintain.

MECHANICAL SCREENS

Mechanical screens of the stationary type, having a mesh of sufficient fineness to afford adequate protection to fish fingerlings, have been found very difficult and expensive to maintain. The chief difficulties are the constant accumulation of leaves and débris and mechanical injury to the screen by large floating pieces of débris.

The objectionable features of the stationary-type mechanical screen have been reduced greatly by the revolving, self-cleaning type of screen, which has been available since 1918. However, the revolving screen has not solved the fish-protection problem and leaves much to be desired in the screening of dangerous waterways.

ELECTRIC SCREEN

The idea of using an electrified area in water to direct the movements of fish is not new. At least three and perhaps more United States patents have been granted on methods of using electricity for this purpose. The most recent of these patents was applied for in March, 1922, and was granted in November, 1924 (Burkey, 1924). Hence, no claim is made that the idea of an electric fish screen is new or novel.

Many installations have been made of electric fish "stops" in Washington, Oregon, and California. Some of these installations have been considered successful; others have been pronounced absolute failures. As a result of these conflicting opinions, the electric fish "stop" came into disrepute in some localities and in some instances was abandoned entirely as impractical. Investigation disclosed the fact that, virtually without exception, the installation of electric "stops" had been made by those who had little or no knowledge of electricity, and there was an absolute dearth of information about the voltage gradients fish were susceptible to in water and the voltage gradients required to produce paralysis and death. The only fact that was known definitely was that virtually every installation succeeded in killing some fish. Hence, the electric fish "stop" rapidly gained a reputation as a destroyer

rather than a preserver of fish. In the light of these facts, J. E. Yates, assistant engineer of the Pacific Power & Light Co., determined to have an investigation made to find, as far as practical, the facts about the electric fish screen. The results of this investigation are given in this report.

ACKNOWLEDGMENTS

Thanks are due especially to J. E. Yates for advice, assistance, and suggestions given during the investigation. Both the Oregon Fish Commission and the Oregon Game Commission have shown great interest in the experiments. The Oregon Fish Commission very generously lent facilities at the Bonneville fish hatchery and provided the fish used in the experiments. Eugene Howell, superintendent of the Bonneville hatchery, and his assistants gave invaluable help with the experimental work. Dean John N. Cobb, of the University of Washington, furnished drawings of one of the electric "stops" used in irrigation canals in Washington. H. B. Holmes, biologist with the United States Bureau of Fisheries, gave much valuable counsel and had great interest in the entire investigation. The Pacific Power & Light Co. financed the work.

PROBLEMS INVESTIGATED

The following problems were studied during the course of the experimental work at Bonneville, Oreg.:

1. What uniform voltage gradient in water will cause a fish to become paralyzed, and how does this voltage gradient vary with the length of the fish?
2. How does the voltage gradient and duration of application affect the mortality of fish subjected to excessive voltage gradients?
3. Do fish subjected to electric shocks in various degrees suffer any after effects other than those immediately observable?
4. What influence does the resistivity of the water in which the fish are immersed have upon the voltage gradient required to produce paralysis?
5. What variation in water resistivity is found in various rivers and streams?
6. Do fish, when swimming into an electrified area, such as that around an electric screen, sense the direction of the danger?
7. Does the relation of the lines of electric-current flow and the equipotential surfaces with respect to the opening protected and the direction of water flow in the stream have any influence on the effectiveness of an electric screen?
8. Will an electric screen effectively prevent fish entering a protected area?

EXPERIMENTAL DATA

VOLTAGE GRADIENT REQUIRED TO PRODUCE PARALYSIS

One of the most fundamental things needed to be known in connection with the application of electricity to fish screens was the order of magnitude of the voltage gradient required to produce paralysis and cause fish to lose all control of movement. To obtain these data, an aquarium with glass sides and wood bottom and ends was fitted with two parallel metal plates having as nearly as practical the same area as the cross section of the aquarium. These plates were connected with the secondary

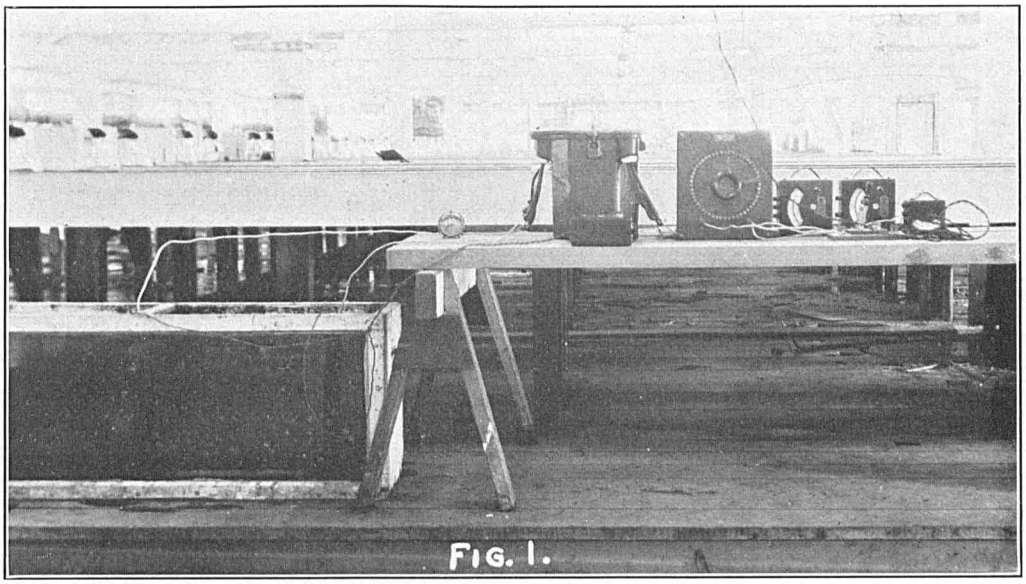

FIG. 1.—Apparatus for uniform voltage gradient tests

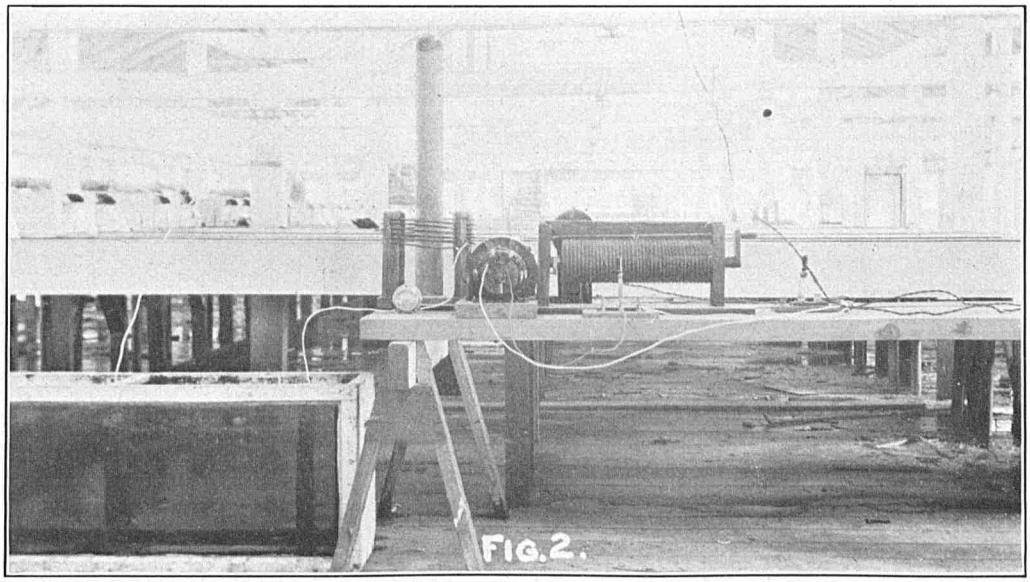

FIG. 2.—High-frequency apparatus

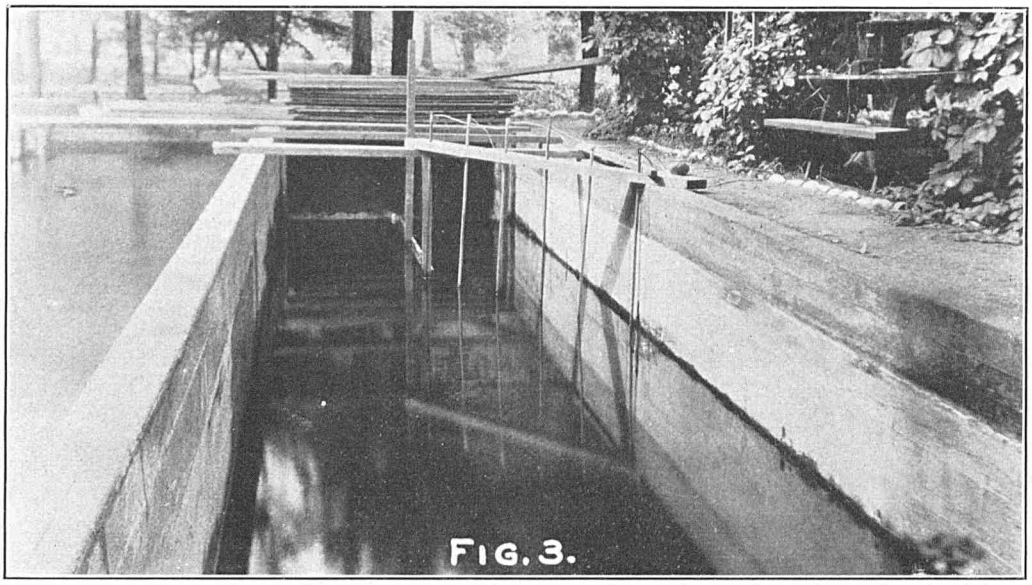

FIG. 3.—Electric screen in concrete pool

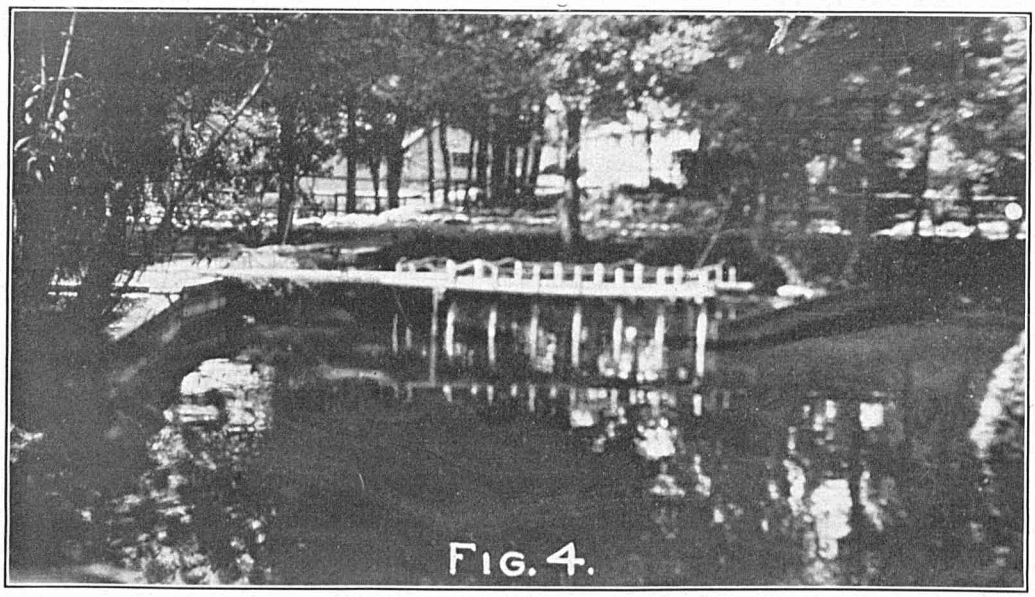

FIG. 4.—Electric screen in pond number 12

terminals of an insulating transformer. The insulating transformer was used to insure against leakage to ground from one plate, due to the grounded neutral of the 110–220 volt lighting circuit. A variable voltage from zero to the maximum value required was obtained by the use of a resistance potentiometer supplying the primary of the insulating transformer. A picture of this apparatus as set up is shown in Figure 1. This arrangement of parallel plates supplied from a variable voltage supply makes it possible to obtain a uniform voltage gradient in the aquarium of any desired value from zero to the maximum necessary in these experiments. All of the tests described in this report, unless otherwise specified, were made with 60-cycle alternating current. The voltages and the voltage gradients are root mean square values.

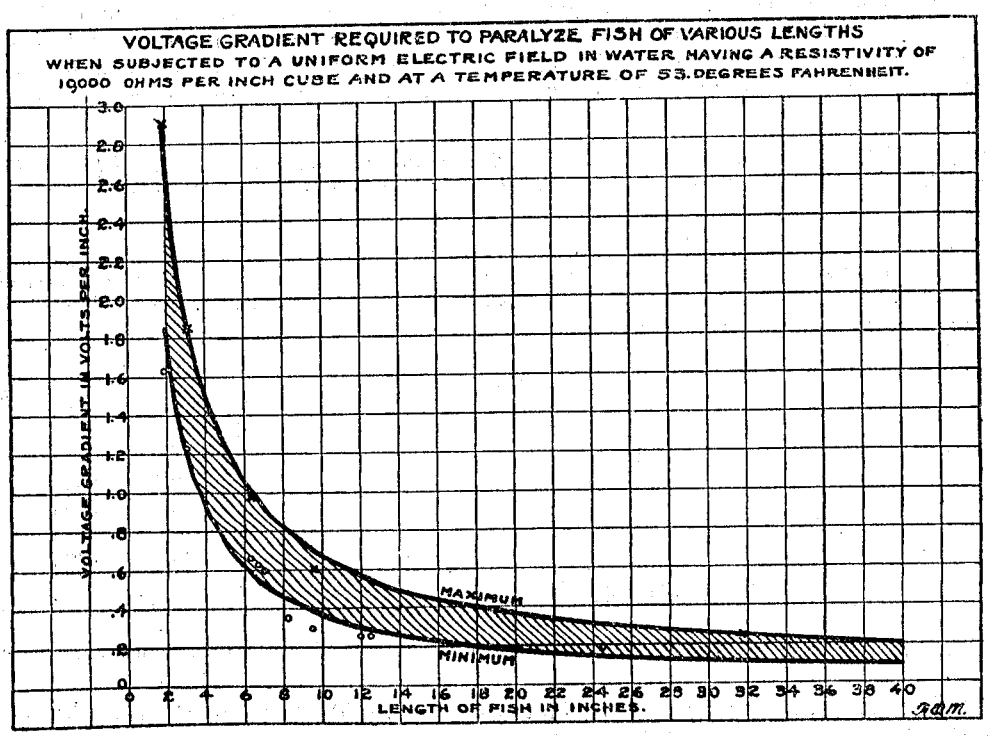

FIG. 5

The method of determining the paralysis voltage was to place a number of fish selected for uniformity of size in the aquarium between the parallel plates and raise the voltage in small increments, holding each increment one minute. When the first fish became paralyzed the plate voltage was recorded as the minimum paralysis voltage. The increase in voltage was continued until the fish were paralyzed and the plate voltage again recorded, this time as the maximum paralysis voltage. From these voltages and the known plate spacing the minimum and maximum voltage gradients per inch to produce paralysis were calculated. The lengths of the fish used in the experiment were measured carefully then from the tip of the snout to the end of the middle rays of the caudal (tail) fin. These measurements were made in inches. The average length of the test group was calculated and recorded. These tests were repeated on many fish ranging in length from 1.87 to 31.75 inches. A

summary of the results is tabulated in Table 1, tests 1 to 14, inclusive, and shown graphically in Figure 5. These data bring out two very interesting facts. First, the voltage gradient required to produce paralysis is very low. Second, the voltage gradient required to produce paralysis is inversely proportional to the length of the fish. In other words, the long fish require a much lower field strength to paralyze them than the short ones. This is the opposite of the conception held by many previous to these tests. In fact, the most recent patent found covering an electric fish "stop" makes the following statement (Burkey, 1924):

> With the use of the transformer it is possible to have an electric current at the inlet end of the fish "stop" of a low amperage for the purpose of stopping or turning back small fish and thereby obviate any possible chance of injuring or killing small fish by coming in contact with electrical current of too high amperage. The electrodes, being arranged in three series and connected to the transformer, permit electrical currents to be passed through the water of progressively increasing amperage, so that when large fish are not stopped or turned back by the low amperage the intermediate series of electrodes will supply electrical current of sufficient amperage to turn back or stop such sized fish.

TABLE 1.—*Voltage gradient required to paralyze fish of various lengths when subjected to a uniform electric field in water having a resistivity of 10,000 ohms per inch cube and at a temperature of 53° F.*

Test No.	Fish			Voltage gradient, in volts per inch, to paralyze the fish	
	Species	Number	Length		
			Inches	*Minimum*	*Maximum*
1	Rainbow and loch leven	30	1.87	1.630	2.910
2	Chinook	30	3.10	1.230	1.850
3	Rainbow	3	6.25		.975
4	do	3	6.29	.666	
5	do	3	6.67	.625	
6	do	1	7.00	.596	
7	do	1	8.25	.358	
8	do	1	9.50	.296	
9	do	1	9.50		.592
10	do	1	12.00	.250	
11	do	1	12.50	.292	
12	do	1	12.50	.250	
13	Chinook, male	1	24.50	.188	
14	Chinook, female	1	31.75		.250

NOTE.—The rainbow trout were *Salmo irideus;* the loch leven trout were *Salmo levensis;* and the Chinook salmon were *Oncorhynchus tschawytscha.*

It is obvious, in the light of the facts as given by Table 1 and Figure 5, that the situation is just the reverse of that anticipated by the fish-stop inventor quoted above.

The equation for the "minimum" length-voltage gradient for paralysis curve has been calculated and found to be

$$g=3.70L^{-0.99}$$

which, within permissible limits of error, may be written

$$g=\frac{3.70}{L}$$

where g = voltage gradient per inch to produce paralysis and L = length of fish in inches.

Thus it is seen that there is a very simple and interesting relation between the length of fish and the voltage gradient required to produce paralysis. This equation

applies for water having a resistivity of 10,000 ohms per inch cube, but for other resistivities the constant term 3.70 must be modified, as will be shown later under the discussion of the influence of water resistivity upon paralysis-voltage gradient.

It has been suggested that different species of fish may require different voltage gradients to produce paralysis. This point should be investigated further. Tests were made on four different species at Bonneville, and all gave results that fell within the range between the minimum and maximum curves. It is probable that no greater variation will be found between the different species involved in protection problems than is found between individuals of the same species. That there is considerable variation between individuals is shown by the separation of the maximum and minimum curves of Figure 5. This variation is due to several factors, among which may be mentioned slight variation in the length of individuals in a test group, variation in the condition and vitality of individuals and the position of the fish with respect to the lines of current flow, and the equipotential surfaces in the electric field. Great care was exercised to obtain healthy, normal fish. Some of the rainbow trout at Bonneville were found to be infested with an external copepod parasite, which attacks the mouth and gills. For this reason all of the rainbow trout used were examined carefully for this parasite, and those infested to a degree that would affect their vitality were rejected.

HIGH-FREQUENCY TEST

A high-frequency oscillator was set up, as shown in Figure 2, and a group of 30 chinook-salmon fingerlings, averaging 3.04 inches in length, was subjected to a 500,000-cycle electric field. Plate voltages more than 100 times those used at 60 cycles were applied. None of the fish gave any indication of feeling the existence of an electric field in the water. This phenomenon probably is due to the fact that virtually all of the current at this high frequency is flowing on the surface of the water between the electrodes, and consequently there is no appreciable electric field in the water.

CONTINUOUS-CURRENT TEST

A continuous-current test was made on a group of 30 chinook-salmon fingerlings, using the direct-current exciter in the hatchery hydraulic-power plant as a source of continuous potential. The voltage gradients for paralysis were 1.33 volts per inch minimum and 2.0 maximum. The average length of the fish was 3.0 inches. These values check the 60-cycle alternating-current tests very well, as shown by the maximum and minimum curves in Figure 5.

DURATION OF APPLICATION AND MORTALITY

Returning to the 60-cycle alternating-current source of supply, a series of tests was made to determine the influence of the time of voltage application on the number of fish killed. These tests were made on chinook-salmon fingerlings having an average length of 3.1 inches. They were made by subjecting 14 groups of approximately 30 fish each to a definite voltage gradient for a fixed period of time. The voltage gradients were selected from below the paralysis value to values of approximately twice this voltage gradient, and two arbitrary periods of application (1 minute and 5 minutes) were chosen. An entirely fresh lot of fish was used for each test to eliminate any cumulative effects from repeated voltage applications. The results of these tests

are summarized in Table 2. These data show conclusively, as one would expect, that the duration of application of the potential has a decided effect upon the mortality of the fish when voltage gradients above the paralysis value are applied. A voltage gradient of 1.48 volts per inch, used in test No. 19, paralyzed 26 of the 30 fish in one minute but did not kill any of them. Essentially the same voltage gradient, 1.46 volts per inch, used in test No. 27, paralyzed all of the fish, and after a 5-minute application 69 per cent of the fish did not recover. The duration of the period of complete paralysis or suspended animation appeared in every case to be the greatest factor in determining recovery from electric shock. Virtually, without exception, it was observed that when a group of fish was paralyzed the recovery was in the inverse order of the paralysis—that is, the fish paralyzed first were last to recover and those paralyzed last were first to recover.

TABLE 2.—*Influence of voltage gradient and duration of application on mortality of chinook-salmon fingerlings 3.1 inches long when subjected to a uniform electric field in water having a resistivity of 10,000 ohms per inch cube and at a temperature of 53° F. Electrode plates, 212 square inches area, spaced 12 inches apart*

Test No.	Number of fish	Plate voltage	Voltage gradient, volts per inch	Duration of application, minutes	Fish killed	
					Number	Per cent
17	30	14.4	1.20	1	0	0
18	27	16.0	1.33	1	0	0
19	30	17.8	1.48	1	0	0
20	30	19.9	1.66	1	3	10
21	30	22.2	1.85	1	3	10
22	31	24.5	2.04	1	12	38.7
23	30	29.7	2.48	1	17	56.6
24	30	5.57	.464	5	0	0
25	30	10.25	.854	5	0	0
26	30	15.0	1.25	5	0	0
27	29	17.5	1.46	5	20	69
28	29	20.4	1.70	5	18	62
29	30	23.0	1.92	5	20	66.6
30	29	25.5	2.12	5	23	79.3

OBSERVATIONS DURING PARALYSIS AND RECOVERY

Some interesting observations were made of the characteristic behavior of fish during the application of potential and during the recovery from an electric shock. These will be given here. When the electrode voltage is increased gradually from a very small value the fish begin to show signs of feeling the potential at from 10 to 20 per cent of the value for paralysis. This is indicated by short, quick, caudal (tail) fin movements and slight shifts in position. At from 50 to 80 per cent of the paralysis voltage they become quite active, swimming about in all directions, seeking to avoid the uncomfortable electric field. Just before reaching the paralysis voltage, the fish are extremely active, dashing about trying to escape the field. Then they become paralyzed, the pectoral fins stand motionless and virtually at right angles with the body; the fish then turns belly up and sinks to the bottom, where it lies on one side. In some instances the gill action apparently stops entirely, while in others it continues feebly. The entire fish turns perceptibly lighter in color while paralyzed. The change in color is due to changes in the distribution of the pigment in the chromatophores of the skin (Kuntz, 1917). These chromatophores are probably under

the direct control of the sympathetic nervous system and hence are disturbed very seriously by a severe electric shock. The first indication of recovery after the potential is removed is a reestablishment of gill action, or a strengthening of it if the gill action has not stopped entirely. After the gill action has reached nearly normal the body begins to flex, and in a short time the normal swimming position is resumed.

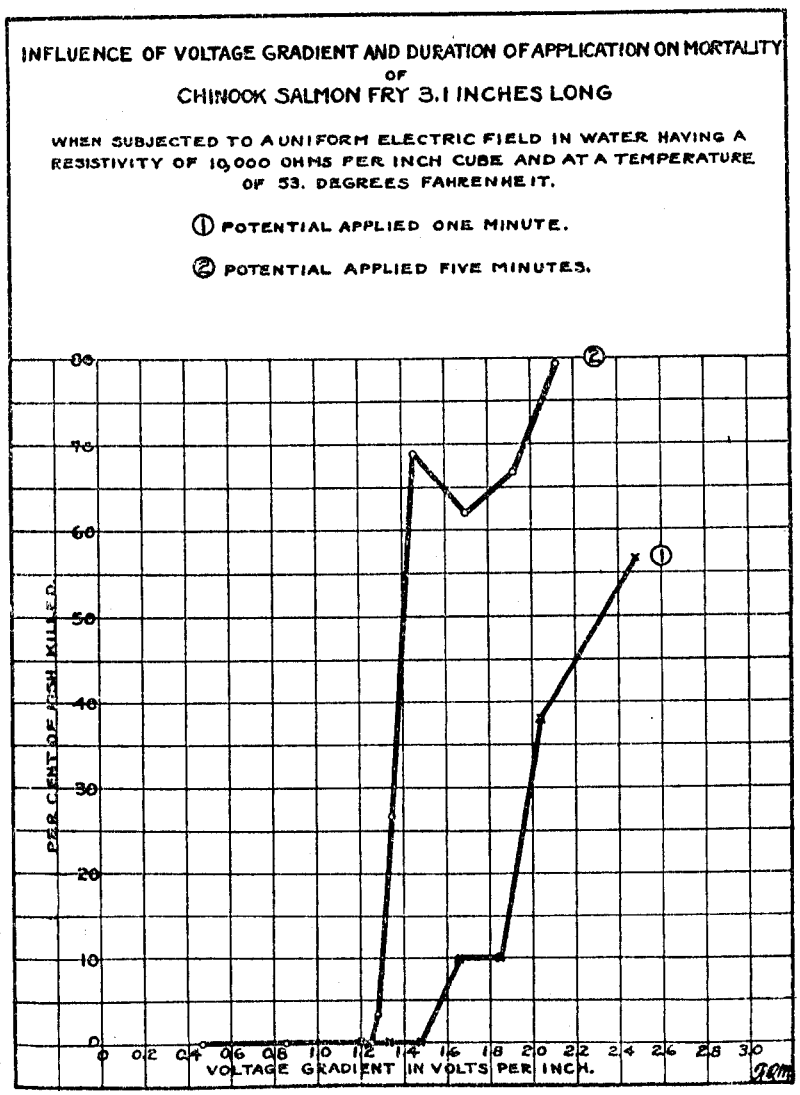

FIG. 6

The movements are slow and sluggish at first, but, except in the most severe cases, normal activity is resumed quickly. This recovery from electric shock requires varying amounts of time from a few seconds to 45 or more minutes. The longest time of recovery accurately recorded during the tests was 45 minutes for a 7-inch rainbow trout.

OBSERVATIONS AFTER ELECTRICAL TESTS

All of the fish used in tests 1 to 30, inclusive, except those killed outright, were kept, segregated by test numbers, in the running water of the hatchery troughs for observation. Check groups taken from the same hatchery pools, which had not been subjected to any potential, were used for comparison. These fish, totaling 407 in number, were observed very carefully twice daily for 10 days. During this period the fish that had been subjected to the electrical tests did not develop a single symptom that did not develop in the check groups as well. During the first two days of observation one fish that had been subjected to a high-voltage gradient became

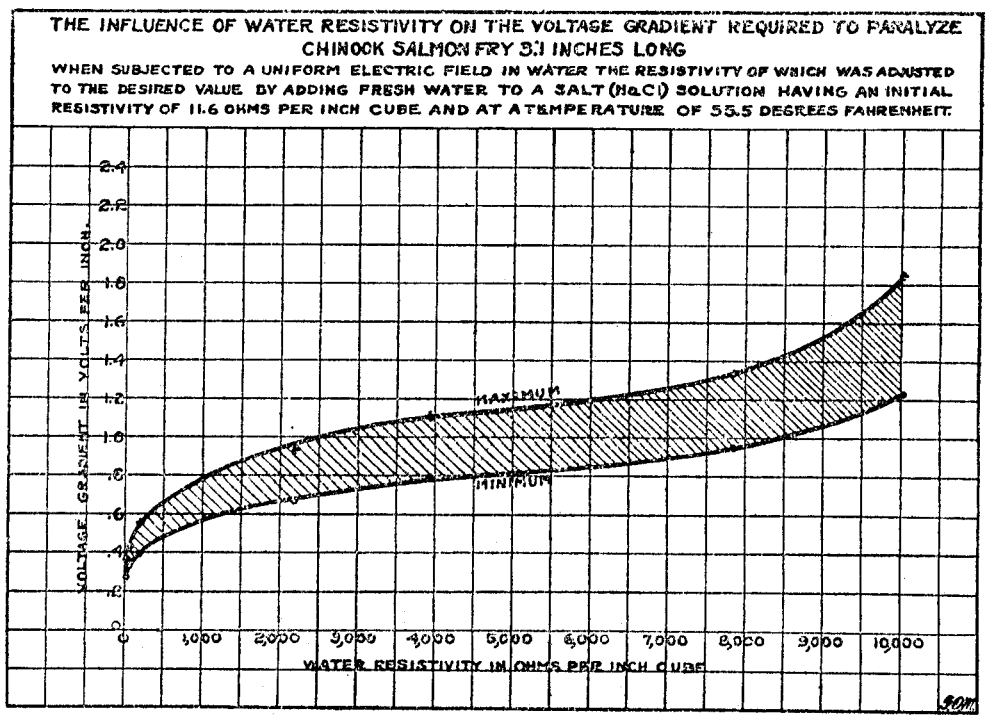

FIG. 7

blind, and it was thought at first that it was due to an electrical injury. Later, however, fish in the check groups became blind in the same manner. During the observation period 9 of the 407 fish became blind in one eye. This blindness probably was caused by mechanical injury in the close confinement of the hatchery troughs. The male and female chinook salmon used in tests 13 and 14 of Table 1 were taken from a group of 21 being held in one of the ponds on Tanner Creek for spawning purposes. These salmon had scars by which they could be identified, and after reviving from an electrical test they were returned to the pond. These fish spawned later, and Eugene Howell, the superintendent of the hatchery, reported that milt and eggs were normal and did not show any evidence of sterilization.

INFLUENCE OF WATER RESISTIVITY ON THE PARALYSIS-VOLTAGE GRADIENT

A series of paralysis-voltage gradient tests were made with chinook-salmon fingerlings, using water varying in resistivity from 11.6 to 10,030 ohms per inch cube to determine the influence of water resistivity upon the paralysis-voltage gradient. The results of these tests (Nos. 31 to 37, inclusive) are summarized in Table 3 and shown graphically in Figure 7. The water resistivity was adjusted to the desired value in these tests by first making a salt (NaCl) water solution that had the resistivity of sea water; fresh water was then added to obtain the desired increments in resistivity. These data show a rapid change in the voltage gradient required to paralyze fish at low values of water resistivity, a slower change at intermediate resistivities, and a rapid change again at high resistivities. The range of resistivities covered by this investigation, it should be noted, is from sea water to high-resistivity mountain-stream water, and in this range the minimum paralysis-voltage gradient changes from 0.27 to 1.23 volts per inch, or 4.55 times. It is necessary then to introduce a water-resistivity correction factor in the previous equation. It may now be written

$$g=\frac{3.70\ W}{L}$$

where g = voltage gradient per inch to produce paralysis, L = length of fish in inches, and W = correction factor for water resistivity. (See Table 4 for values of W for different water resistivities from 10 to 10,000 ohms per inch cube.)

TABLE 3.—*Influence of water resistivity on the voltage gradient required to paralyze chinook-salmon fingerlings 3.1 inches long when subjected to a uniform electric field in water, the resistivity of which was adjusted to the desired value by adding fresh water to a salt (NaCl) solution having an initial resistivity of 11.6 ohms per inch cube and at a temperature of 55.5° F.*

Test No.	Number of fish	Water resistivity, ohms per inch cube	Voltage gradient, in volts per inch for paralysis	
			Minimum	Maximum
31	30	11.6	0.271	0.366
32	30	53.2	.333	.423
33	30	194.0	.396	.560
34	30	2,180.0	.666	.937
35	30	3,930.0	.791	1.110
36	30	7,850.0	.950	1.339
37	30	10,030.0	1.230	1.850

TABLE 4.—*Correction factor, "W," for various water resistivities for the minimum voltage-gradient equation* $g=\frac{3.70W}{L}$

Water resistivity, ohms per inch cube "ρ"	Correction factor for water resistivity "W"	Water resistivity, ohms per inch cube "ρ"	Correction factor for water resistivity "W"
10	0.210	3,000	0.612
50	.268	4,000	.654
100	.297	5,000	.679
200	.335	6,000	.712
300	.365	7,000	.755
500	.402	8,000	.805
1,000	.477	9,000	.897
2,000	.561	10,000	1.000

WATER RESISTIVITY OF VARIOUS STREAMS

The resistivity of the water has such an important influence upon the voltage gradients and voltages that should be used on electric fish screens that it is very important to know something of the variation in resistivity found in various streams.

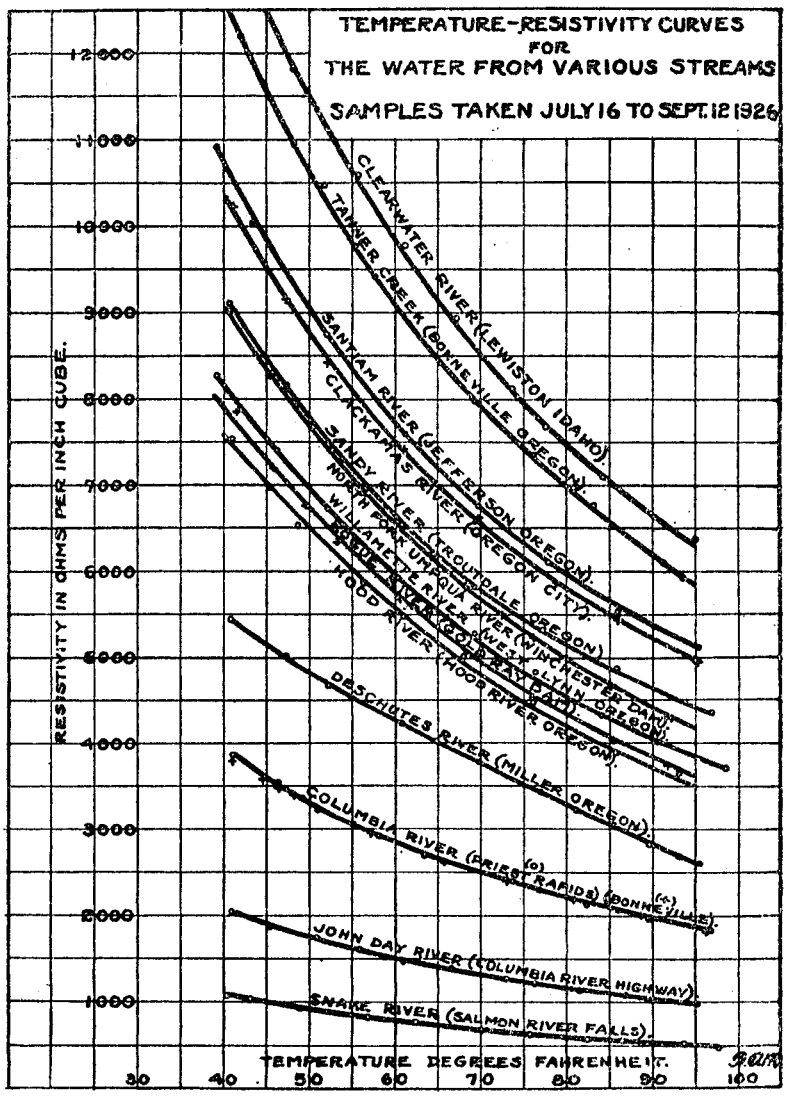

FIG. 8

To obtain this information, samples of water were secured from 12 rivers, 1 creek, and the Pacific Ocean.

Temperature-resistivity data were taken for each of these samples by chilling the water to approximately 40° F., then measuring the resistivity as the sample was warmed in increments to approximately 95° F. All water resistivities used in this investigation were measured by the Kohlrausch U-tube method, using a double com-

mutator with the resistance bridge to insure the elimination of all polarization effects (Kohlrausch, 1883). These temperature-resistivity data for the various streams are plotted with rectangular coordinates in Figure 8. An examination of these curves shows that there is a great variation in the resistivity of the water from various streams. The Snake River water, for example, has a resistivity of 800 ohms per inch cube at 60° F., while the Clearwater River water has a resistivity of 9,850 ohms,

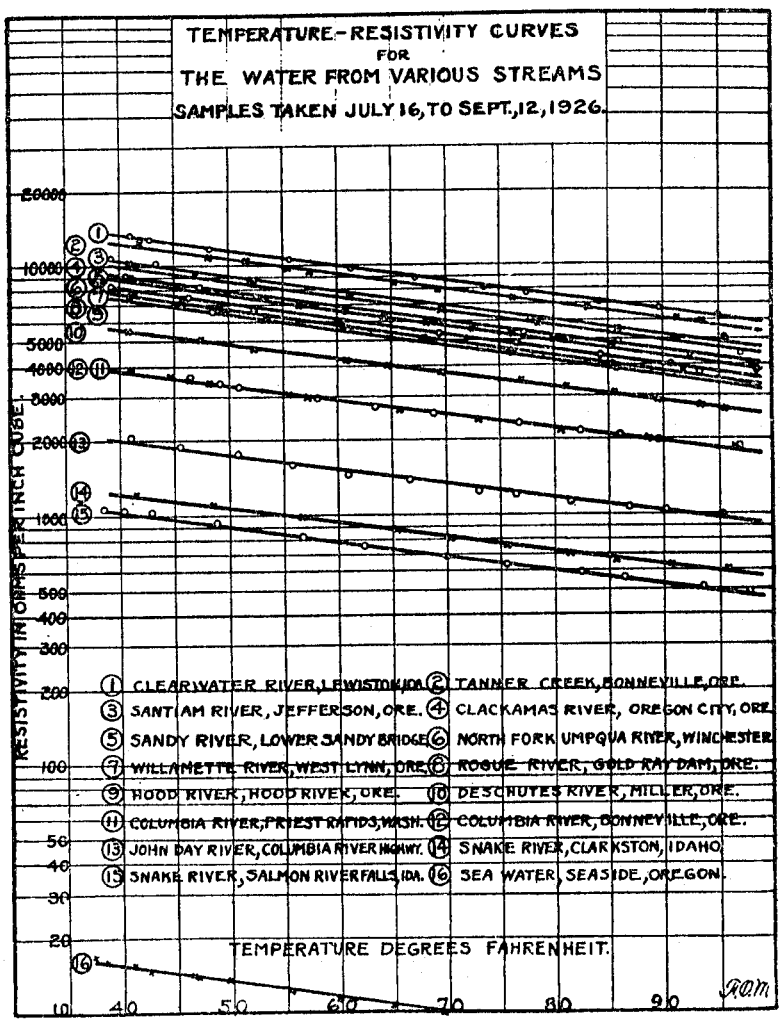

FIG. 9

which is 12.3 times as great at the same temperature. This wide variation in resistivity is due, of course, to dissolved salts taken up by the water in the stream and its tributary drainage basin. An inspection of these curves shows that all of the streams having low-resistivity water rise east of the Cascade Mountains and pass through semiarid alkali sections. The Clearwater River rises in the Bitter Root Mountains of Idaho. The other streams rise in the Cascade Mountains and are fed, in general,

by melting snow and glaciers, with the result that they are grouped fairly close together in water resistivity and the value is relatively high.

The resistivity of the sea-water sample from Seaside, Oreg., was so low that it could not be plotted in Figure 8. The resistivity of the sea water at 60° F. was 11.2 ohms per inch cube, or 1/880 that of the Clearwater River water at the same temperature.

Figure 9, a semilogarithmic plot of these temperature-resistivity data for the waters from all of the sources investigated, shows two very interesting relations. First, all of the curves are straight lines; second, all of the curves are parallel. The significance of all of the curves being straight lines when plotted this way is that the temperature-resistivity characteristic within the limits of temperature investigated can be represented by an exponential equation of the form

$$\rho = A\epsilon^{-b\Theta}$$

where ρ = the resistivity in ohms per inch cube, Θ = the temperature in degrees Fahrenheit, $\epsilon = 2.7183$ base of Naperian logarithms, A = a constant, and b = a constant.

The significance of all of the curves being parallel is that the slopes are all the same; therefore, the constant term b in the exponent of this equation is the same for sea water and the water from every stream investigated. The numerical value of the constant b was calculated and found to be 0.014. The values of the constants A for the various kinds of water were calculated and are tabulated in Table 5. With these values of the constant term A and 0.014 for the constant term b in the above equation, the resistivity of any of the waters investigated can be calculated for any temperature from 40 to 100° F., with a maximum error not greater than 3 per cent. Therefore, the temperature-resistivity characteristics for the waters studied can be represented over the range of temperature from 40 to 100° F. by the following equation:

$$\rho = A\epsilon^{-0.014\Theta}$$

where A is a constant having a different value for the water from each stream and for the waters investigated has a minimum value of 26.9 and a maximum value of 23,100.

TABLE 5.—*Constants for water temperature-resistivity equation* $\rho = A\epsilon^{-b\Theta}$.

Stream	Location at which sample was taken	Constant A	Constant b
Sea water (Pacific Ocean)	Seaside, Oreg	26.9	0.014
Snake River	Salmon River Falls, Idaho	1,840.0	.014
Do	Clarkston, Idaho	2,240.0	.014
John Day River	Columbia River Highway, Oreg	3,630.0	.014
Columbia River	Bonneville, Oreg	6,850.0	.014
Do	Priest Rapids, Wash	6,850.0	.014
Deschutes River	Miller, Oreg	10,000.0	.014
Hood River	Hood River, Oreg	12,970.0	.014
Rogue River	Gold Ray Dam, Oreg	13,500.0	.014
Willamette River	West Lynn, Oreg	14,130.0	.014
North Fork Umpqua River	Winchester, Oreg	15,500.0	.014
Sandy River	Lower Sandy Bridge, Oreg	15,850.0	.014
Clackamas River	Oregon City, Oreg	17,800.0	.014
Santiam River	Jefferson, Oreg	18,400.0	.014
Tanner Creek	Bonneville, Oreg	21,630.0	.014
Clearwater River	Lewiston, Idaho	23,100.0	.014

Seasonal variations will occur in the resistivity of the water in a stream. In some streams this variation will undoubtedly be much larger than in others. One stream that has been investigated has a seasonal variation in resistivity of 13 per cent at a constant reference temperature. The maximum resistivity occurs during the period of maximum run-off. Fortunately, electric fish screens do not need to be designed within very close limits, and no trouble is anticipated from variations in the water resistivity of a stream.

DO FISH SENSE THE SOURCE OF AN ELECTRIC FIELD AND AVOID IT?

Another fundamental fact that must be known is whether or not fish, swimming into an electrified area, sense the direction of danger. In an effort to determine this point several tests were made in the outside pools at the Bonneville hatchery. The first four tests were made in a rectangular concrete pool 8 feet wide, 4 feet deep, and 48 feet long, including the spillway. Twelve feet of the lower end of this pool next to the spillway were divided into two 4-foot channels by a tight partition of 1 by 12 inch boards. Facing downstream, the right-hand channel was selected to be protected by the electric screen. The arrangement of this pool and the second screen used are shown in Figure 3.

The first screen was made of four ½-inch standard-pipe electrodes spaced 18 inches apart and in a single row, making an angle of 60 degrees in the direction of stream flow. Alternate electrodes were connected and made the same electrical polarity; this arrangement made adjacent electrodes opposite in polarity. About 200 chinook-salmon fingerlings 10 months old were liberated at the upper end of the pool. When undisturbed they avoided the electrified area around the screen fairly well, but when frightened they would swim through it into the protected channel. This screen was defective in three ways, as will be shown later in the discussion of the proper relation of the lines of current flow and equipotential surfaces with respect to the direction of water flow and the plane of the protected opening and the proper size of electrodes. First, the lines of electric-current flow were in the wrong direction with respect to the water flow; second, they were in the wrong direction with respect to the protected opening; and third, the electrodes were too small in diameter.

The second screen test was made in the same pool, and all of the conditions were kept the same, except that the number of electrodes was increased to six and the angle of the line of electrodes with the direction of water flow was reduced from 60 to 30 degrees. Approximately 2,000 chinook-salmon fingerlings 10 months old were liberated in the open end of the pool and observed. They seemed to avoid the screen fairly well, although some would swim through into the protected channel. At 4.30 p. m. the protected area was cleared of fish and 30 volts left on the electrodes for the night. The next morning at 8 o'clock 50 fingerlings were in the protected area and 6 had been electrocuted during the 15.5 hours the screen had been on. The fish were then driven back and forth past the screen, and they avoided the electrified area fairly well but would dash through at times. This screen was still defective in regard to the size of the electrodes. The direction of the lines of current flow, however, had been improved by making them more nearly parallel with the direction of stream flow and more nearly perpendicular to the plane of the protected opening. Leaving all conditions except the screen as they were before, a third screen was constructed,

consisting of two parallel rows of ½-inch standard pipe spaced 18 inches apart in the rows and the two rows 2 feet apart. The angle of the electrode rows with the direction of stream flow was kept at 30 degrees, as before. The electrodes of each row were connected parallel and the two rows made opposite in polarity. This arrangement of electrodes put the lines of current flow approximately in the direction of stream flow, and consequently in the direction the fish approach the screen. With some trout used in the previous test in the open channel, the electrodes were energized with 24.5 volts and left on from 4.30 p. m. until 8 a. m. The fish did not enter the protected channel. It was observed that trout that had passed through the electric field of the screen could not be driven through it again except with great difficulty. For this reason a new group of 12 rainbow trout was substituted for those that apparently had become screen shy. When first liberated, 5 of the 12 were frightened and dashed through the screen. They were then driven out into the open end of the pool and the potential left on over night. The fish did not reenter the screened area during the night, and the next morning we were unable to drive any of them through the screen.

The fourth screen used was but a very slight modification of the third. One electrode was added to fill a rather large opening on the by-pass channel side of the screen. The electrode voltage was adjusted to 23 volts, and approximately 2,500 chinook-salmon fingerlings were put in the outside channel at 11.30 a. m. These fish were allowed to move about as they pleased. Frequently the entire school would swim directly toward the screen but always turned away when within from 18 to 24 inches of the first row of electrodes. They were continually feeding on elm beetles, which were blown on the water from the elm trees above the pool, but they would never venture through the screen for those in the protected area. An attempt was then made to attract them through the screen by throwing a mixture of ground salmon and salmon eggs between the electrodes and in the protected area. They could be drawn into the screen by throwing the food outside and leading up to it, but they would dash out without taking the food and never passed beyond the second row of electrodes. The only way the young salmon could be driven through the screen was by fright. A few were driven through the screen by waiting until a school was immediately in front of the screen and then making a sudden motion toward them with a pole, net, or other device.

The last two screens tried were by far the most effective. This undoubtedly was due to a more effective use of the electric field by arranging the lines of current flow parallel with the stream flow and at right angles with that of the protected opening. The tests in the concrete pool, however, were not as conclusive as they might have been, because conditions were unnatural. The water velocity was extremely low; in fact, it was virtually still water, hence the fish did not line up with the direction of water flow as in a stream. The pool was near the main hatchery driveway, and the fish were continually frightened and disturbed by tourists and therefore were unnatural in their behavior. However, those who witnessed the tests with the third and fourth screens were convinced that the fish did have a directional sense of the location of the source of the electric fields and a decided inclination to avoid them. These observations led to the decision to install a screen under more natural and normal conditions for further observations and tests. This screen and the results obtained will be discussed later in this report.

DIRECTION OF THE ELECTRIC FIELD WITH RESPECT TO THE PROTECTED OPENING AND THE STREAM FLOW

The experience with the four electric screens tested in the concrete pool and the tests conducted in the aquarium demonstrated clearly the importance of considering the direction of the lines of current flow and the equipotential surfaces in the water. The lines of current flow and the equipotential surfaces for two parallel gratings of opposite polarity and consisting of parallel cylindrical electrodes immersed in water or any electrolyte of uniform resistivity are shown by Figure 10. The lines of current flow originate in one electrode and terminate in the one of opposite polarity. The lines of current flow in Figure 10 are drawn to include one-thirty-sixth of the current from one electrode between adjacent lines of current flow. The equipotential surfaces start as eccentric circular tubes about the electrodes, change to elliptical tubes, then to curved surfaces passing in front of the electrodes along the plane of the grating, gradually straightening out into a plane surface midway between the gratings. Figure 10 is drawn as a plane surface at right angles to these equipotential surfaces, hence they appear as lines in the drawing. These equipotential surfaces are drawn so that one-fortieth of the potential between the gratings is included between adjacent equipotential surfaces. Such a graph is very helpful in the study of the electric field between gratings, because the distance between the lines of current flow is a measure of the current density, and the distance between the equipotential surfaces is a measure of the rate of change of potential or voltage gradient. The nearer the lines of current flow are together the greater the current density, and the nearer the equipotential surfaces are together the higher the voltage gradient.

It should be noted that the lines of current flow and the equipotential surfaces always intersect at right angles. The equipotential surfaces, as the name indicates, are surfaces in which there is no change in potential. It is obvious, then, that a fish swimming in electrified water parallel with the equipotential surfaces is subjected to a potential difference only equal to that spanned by the thickness of his body, and the current that flows through his body is from side to side at right angles with the spinal column and major nerve channel. On the other hand, a fish swimming in electrified water at right angles with the equipotential surfaces and parallel with the lines of current flow is subjected to a potential difference equal to that spanned from the tip of his snout to the end of his tail, and the direction of current flow is lengthwise through the body in the direction of the spinal column and major nerve channel. The ratio of the length to the thickness of a fish is very large for most species. Then, in consideration of what has been said about the two positions of a fish in an electric field, it is obvious that when at right angles with the equipotential surfaces and parallel with the lines of current flow he will be subjected to a potential difference several times that when he is at right angles to this position. Furthermore, in this position the direction of current flow is in the direction of the spinal column and main nerve channel and is probably much more effective in producing a disagreeable sensation.

In all of the tests when moderate values of potential were used (so the fish were not in too great distress) there was always a decided tendency to line up with the equipotential surfaces. This is, of course, the most comfortable position if there is no way to escape from the field entirely.

The above observations show the necessity, when using an electric screen for protecting an opening, of having the equipotential surfaces parallel with the plane of the opening and the lines of electric-current flow perpendicular to this plane.

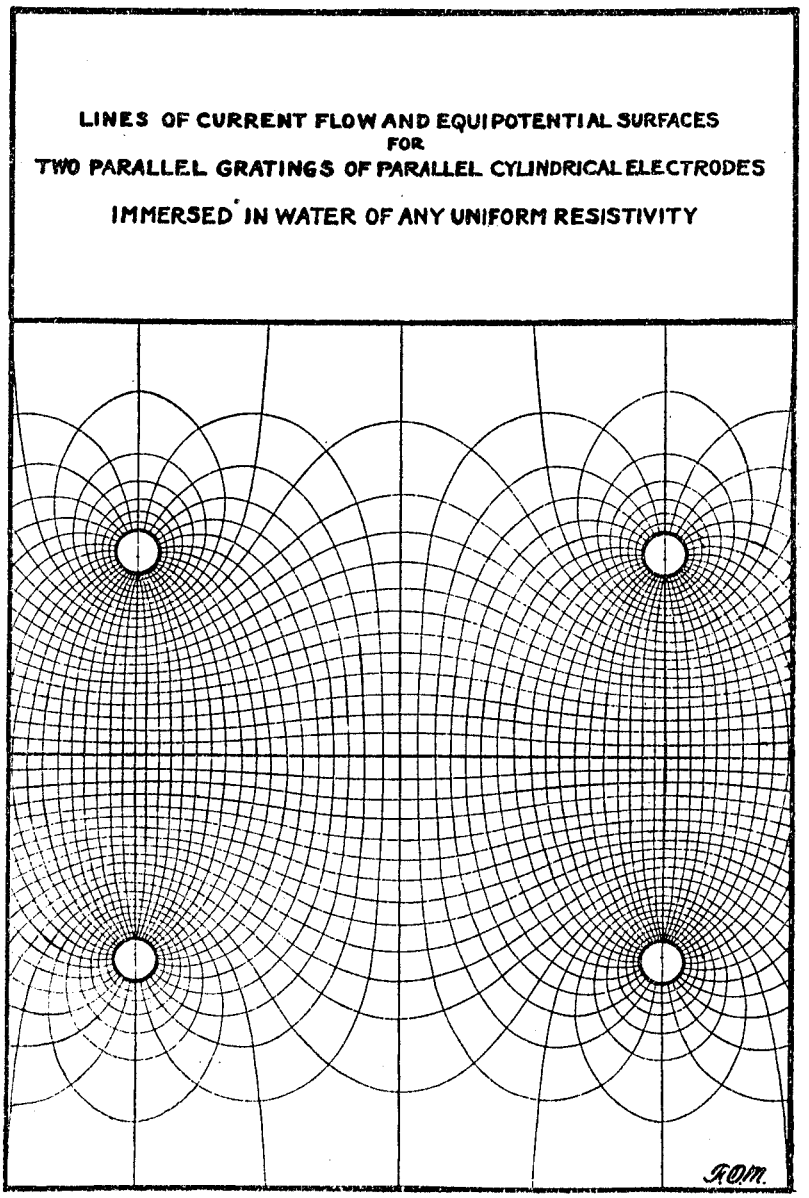

FIG. 10

When in swift water fish hold their bodies parallel with the direction of stream flow for ease in swimming. This fact must also be taken account of when installing an electric screen. The lines of electric-current flow must be parallel with the direction of water flow and the equipotential surfaces at right angles to the direction of water flow.

When an electric screen is installed in such a way that the field has the correct relation to both the opening protected and the direction of water flow, as explained above, fish entering the electric field of the screen are almost compelled to enter parallel with the lines of current flow and at right angles to the equipotential surfaces. This is the position of maximum discomfort and hence is most effective in discouraging further progress toward the protected opening.

Heretofore no attention has been given to the relation of the electric field to the protected opening and to the direction of stream flow. As far as is known, all of the electric "stops" have been installed, either with a plate (or metal screen) on each side of the protected opening (these plates being of opposite polarity), or several electrodes have been used in one or several rows across the opening, the electrodes in the rows alternating in polarity. Both of these schemes, it will be observed, produce an electric field in which the lines of current flow are parallel with the plane of the opening and the equipotential surfaces are perpendicular to this plane. This arrangement, as shown above, is the most ineffective that it is possible to make, and if any success has been attained at all by this arrangement it augurs well for electric screens installed with the field in the proper relation to the opening and water flow.

ELECTRIC SCREENS SHOULD BE USED AS DEFLECTORS, NOT STOPS

Another serious error that has been made in the installation of electric "stops" has been the attempt to use them as impenetrable barriers in canals, sometimes miles from the intake at the supply stream. This, in general, is not good practice even if successful in stopping the fish, especially for young salmon fingerlings that are impelled by instinct to migrate downstream toward the ocean. They may be held for months by such a trap and may never return upstream to the intake and main stream leading to the ocean. A short interruption of the potential supply on an electric screen so installed would allow fish to escape past the screen, making successful screening action for months of no avail. It is recommended that electric screens, when used, be installed as deflectors, by-passing fish around the openings to artificial waterways dangerous to their well-being, always keeping the fish, as far as possible, in the natural stream channels.

LAST FISH-SCREEN TEST AT BONNEVILLE

Following the fish-screen experiments in the concrete pool, which have been described, it was decided to make an electric-screen test with more fish and under as nearly as practical natural stream conditions. After an examination of the ponds and waterways at the Bonneville hatchery it was decided that ponds Nos. 12, 15, and 16, with their interconnecting waterways, offered the best available location for the fifth and last electric-screen test made during this investigation. A map is included in this report (fig. 11), showing the arrangement of these ponds, the location of the electric screen, and the quantities of water flowing in the various interconnecting channels. The arrangement shown by the map was chosen because the application of the by-pass or deflector principle of using the electric screen could be applied readily. The water flowing through pond No. 12 into pond No. 15 and finally discharging into pond No. 16 represents the natural stream channel, and the flow from pond No. 12 through the west waterway into pond No. 16 represents the artificial waterway

from which the fish were to be protected. The water flow in the two paths was adjusted to the desired value by regulating the water level in pond No. 15 with stop boards at the discharge into pond No. 16. The flow of water through the electrically screened channel purposely was made 39 per cent higher than through the open channel, because it was thought that would make protection more difficult on account of

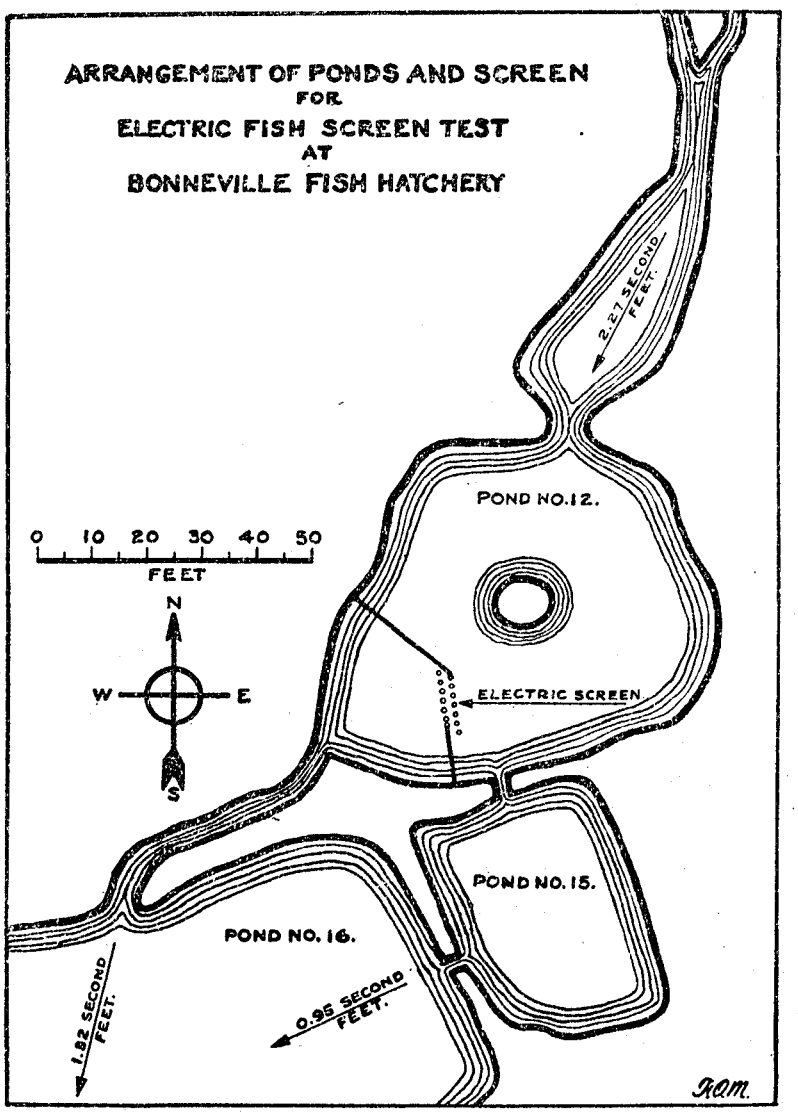

FIG. 11

the inclination of the fish to follow the maximum water flow. A wire screen was installed in the west outlet of pond No. 12 to prevent the fish that went through the electric screen into the protected area from escaping into pond No. 16. This screen made it possible to check the effectiveness of the electric screen. The 15,000 chinook-salmon fingerlings used in the experiment had been reared in pond No. 12

and therefore were normal in their activity there. The area screened was frequented by large numbers of fish before the screen was installed.

The screen installed for this test consisted of fourteen 2½-inch standard-pipe electrodes (2.875 inches outside diameter) in two rows of seven electrodes each. The electrodes were spaced 18 inches, center to center, in the rows, and the two rows were 24 inches, center to center. The electrodes of the second row were staggered 9 inches with respect to the first row, making them come opposite the centers of the openings between the electrodes of the first row. The electrodes were supported, through holes in 2 by 10 inch planks, 18 inches above the water level and projected to within 2 inches of the bottom of the pond. The electrodes in each row were connected by means of 14-gauge wire and made the same electrical polarity. The two rows of electrodes were

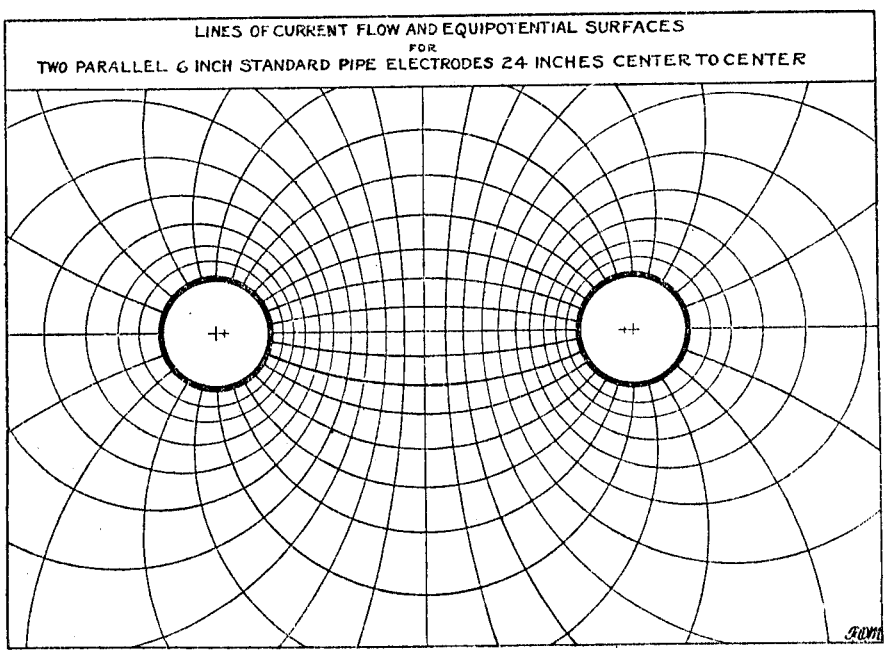

FIG. 12

of opposite polarity. The opening protected by this electric screen was 9 feet 3 inches wide.

The installation of the screen was completed at 10 a. m., August 7. The fish were attracted out of the screened area by feeding on the opposite side of the pond, and 25 volts at 60 cycles were put on the screen from a 3-kilovolt-ampere ungrounded supply transformer. A graphic recording voltmeter was connected to the potential supply to check the continuity of the electrical supply to the screen.

When the screen was first electrified the fish would drift down toward it in large schools, and as soon as the outer fringe of the school struck the electrified area it would swim out swiftly, giving warning of the danger, and the whole school would move away. The school would soon drift back into the electrified area and repeat the above movement. At times fish that drifted too far into the electrified area would become bewildered and swim through the screen. The number swimming through

in this manner was very small; usually none went through; on some occasions one, two, or three; and the largest number observed to go through in six hours of observation on August 17 was six. One very interesting thing about the fish that went through the screen is that almost invariably upon finding that they were separated from the main school they would dash back through the screen to join the school.

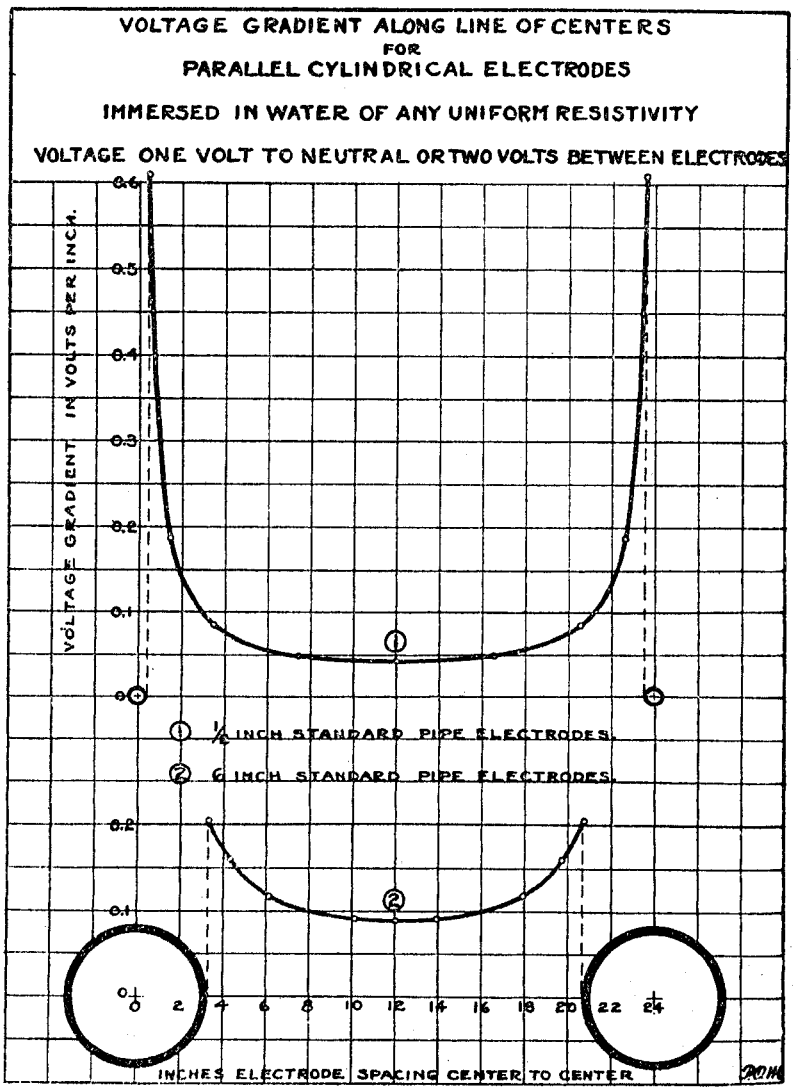

FIG. 13

The result was that during the first day there were never more than 30 fish in the protected area.

At 11.30 a. m., August 18, the second day of operation of the screen, a short circuit occurred in some very poorly insulated scrap wire it had been necessary to use in making the power extension to the transformer supplying the screen. This took the

voltage off the screen until 6 p. m., during which period between 3,000 and 4,000 fish went into the protected area. These fish were coaxed out of the protected area by feeding before the screen was electrified again. This accidental interruption of the screen power supply showed two things: First, it is important to have a reliable source of supply, and, second, the screen was effectively keeping the fish out of the

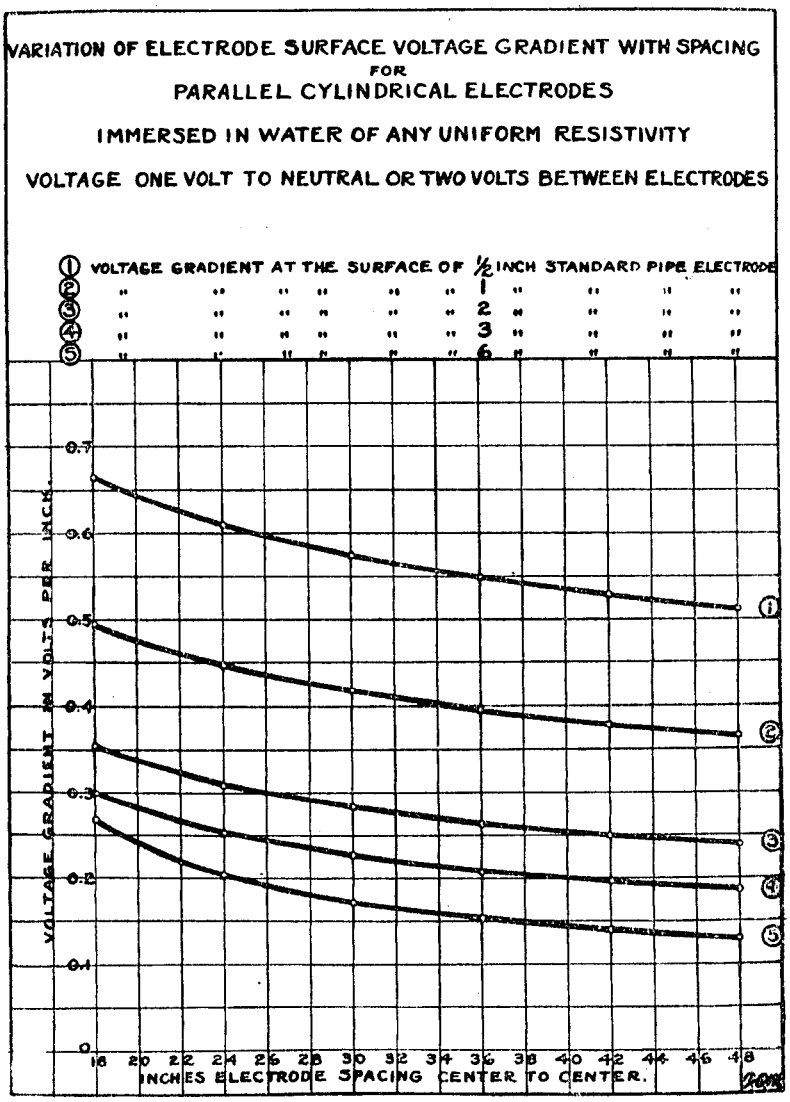

FIG. 14

protected area. Following this interruption the screen was kept electrified continuously for 10 days. During this period sunshine and cloudy and rainy weather were experienced. One very hard rain, lasting about 36 hours, occurred on August 25 and 26. This afforded an opportunity to see whether weather conditions had any influence on the effectiveness of the screen equipment, and as far as could be observed it did

not have any effect. A very accurate record was kept of the fish killed during this test. The hatchery attendants were instructed not to remove any dead fish from pond No. 12 without having them properly recorded. For the entire period of 11 days (this includes August 17, the first day of the test, which was eliminated from the 10-day continuous run by a short circuit in the temporary alternating-current supply

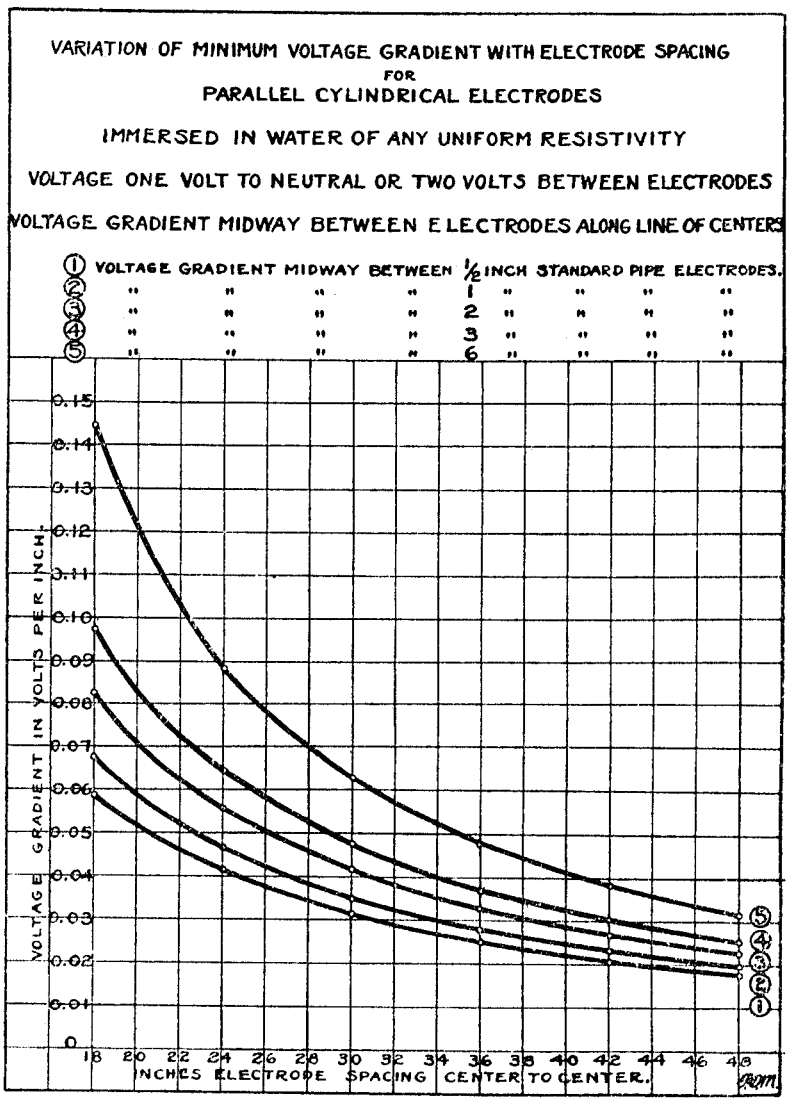

FIG. 15

line on August 18), from August 17 to August 27, inclusive, 29 fish were killed by the electric screen, or less than 0.2 per cent of the 15,000 fish in pond No. 12—a negligible number. The maximum number of fish killed in one 24-hour day was six; on two days no fish were killed; and the average number killed per day for the 11-day period was 2.64. By the use of larger-diameter electrodes (thereby obtaining a more uniform voltage gradient) even this small number of fish killed could have been reduced,

if not entirely eliminated. At the time the screen equipment was disconnected (on August 28), as nearly as could be estimated 500 of the 15,000 fish were in the protected area. These had accumulated gradually during the 10-day period. The screen kept 97 per cent of the fish from the protected area, which is an excellent record. This installation was witnessed by John C. Veatch, of the Oregon Fish

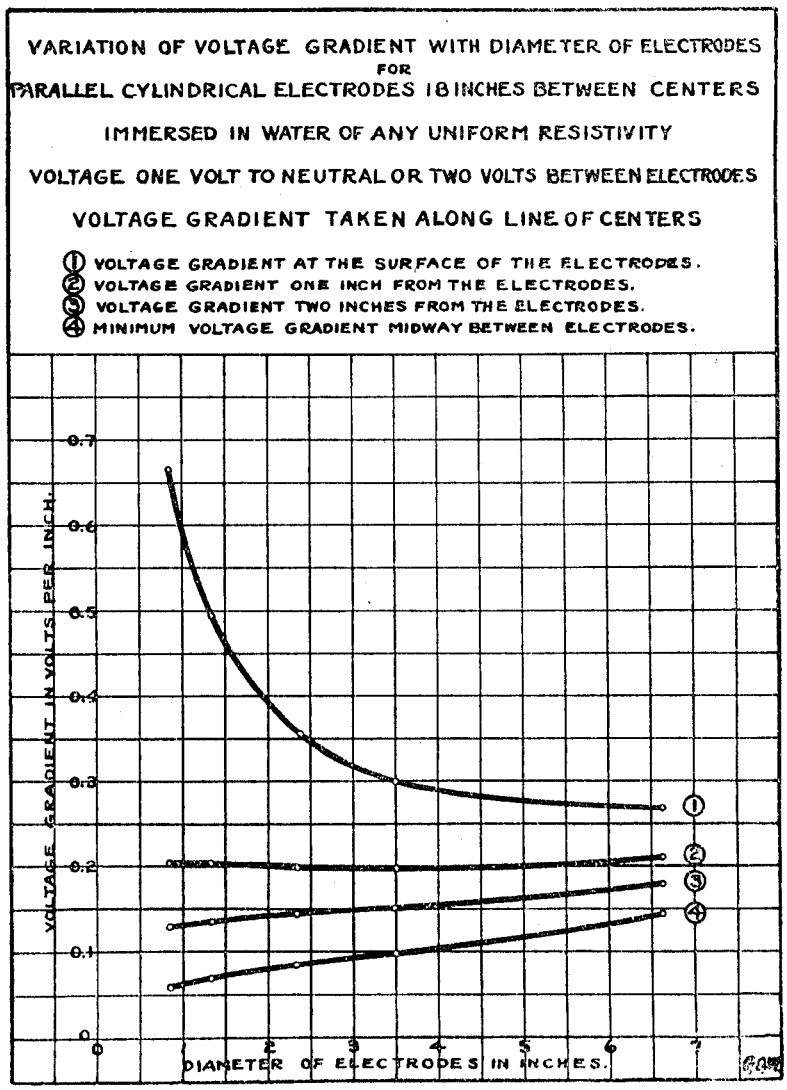

FIG. 16

Commission; Edward Balaugh, master fish warden of Oregon; E. F. Averill, master game warden of Oregon; H. B. Holmes, biologist with the United States Bureau of Fisheries; and many others. Eugene Howell, superintendent of the Bonneville hatchery, and some of his assistants made daily observations, and J. E. Yates made observations on several different days during the progress of the test.

DESIGN OF ELECTRIC FISH SCREENS

In this discussion of the design of electric fish screens no attempt will be made to discuss the details of mechanical construction, because these may be altered greatly by local conditions. The electrical design, however, is fundamental and contains

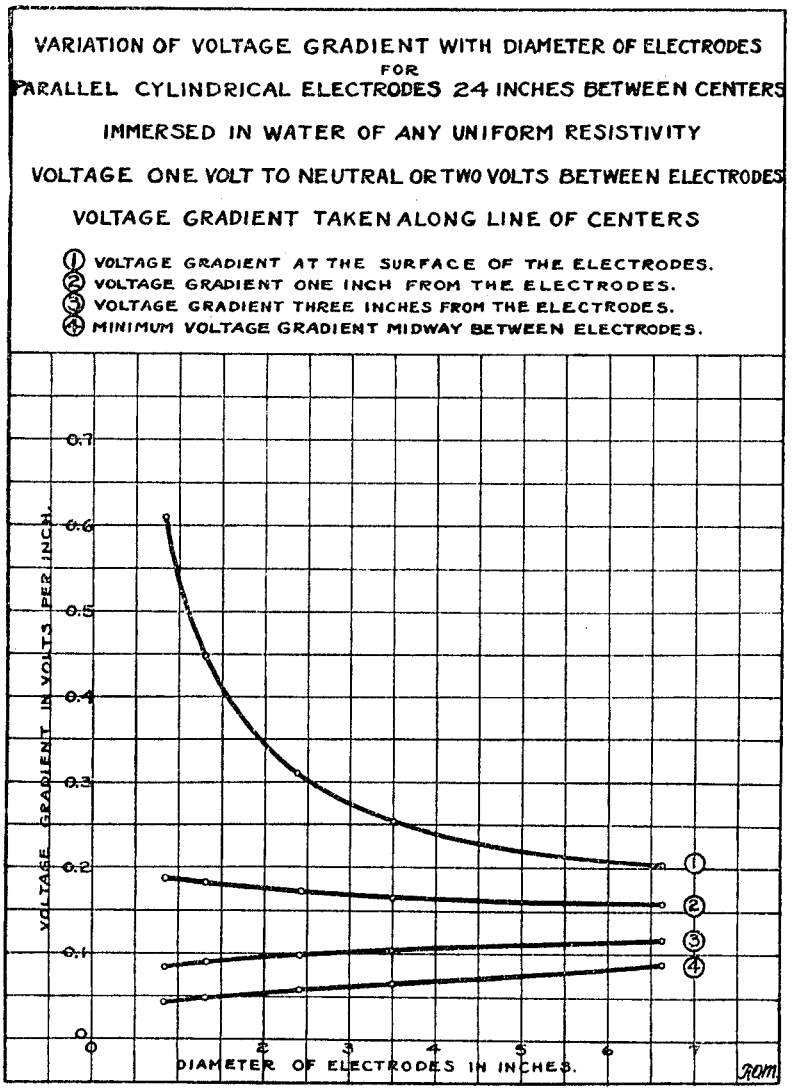

FIG. 17

conditions that must be met to obtain satisfactory operation. These conditions, stated very briefly, are as follows:

1. An insulating transformer should be used between the power supply and the screen to avoid a useless current flow from the electrodes to ground.

2. The lines of current flow in the electric field must be perpendicular to the plane of the protected opening and the equipotential surfaces parallel with this plane. (See figs. 10 and 12.)

3. The lines of electric-current flow must be parallel with the direction of the water flow. (See figs. 10 and 12.)

4. The voltage gradient in the electric field should be kept as uniform as practical by the selection of proper electrode sizes and spacing. (See figs. 13 to 21, inclusive.)

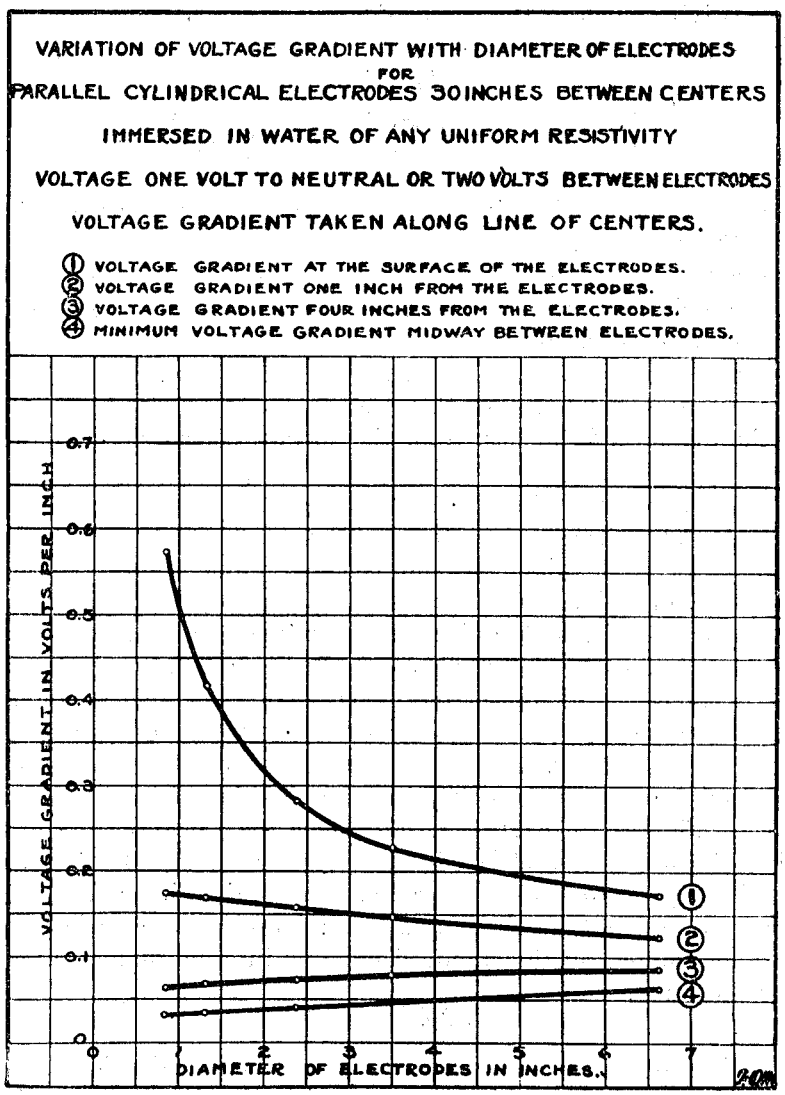

FIG. 18

5. The voltage gradient must be suitable for the size fish to be protected. If the fish to be protected vary greatly in length, it may be necessary to use a double screen. (See equation on p. 107.)

6. The spacing between electrodes in the rows is determined largely by the opening desired for débris to pass through.

7. The spacing between rows of electrodes should be approximately 1.33 times the spacing of the electrodes in the rows.

8. The electrodes should be from 2 to 12 inches above the bottom of the stream. This distance depends upon the spacing of the electrodes and upon the character of the stream bed.

The voltage gradient along the line of centers between two parallel cylindrical electrodes (which is the locus of the maximum voltage gradients) in an electrolyte of uniform resistivity, such as the water of streams, can be calculated by the use of the following equation:

$$g=\frac{E_n\sqrt{S^2-4\,r^2}}{\left\{(r+x)\,(S-2r)-x^2\right\}\log_{\epsilon}\left[\frac{S}{2r}+\sqrt{\left(\frac{S}{2r}\right)^2-1}\right]}$$

Where

g = the voltage gradient in volts per inch at distance x from the surface of the electrode.

E_n = the voltage to neutral (one-half electrode voltage for a single-phase circuit) root mean square values of the alternating voltages were used in this investigation.

S = the spacing, in inches, between electrode centers.

r = the radius, in inches, of the electrodes.

x = the distance, in inches, from the surface of the electrode at which the voltage gradient g is to be calculated.

ϵ = 2.7183, the base of Naperian logarithms.

To facilitate the electrical calculation of fish screens and to show how the various factors, such as electrode diameter and spacing, influence the voltage gradient, Figures 12 to 21, inclusive, were calculated and plotted. Figure 12 is the plot of the lines of current flow and equipotential surfaces for two standard 6-inch pipe electrodes, spaced 24 inches, center to center. In Figure 13, 1 and 2 are the voltage-gradient curves along the line of centers for ½-inch and 6-inch standard-pipe electrodes. These curves clearly show the importance of using large-diameter electrodes for improving the voltage gradient. Figures 14 and 15 show the variation of the maximum and minimum voltage gradients along the line of centers for various electrode spacings. Figures 16 to 21, inclusive, show the variation of voltage gradient along the line of centers, with electrode diameter for 18, 24, 30, 36, 42, and 48 inch electrode spacing, center to center. The diameters plotted in these curves are actual outside diameters and not nominal pipe sizes; however, the various sizes of pipe electrodes are designated by the standard nominal internal diameter by which they are known to the trade.

CONCLUSIONS

The following conclusions were reached from this investigation:

1. A very simple relation exists between the minimum voltage gradient required to paralyze fish and their length, which can be expressed by the equation

$$g=\frac{3.70\,W}{L}$$

where g = voltage gradient in volts per inch, W = water-resistivity correction factor, and L = length of fish in inches.

2. When voltage gradients above the paralysis values are applied to fish, the mortality increases with increased time of application.

3. Fish subjected to electric shocks in various degrees, if not killed outright, quickly recover and do not suffer any serious after effects.

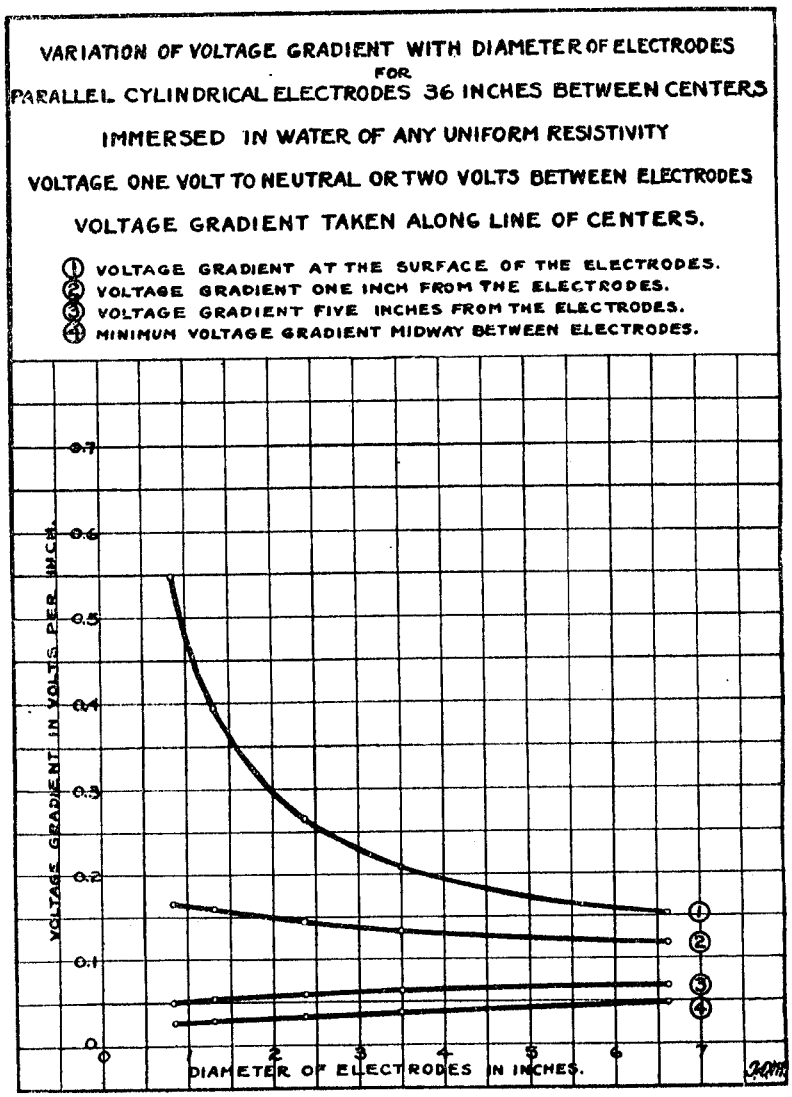

FIG. 10

4. The resistivity of the water in which fish are immersed has an important influence upon the voltage gradient required to produce paralysis, as shown by the values of the water-resistivity correction factor, "W" in Table 4.

5. Very large variations are found in the resistivity of the water from various streams. The largest fresh-water variation found was one river water that had a

resistivity 12.3 times that of the lowest stream-water resistivity found. The highest resistivity river water had a resistivity 880 times that of sea water. In spite of this wide variation in resistivity, the temperature-resistivity curves for waters from all of the 16 sources of water studied can be represented over the range of temper-

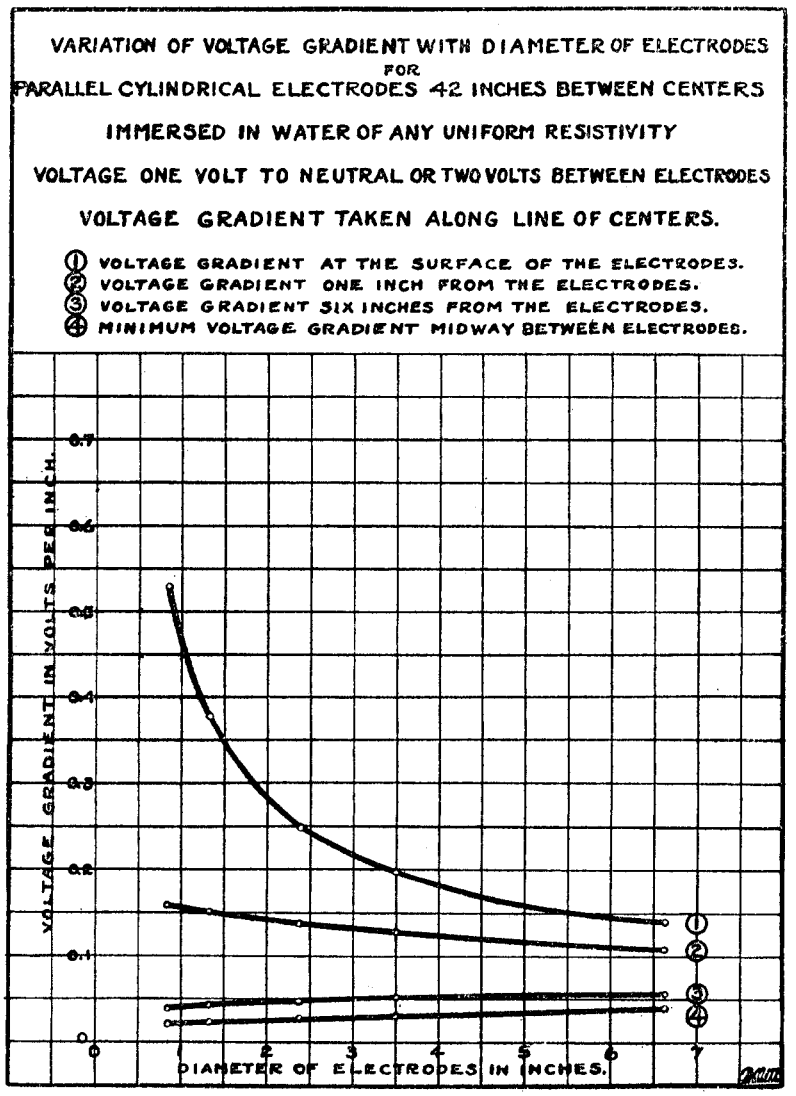

FIG. 20

ature from 40 to 100° F. by the equation

$$\rho = A\epsilon^{-0.014\,\Theta}$$

where ρ = the resistivity in ohms per inch cube, A = a constant different for each kind of water (see Table 5), ϵ = 2.7183 base of Naperian logarithms, and Θ = the water temperature in degrees Fahrenheit.

6. When swimming into an electrified area fish do have a sense of the direction of danger and try to avoid it.

7. To be effective, an electric screen must have the lines of current flow perpendicular to the plane of the protected opening and the equipotential surfaces parallel

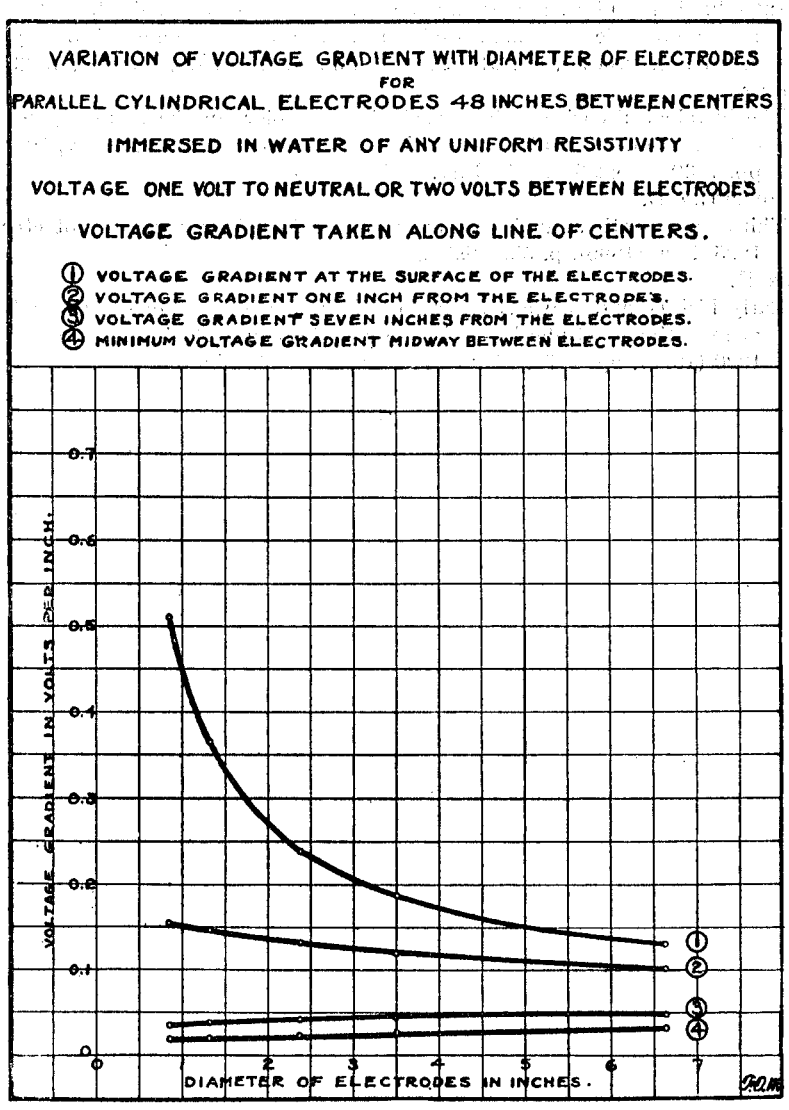

FIG. 21

with this plane. The lines of electric-current flow must also be parallel with the direction of stream flow.

8. The experimental electric fish screens have been very successful. Actual stream installations should now be made, carefully observed, and developed.

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NATURAL HISTORY AND CONSERVATION OF REDFISH AND OTHER COMMERCIAL SCIÆNIDS ON THE TEXAS COAST

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INTRODUCTION

GENERAL PROBLEM

In the summer of 1925 the United States Bureau of Fisheries, heeding a demand from Texans for more specific information as to the actual status of their coastal marine fisheries, conducted a short survey of those fisheries. The results of the study were presented in a Preliminary Report on the Marine Fisheries of Texas, by Higgins and Lord (1926), in which the character of the fisheries was discussed in the light of their past and present yields. A logical recommendation given in this report was for the immediate initiation of biological investigations that would include primarily extended study of the life histories of various marine food fishes of the State.

Having complete control of its commercial fisheries, Texas has been alarmed for some time as to the possibility that serious depletion of its shore fisheries would occur before any steps could be taken to insure a permanent supply of food fish. Many prohibitive laws have been passed, unfortunately, without sufficient knowledge of the life histories of the fish to allow rational conservation of the fish stock as well as intelligent utilization and development of the fisheries. The people most interested in the future welfare of the marine resources of Texas are beginning to realize that a fundamental prerequisite for adequate fisheries legislation is an accurate, unbiased knowledge of the life histories of the food fish entering into the fisheries.

AIM OF THE INVESTIGATION [1]

The natural histories of the three leading food fishes of coastal Texas—the redfish (*Sciænops ocellatus*), the black drum (*Pogonias cromis*), and the spotted sea trout (*Cynoscion nebulosus*)—have been little understood in any section of the distribution of these species. Along the Texas coast serious debates often arise as to the habits of the redfish, drum, and spotted trout, with special reference to the location of spawning areas and the distribution of young and adult fish. Reliable information concerning the life histories of these most valued shore fishes is of much interest, both from a popular standpoint and the point of view of those individuals that are intrusted with the conservation of the natural resources of Texas. To furnish this sound basis for conservation, the first of a series of scientific fishery investigations was undertaken to ascertain, primarily, the location of the spawning grounds, rate of growth, seasonal distribution, and movements of the redfish, black drum, and spotted sea trout.

As a result of the support of the Texas game, fish, and oyster commission, which consisted in furnishing a fishing boat and crew, various launches, as well as other equipment and services, the bureau is able to present the following paper, embodying the results and conclusions of 14 months' field observations and collections along the coast of Texas. These observations, conducted continuously from April, 1926, to June, 1927, included studies on the natural history of the croaker (*Micropogon undulatus*) and the spot (*Leiostomus xenthurus*), fishes of secondary commercial importance in Texas but of considerable value along the Atlantic coast.

DESCRIPTION OF TEXAS COAST

The entire coast line of Texas, from the mouth of the Sabine River in the north to the mouth of the Rio Grande in the south, extends along the Gulf of Mexico for nearly 400 miles. The greater portion of the coast is bordered by a chain of low, sandy barrier islands, which separate the many coastal bays and lagoons from the Gulf of Mexico and through which run the various passes that connect the inland waters with the Gulf. The coast line following the winding shores of these many bays, lagoons, and coves extends about 2,000 miles along the mainland.

A central coastal section, extending, roughly, from Copano Bay on the north to Baffin Bay on the south, provides an extremely diverse system of intercoastal and Gulf waters. Many types of marine environment are to be found within this general area, in which the greater part of the field work centered and which, for the purposes of the investigation, appeared to satisfy the demand for an area of observation that would be representative of the entire coast line.

[1] Appreciation and thanks are due to the following individuals for assistance and advice, which enabled the investigator to progress in his task more rapidly than would have been possible if their interest and help had been lacking: Turner E. Hubby, former commissioner of the Texas game, fish, and oyster commission; William J. Tucker, present commissioner of the State commission; C. W. Gibson, of the Lone Star Fish & Oyster Co., Corpus Christi, Tex.; Robert E. Farley, deputy of the Texas game, fish, and oyster commission; Lawrence Gates of Corpus Christi, Tex. Special thanks are due to the city of Corpus Christi for the extended use of one of the rooms in the city hall as an office and laboratory. Many individuals and fish companies in the vicinity of Corpus Christi contributed greatly to the success of the investigation by their willingness to give advice and information.

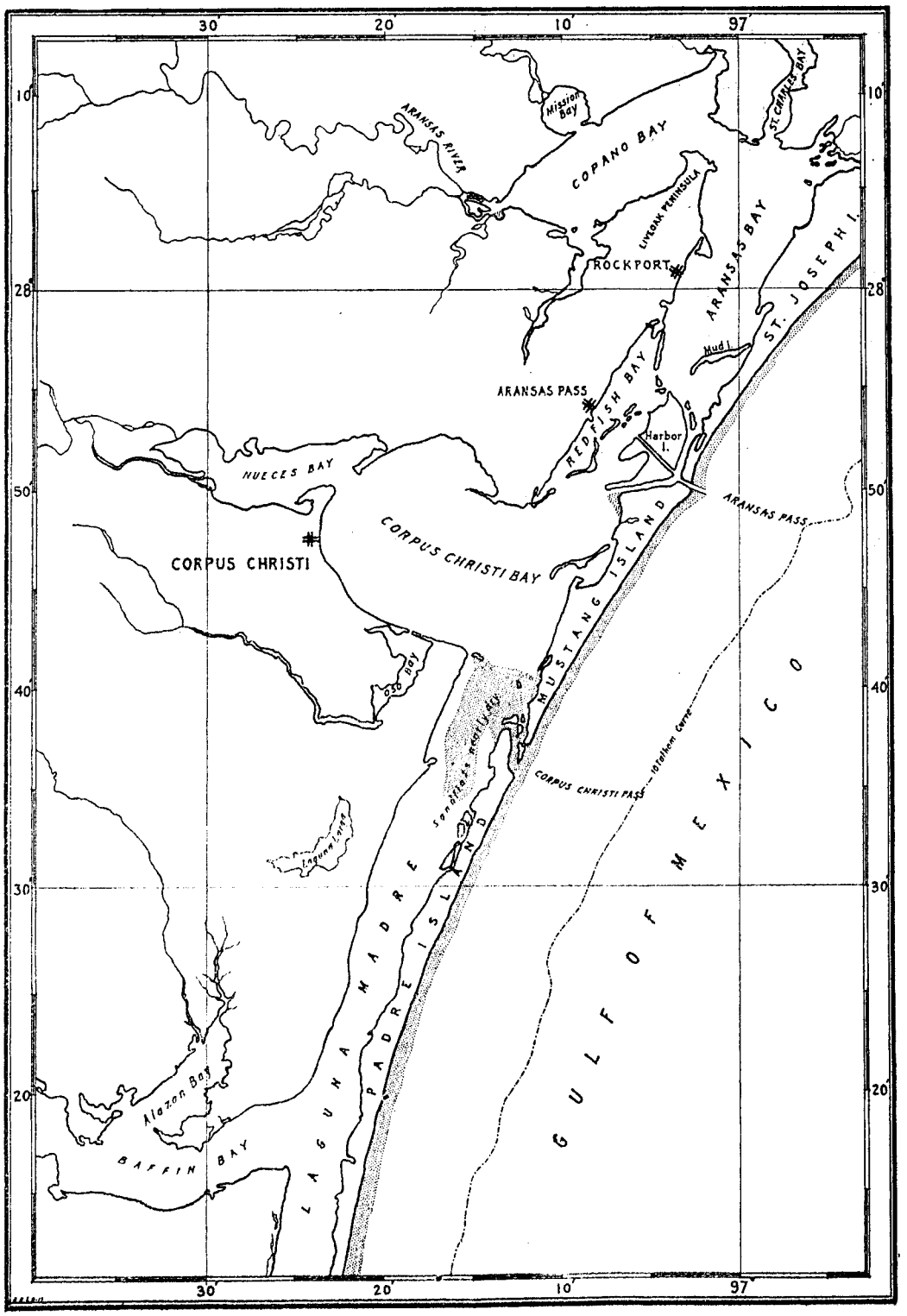

FIG. 1.—Section of the Texas coast covered by the investigation

The Gulf of Mexico is the fundamental source of all the marine life found within the intercoastal waters. Without the incoming tides the shallow bays and lagoons would be subject to such extreme temperatures and salinities as to render the existence of much marine life highly improbable. At the present time Laguna Madre, a long, narrow lagoon having poor circulation of water with the Gulf of Mexico, often reaches such high salinity through excessive evaporation in summer as to kill thousands of fish trapped in the lagoon by shallow water. In spring large quantities of Gulf water pour into the bays, bringing along a new supply of marine organisms, which usually linger within the intercoastal waters until the approach of cold weather.

Water from the Gulf enters the bays by the passes or inlets through the barrier islands. Because of the relatively slight tidal action, many of the more remote bays and lagoons do not attain a salinity equal to that of the Gulf and approach the character of brackish water. Two passes—Aransas and Corpus Christi—are included in the section of Texas coast represented in Figure 1.

Aransas Pass is an artificial or dredged channel, which has been enlarged from a relatively shallow, natural inlet to a deep, jettied pass, through which merchant ships go on their way to the inland port of Corpus Christi. The pass is about 2 miles long, 1,000 feet wide, 30 feet deep, and is protected against erosion by a pair of rock jetties stretching out into the Gulf about a mile from the shore line. Many observers believe that natural entrance of schools of fish into the bays is hindered by these barriers along the shore line. While no data exist to support or deny this contention, the writer found that the rocks at Aransas Pass had a decided tendency to impede the entrance of many larval and young croakers and spots into the bays. The deepened condition of the pass, resulting from continual dredging, allows more water to enter than would be possible if the pass were continually filled with sand, such as is the case with most of the natural passes along the coast. The effect of the dredging in the pass, however, could hardly be called beneficial to the particular species of fish found to spawn at the mouths of the passes.

Corpus Christi Pass, lying at the head of Laguna Madre and about 20 miles south of Aransas Pass, is a small, natural channel through which not even a small power boat can navigate on account of the ever-present sand bars in and about the pass. At the time of the investigation in 1926 and 1927 this pass was about 1,000 feet long, 100 feet wide, and about 6 feet deep in the middle of the channel. It may change its shape and depth after each severe storm and at times may be almost closed by sand bars.

Tidal action usually gives the passes along the coast but one strong incoming tide a day, and little or no water enters if the tide is opposed by strong winds. With the passes serving as main highways between the Gulf and the intercoastal waters, their condition is of the utmost importance if a continual interchange of water is to be maintained.[2]

[2] According to Marmer (1927, p. 434), the range of the tide at Galveston, Tex., averages but 1 foot, as compared with 4½ feet at New York and 9 feet at Portland, Me. On the Atlantic coast the two high waters and also the two low waters of a day are approximately the same, the morning and afternoon tides resembling each other in all respects. In the Gulf of Mexico, however, the two high waters do not differ much, but morning and afternoon low waters are so strikingly different that frequently the higher of the two low waters merges with one of the high waters, and at such times there is but one high water and one low water in a day.

The largest as well as the deepest of the intercoastal waters included in the general area of study comprised three main bays: Corpus Christi Bay, with its tributaries covering about 185 square miles, and Aransas and Copano Bays, covering with their tributaries about 163 square miles. The depth of water in these bays scarcely exceeds 15 feet, and numerous oyster reefs make much of the total area unnavigable to all but boats of the shallowest draft. The bottoms generally consist of hard sand with soft mud present in the vicinity of river mouths, and the water is often turbid, due to the heavy winds that sweep the coast.

Protected indentations of these larger bays, commonly called coves, are interesting in that generally they are preferred by fish to the more open, larger bays on account of the quiet, shallow water, well supplied with aquatic vegetation and organisms suitable for fish food.

A unique system of smaller bays tributary to the larger ones is common along certain sections of the coast. These smaller bays, typified by Oso and Nueces Bays, which empty into Corpus Christi Bay, are extremely shallow and muddy and inci-

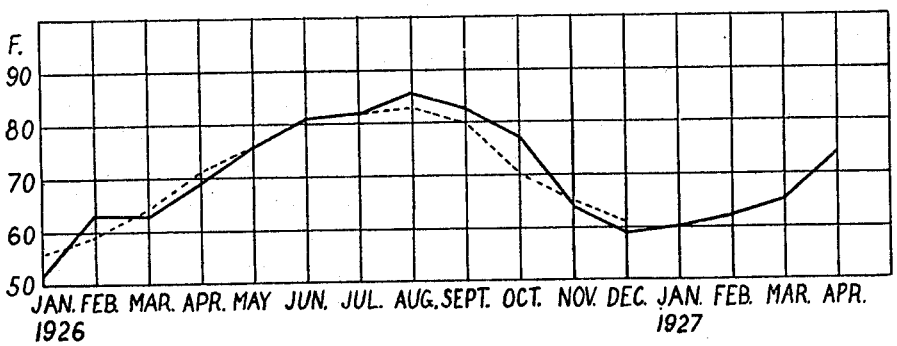

FIG. 2.—Mean air temperature at Corpus Christi, Tex. Solid line, January, 1926, to May, 1927; dotted line represents the averaged monthly mean temperature from 1888 to 1926. (From U. S. Weather Bureau records)

dentally harbor the bulk of the black-drum population. Their average depth is rarely over 3 feet, and excessive turbidity prevails on account of the quantity of silt brought down by the fresh-water rivers and creeks that empty into these bays.

Stretching from the southeast corner of Corpus Christi Bay to the mouth of the Rio Grande, a distance of over 180 miles, is the tortuous, extremely shallow Laguna Madre. This lagoon, except in the vicinity of Baffin Bay, has a depth rarely over 2 to 4 feet, with a grassy or mud bottom, according to the proximity of sediment-laden rivers or creeks. The northern half of the lagoon reaching from Corpus Christi Bay to Penascal Point in Baffin Bay (an enlarged and deeper portion of Laguna Madre), provides a fine foraging ground as well as a natural trap for the fish that frequent this body of water; while the general inaccessibility of the region allows the fish considerable protection from fishing activities. This portion of the lagoon has long been a problem to conservationists, since a heavy mortality of fish life often occurs during the summer months from the excessive salinity of the water, resulting from evaporation and lack of rain.

From Corpus Christi Bay to Baffin Bay the lagoon generally is open to navigation of shallow-draft sailboats; but below Baffin Bay it becomes nothing more than a

semidry mud or sand flat, which extends south to a point about 30 miles above Point Isobel, Tex. Consequently, very little circulation of water occurs in the vicinity of Baffin Bay. The only sources of fresh water are the small creeks emptying into the bay, and of salt water, the drift of sea water from Corpus Christi Pass and Bay southward. With little rainfall on this particular section of the coast, the salt water predominates nearly all the year in and about Baffin Bay as well as in the more northern portions of the lagoon.

During the summer of 1925 a period of excessive salinity (indicated by high specific gravity of the water) occurred in Laguna Madre, which caused severe mortality of fish trapped within the lagoon on account of the nearly dry areas between the section of high salinity (Baffin Bay) and the deeper, less saline waters of Corpus Christi Bay and the Gulf of Mexico. Table 1 presents a series of specific-gravity determinations within the particular area of high salinity as well as within other bodies of coastal water not affected. In all, 185 determinations were made throughout the area covered in Figure 1, but only the major stations have been given in Table 1. Waters with a low saline content are denoted by low specific gravity (Nueces and Copano Bays), while waters with a high content of salts are indicated by high specific gravities (Baffin Bay and Laguna Madre). Ordinary Gulf water found about the passes has generally a specific gravity of about 1.026. During July and August, 1925, the specific gravity of the water in Baffin Bay and lower Laguna Madre reached 1.055—twice that of normal Gulf water near the passes.

TABLE 1.—*Excessive salinity of the water in the vicinity of Baffin Bay and Laguna Madre, Tex., during the summer of 1925*

[The specific gravities indicate the relative salinity in various coastal waters. Ordinary Gulf water has a specific gravity of about 1.026. Consult text for details. Determinations by H. F. Prytherch]

Date	Locality	Specific gravity, 17.5° C.	Water temperature° F.	Air temperature °F.	Date	Locality	Specific gravity, 17.5° C.	Water temperature °F.	Air temperature°F.
July 29	Baffin Bay	1.055	87.0	86.0	Sept. 4	Corpus Christi Bay by Oso	1.029	80.0	83.0
30	Laguna Madre	1.055	87.0	84.5	5	Nueces Bay	1.023	84.0	82.0
31	Corpus Christi	1.029	84.0	84.0	5	Aransas Pass	1.027	84.0	83.0
31	Corpus Christi Pass	1.027	85.2	82.6	6	Aransas Bay	1.027	80.0	78.0
31	Corpus Christi Bay by Oso	1.028	86.0	85.0	6	Copano Bay	1.023	84.0	90.0
Aug. 4	Corpus Christi Bay	1.028	83.0	82.5	19	Baffin Bay	1.055	84.0	83.0
5	Aransas Bay	1.025	81.7	81.0	19	Laguna Madre	1.055	85.0	84.0
5	Copano Bay	1.021	82.7	84.0	20	Corpus Christi Pass	1.030	85.0	85.0
12	Baffin Bay	1.055	86.0	88.0	20	Corpus Christi Bay by Oso	1.029	85.0	86.0
12	Laguna Madre	1.060	87.0	84.0	20	Nueces Bay	1.020	87.0	85.0
13	do	1.055	86.0	87.0	21	Aransas Pass	1.027	84.0	80.0
14	Corpus Christi Pass	1.028	87.0	81.0	21	Aransas Bay	1.024	84.0	84.0
14	Corpus Christi Bay by Oso	1.027	86.0	88.0	21	Copano Bay	1.024	84.0	82.5
14	Nueces Bay	1.023	88.0	84.0	Oct. 7	Baffin Bay	1.039	83.0	80.0
14	Aransas Pass	1.028	86.0	83.0	7	Laguna Madre	1.039	85.0	82.0
15	Aransas Bay	1.026	85.0	82.5	8	Corpus Christi Pass	1.025	81.0	84.0
15	Copano Bay	1.023	86.0	85.0	8	Corpus Christi Bay by Oso	1.024	83.0	81.5
Sept. 3	Baffin Bay	1.055	88.5	86.0	8	Nueces Bay	1.017	84.0	82.0
3	Laguna Madre	1.044	88.0	87.0	8	Aransas Pass	1.025	83.5	83.0
4	Corpus Christi Pass	1.029	86.0	83.5	9	Aransas Bay	1.021	81.5	79.0

The average precipitation at Corpus Christi for May, June, July, and August, 1925, was but 1.26 inches, compared with the normal average for these months of 2.38 inches. This reduction of nearly one half of the normal rainfall during the summer of 1925 accounts, at least partially, for the excessive salinities that prevailed in Laguna Madre. Table 1 indicates a falling specific gravity within Baffin Bay and Laguna

Madre during October, 1925, and this was due largely to the rainfall during September, which measured 8.12 inches, compared with the normal for the month of 4 inches.

In the summer of 1926, with the average precipitation during May, June, July, and August at Corpus Christi slightly above normal (2.78 inches), there appeared no evidence of excessive or destructive salinity within Laguna Madre. Obviously, the amount of rain fall during the summer months determines to a great degree the conditions, both physical and biological, that obtain within this unique salt lagoon.

There remains to be mentioned another type among the coastal waters of Texas. This is represented by the bayous or channels running into the mainland and islands from the various bays or connecting the bays with one another. These bayous are generally from 10 to 100 feet long, much less in width, and are generally deep, owing to the action of tidal or wind currents, which keep the water running from one bay to another. Such bayous provide a most important refuge and feeding ground for young fish of many species, which enter from the spawning grounds in deeper areas. Table 2 presents an interesting catch made within a small bayou or creek in one haul with a small minnow seine and illustrates the variety of marine fish that prevails within such an environment.

TABLE 2.—*Young fish taken in one haul of a 50-foot seine in a small creek, 2 to 4 feet deep, off Copano Bay on May 18, 1927*

Common local name of fish	Scientific name	Common local name of fish	Scientific name
Skipjack	Elops saurus.	Anchovy, or "minnow"	Anchovia mitchilli.
Menhaden	Brevoortia patronus (?).	Swellfish	Spheroides nephelus.
Spotted sea trout	Cynoscion nebulosus.	Flounder	Species unknown.
Redfish	Sciænops ocellatus.	Hog choker	Achirus fasciatus.
Black drum	Pogonias cromis.	Mullet	Mugil cephalus.
Sand trout	Cynoscion nothus (?).	Catfish	Galeichthys milberti.
Sand perch	Bairdiella chrysura.	Alligator gar	Lepisosteus tristoechus.
Croaker	Micropogon undulatus.	Goby	Species unknown.
Spot, or flat croaker	Leiostomus xanthurus.	Gizzard shad	Dorosoma sp.
Jackfish	Caranx hippos.	Unknown	Polynemus ostonemus.
Electric fish	Porichthys porosissimus.	Needlefish	Tylosurus marinus.

METHODS

AREA OF STUDY

While the territory encompassed in Figure 1 and briefly described on preceding pages was believed to cover typical environments in which the redfish, black drum, and spotted sea trout occur, it seemed desirable to divide this extensive area into compact units or "key" stations, which could be examined regularly and efficiently for existing fish populations. A careful study of the fish life occurring at these "key" stations should yield a series of facts that finally could be patched together into a life history of the species of fish under consideration.

The greater part of the experimental collecting centered in and about these "key" localities, including the two passes, Aransas and Corpus Christi; adjacent waters to these passes, such as Harbor Island Channel and Bayou, Packery Channel, and the Gulf of Mexico; the more open bays, such as Corpus Christi, Aransas, and Copano, together with various coves (Shamrock and Ingleside) that form restricted portions of these bays; the more remote intercoastal waters, such as Oso and Nueces Bays, with Laguna Madre; and the many brackish rivers and creeks flowing into

the intercoastal bays and lagoons. Incidental but important collecting also was conducted in the waters of Baffin, Alazan, Mesquite, Espiritu Santo, Lavaca, and Matagorda Bays, as well as about Cedar Bayou and Cavallo Passes and along the shores of the Gulf of Mexico from Cedar Bayou Pass to Corpus Christi Pass. Much of the territory fished was closed to all forms of net fishing and consequently provided ideal conditions for an examination of the natural fish populations.

SAMPLING OF FISH POPULATION

A perfect method of sampling an unknown fish population requires in the beginning a perfect knowledge of this population. No detailed observations on the natural abundance and distribution of the redfish, black drum, or spotted sea trout in any particular localities along the Texas coast had ever been recorded, and what information was available was extremely fragmentary and unreliable. The field operations, as a matter of sheer necessity, had to be devoted largely to an effort to secure at definite intervals adequate samples of young and adult fish for data on maturity, time and place of spawning, age, rate of growth, and seasonal distribution and movements. Where and how these fish were to be captured constituted one of the first problems for the investigator to solve.

All catches made by any type of gear were supervised individually by the writer, and the results were tabulated and filed for future compilation and study. Since the investigator was in touch with the collecting operations, he was able to sense, by the changing composition and character of the catch in various localities, any unusual movements of the fish. As a rule, all food fishes captured were measured by the writer for total length from the tip of the snout to the end of the mid-caudal (tail) fin ray, and the sex was determined if the sexual elements were in evidence. All fish above 5 centimeters were measured in centimeters, while those under this length generally were measured in millimeters. Due to the great abundance of larval and young fishes of most species, but a small percentage of the total number secured was measured for consideration in this paper.

Several explanations may be offered for the lack of egg collections, which apparently are the first things to be sought in an attempt to understand the life history of any marine fish. Physical difficulties in employing the typical egg-collecting gear (the fine silk tow nets) were very serious throughout the investigation, owing to the shallow water and to the hordes of Medusæ, or jellyfish, that filled and broke the nets during the warm months of the year. So abundant are these Medusæ that bathing beaches on Corpus Christi Bay must be screened to prevent the bathers from becoming severely poisoned by contact with the pests. Furthermore, the heavy seas, often prevalent at the mouths of the passes in the Gulf of Mexico, prevented the small boat needed for navigation within the shallow bays from operating in the Gulf, where the majority of the marine fishes are believed to spawn.

With the securing of larval and young fish of the species desired, and with the definite indication of the general spawning areas through the nature and distribution of the newly hatched fish as well as the spawning adults, it was not thought practical to seek the fish eggs with the time and resources at hand. In future research, however, an attempt can well be made to collect the eggs of the redfish, black drum, and spotted trout on the basis of the information presented in this paper.

COLLECTING GEAR

Since the fishing gear occasioned the most serious error in obtaining a representative sample from any given locality, strenuous effort was expended constantly to employ nets with a wide range in size of mesh, which would cut this inevitable error to a minimum. Due to the efforts of 4 or 5 experienced fishermen, notable success was had in the operation of the various types of fishing gear. Drag or haul seines of varying sizes were the most practical and effective gear that could be used in the shallow water, while trawls, gill nets, tow nets, trammel nets, and dredges were most applicable in the deeper waters of the bays or the Gulf.

The frequency of use of any particular type of collecting gear was not considered, since all fishing operations were conducted as environmental conditions and scientific needs warranted at the time. Factors such as tides, winds, currents, type of fishing bottom, depth of water, and the kind of material desired were but a few of the limitations influencing the selection of gear. Table 3 presents a list of the types of collecting apparatus most generally used.

TABLE 3.—*Types of collecting gear employed during investigation*

[Several types of dredges and bottom trawl are not included]

Gear	Length, in feet	Depth, in feet	Size of mesh	Size of twine
Experimental seine	450	10	150-foot center, 1 inch square 300-foot ends, 1½ inches square	All No. 9 cotton.
Do	480	12	160-foot center, ¾ inch square 320-foot ends, +¾ inch square	Center No. 9 cotton. Ends No. 6 cotton.
Do	30	4	10-foot center, ¼ inch square 20-foot ends, ¾ inch square	All No. 6 cotton.
Do	50	4	20-foot center, ¼ inch square 30-foot ends, ½ inch square	Center No. 9 cotton. Ends No. 6 cotton..
Do	10	3	38 meshes per linear inch; oxx	Net made of bobbinet lined with silk cloth.
Commercial drag seine	[1] 600	5	100-foot center, 1 inch square 500-foot ends, 1½ inches square	Center No. 24 cotton. Ends No. 18 cotton.
Petersen trawl	29	7×3-2×1	All ¼ inch square	All No. 6 cotton.
Ring tow nets	9	3	38 meshes per linear inch; oxx	Silk bolting cloth.
Gill net	450	6	All 1½ inches square	No. 18/3 linen.
Do	300	5	All 4 inches square	
Trammel net	400	10	Inner net 1½ inches square Outer nets 4 inches square	Inner net No. 20/3 linen. Outer nets No. 12 cotton.
Commercial shrimp trawl	40	[2] About 35.	Bag ¾ inch square Mouth to bag 1 inch square	No. 18 or 21. No. 9.

[1] Bag of commercial drag seine 16 feet long.

[2] Width.

NATURAL HISTORY OF THE REDFISH, SCIÆNOPS OCELLATUS (LINNÆUS)

REDFISH, RED DRUM, CHANNEL BASS

Perca ocellata Linnæus, Syst. Nat., ed. XII, 1766, p. 483; South Carolina.
Sciænops ocellatus Jordan and Evermann, 1896-1900, p. 1453, Pl. CCXXII, fig. 567; Welsh and Breder, 1923, p. 184; Hildebrand and Schroeder, 1928, p. 276.

DESCRIPTION OF ADULT

The adult redfish has an elongate, rather robust body, with a somewhat elevated back. The head is long, rather low, with snout bluntish. The mouth is horizontal and rather large. No barbels are present on the lower jaw. The color is usually silvery reddish, with each scale having a dark center, these marks forming obscure lateral stripes along the rows of scales. A most characteristic marking on all adult redfish is the presence of a jet black spot at the base of the upper caudal or tail fin. Sometimes several of these spots may be present along the sides of the fish, but one on each side of the upper caudal is generally the rule. (See fig. 8.)

DESCRIPTION OF YOUNG

In larval redfish 4 to 5 millimeters in length (0.2 inch) the yolk sac is present and the dorsal and ventral fin folds are continuous to the caudal fin. The latter is fairly well developed, as are the vertical fins, although the rays of both dorsal and anal are indistinct. Ventrals and pectorals are obscure. One or several prominent groups of brown chromatophores or pigmentation areas are present invariably, and these serve, by their approximate location, to help to identity the young fish at this small size. The most pronounced as well as the most constant group lies ventrally along the posterior base of the anal, while the others lie, when present, one under both the spinous and soft dorsals, and one ventral, slightly posterior to the vent. Often a group of chromatophores appears between the anal and soft dorsal along the obscure lateral line and also between the vent and the spinous dorsal. (See figs. 3 and 4.) Redfish lacking vertical fin rays (fish generally under 7 millimeters) usually can be distinguished from larval croakers (*Micropogon undulatus*) through the fact that the latter possess no dorsal chromatophores, and both of the ventral ones lie closer to each other than ever occurs in the redfish. (Compare figs. 3, 4, 33, and 34.) Larval black drum (*Pogonias cromis*) probably will not be found at the time of the year when larval redfish occur. The dorsal chromatophores of the young larval drum tend not to appear until post-larval stages are reached (at about 7 to 10 millimeters). (Compare figs. 3, 4, 13, and 14.) Anal-ray counts usually are possible on young redfish at a length of 6 to 8 millimeters and above. The count of eight soft anal rays distinguishes the fish from other related species, with the exception of the croaker, which has the same anal count although a different soft-dorsal count.

At about 7 millimeters the yolk sac on young redfish has disappeared, and only a small membrane between the vent and the anal fin remains of the larval fin fold. At this length some fish may have portions of the fin fold still remaining along the edges of the caudal peduncle, however. The chromatophores generally are more pronounced, with small markings appearing on the head and along the sides of the body in no definite arrangement than can be discerned. (See fig. 4.)

Young redfish above 10 millimeters (0.4 inch) rapidly take on much pigmentation, and at 25 millimeters (1 inch) the color pattern has become most distinctive. The ground color at about 25 millimeters is a pale brown, somewhat silvery in fresh specimens. A distinct row of five to seven brown blotches, usually smaller than the eye, lies, for the most part, along the lateral line, one on the opercle, one behind, two or three under the soft dorsal and under the spinous dorsal, and one on the caudal peduncle. A fainter row of these blotches extends along the back from the nape to the caudal peduncle, with the number varying both as to size and number, as well as being more indistinct. A series of dark brown pigment dots extends along the base of the caudal fin, and a series of chromatophores runs along the base of the anal fin. The membrane of the spinous dorsal is punctulated with dark brown, and the soft dorsal is marked likewise, to a somewhat less degree however. Scales and teeth are evident. (See figs. 5 and 6.)

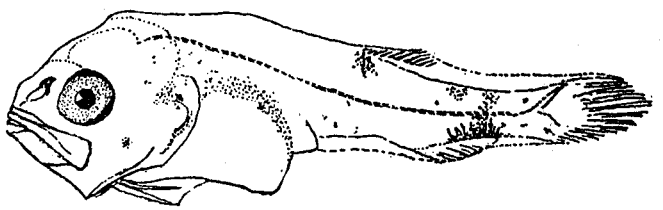

FIG. 3.—Larval redfish. Actual length, 4.5 millimeters

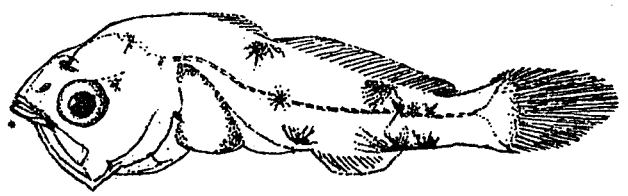

FIG 4.—Young redfish. Actual length, 7 millimeters

At about 36 millimeters (1.5 inches) the color pattern remains generally the same, with the important exception that a pronounced chromatophore enlargement occurs at the base of the upper caudal. This enlargement is the first appearance of the ocellated black spot that is characteristic of the species until death. (See fig. 7.)

The brown lateral blotches enlarge with the fish and generally remain until the latter has reached about 15 centimeters (5.9 inches), when they tend to fade and finally disappear. However, many redfish at 15 centimeters may have lost all traces of the blotches and assumed a dull grayish silver hue with a pronounced bluish iridescence above the lateral line. In a fresh specimen this silvery sheen obscures a mass of finely peppered dots that cover the upper and middle parts of the body and tend to form irregular, undulating, brown stripes along the rows of scales. The anal, pectorals, and pelvics are reddish in cast, with the black ocellated spot on the upper caudal peduncle most distinct.

FIG. 5.—Young redfish. Actual length, 11 millimeters

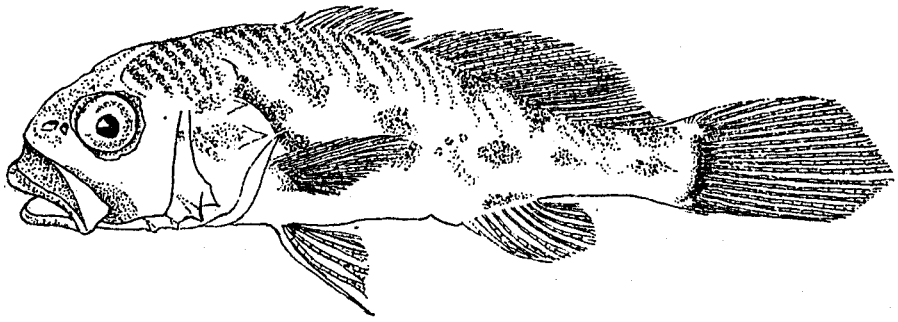

FIG. 6.—Young redfish. Actual length, 24 millimeters

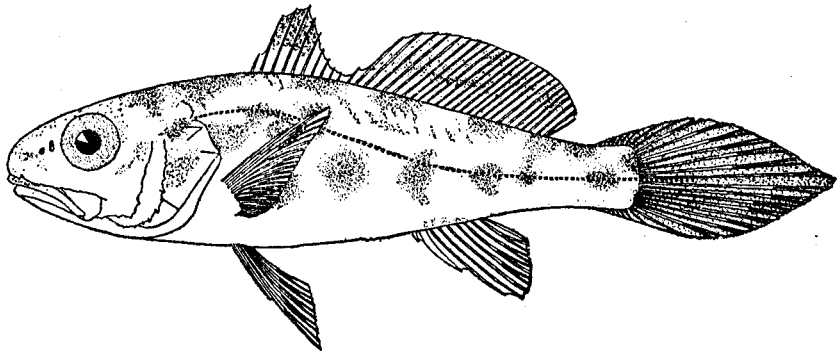

FIG. 7.—Young redfish. Actual length, 4.2 centimeters

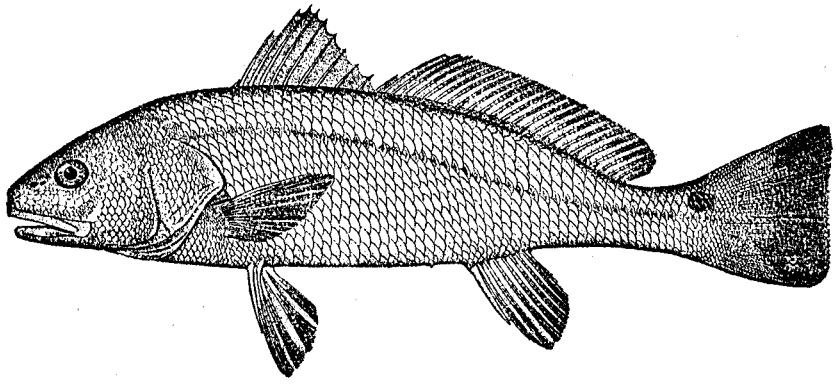

FIG. 8.—Adult redfish

SPAWNING AND EARLY DISTRIBUTION OF YOUNG

In a consideration of the various phases in the life history of the redfish or red drum the spawning habitat of the adult and the distribution of the young fish perhaps are of the most general interest. It has been a subject for much debate in recent years among those who profess an intimate knowledge of Texas coastal waters as to the exact location of the spawning grounds of the redfish, and while the idea is now generally established that the species spawns outside of the barrier islands in the open Gulf of Mexico, no definite observations ever were recorded to support this belief.

From April to September, 1926, a considerable number of redfish, ranging from 4 to 108 centimeters (1.5 to 42.4 inches) in length, were secured from the various bay and Gulf waters (Table 7). Examination of the sexual organs of all fish showed an immature or resting condition. On September 17, however, a large school of adult or "bull" redfish was observed in a regularly fished area in Shamrock Cove off Corpus Christi Bay, and the capture of part of this school revealed, by the presence of well-developed eggs in the ovaries of the females, that spawning time was approaching. Coincidental with the capture of these nearly ripe fish were the reports of fishermen that large numbers of "bull" redfish were traveling along the Gulf beaches and congregating about the mouths of the passes. Intensive fishing in all sections of the coastal area after the capture of these ripening fish failed to reveal any newly-hatched redfish until October 11, when along the shores of Harbor Island, inside of Aransas Pass and near the Gulf of Mexico, several young fish, ranging from 11 to 24 millimeters in length (0.4 to 1 inch), were taken in a few feet of water by a small beach seine. (See Table 4.)

TABLE 4.—*Collections of larval and young redfish (Sciænops ocellatus) during the spawning season of 1926*

Date of capture	Number of fish	Length range, in millimeters	Locality [1]	Miles from nearest pass
Oct. 11	49	11–24	Harbor Island Light	1
Oct. 18	128	6–34	do	½–1
Oct. 20	52	7–21	Lydia Ann Channel	1
	28	13–29	West side, Harbor Island	3–4
Oct. 22	4	23–26	Ingleside Cove	12
Oct. 25	30	10–26	Harbor Island	½–1
Oct. 27	2	25	Corpus Christi Bay by Oso	10
	5	15–29	Shamrock Cove	12
Oct. 28	10	7–18	Laguna Madre	½–1
Oct. 29	63	5–27	do	¼–1
	15	7–26	do	4
	49	5–14	do	1–3
Nov. 4	169	6–40	Harbor Island Light	1
Nov. 9	163	12–50	Harbor Island	1–3
Nov. 15	3	11–15	Laguna Madre	½–1
	15	13–28	Ingleside Cove	12
Nov. 23	132	10–60	Harbor Island	1
Dec. 1	9	17–53	do	1–3

[1] Approximate.

The exact locality where these young redfish were captured is known as Harbor Island Bayou and lies about 1½ miles inside of Aransas Pass. This bayou consists of a small, deepened channel, running from the east shore of the island (Lydia Ann Channel) into the interior of the land for several winding miles. On account of its

suitable depth and sluggish tidal current, the bayou, as well as contributory branches, furnishes an ideal refuge for thousands of larval and young fish. With the incoming tidal current from the Gulf, many marine organisms often are brought into the bayou, voluntarily or otherwise, where they may remain indefinitely or may depart on the next outgoing tide. Many tropical fishes, such as Pterophryne, the sargassum-weed dweller, often frequent Harbor Island Bayou during the height of the tide but generally return to the Gulf during low water.

After a week of seeking the young redfish within many bays with no success another visit to Harbor Island and the adjacent shore lines was made on October 18, when a greater number of larval and young fish were secured than a week previous. Systemic collecting along the grassy shore lines inside of Aransas Pass indicated that areas nearest to and in direct line with the pass yielded the greatest number as well as the smallest size of young. Table 5 illustrates the relative size and abundance of young at various distances from the passes.

TABLE 5.—*Relative size and abundance of young redfish about Corpus Christi and Aransas Passes during October to November, 1926 (from Table 4)*

	Distance, in miles, from nearest pass		
	¼ to 1	2 to 4	5 to 12
Total number of fish taken	636	264	26
Number of fish taken, in percentage	68	29	3
Average minimum and maximum lengths, in millimeters	8–29	11–34	19–28

Corpus Christi Pass, 20 miles south of Aransas Pass, was visited on October 29 to determine whether the newly hatched redfish were coming through the pass into Laguna Madre from the Gulf. The collections obtained were even more extensive than those made at Aransas Pass, for isolated patches of grass bottom in the shallow water immediately inside Corpus Christi Pass offered a temporary refuge for the young fish undoubtedly being brought into the pass from the Gulf of Mexico. Along the sides of the shallow channels radiating from the pass into the waters of Laguna Madre were large quantities of young redfish taken in particular when the tidal current was rushing in from the Gulf.

During the collection of the young fish about the passes (October to November) large numbers of adult redfish were observed milling about at the mouths of the passes. Several fish from these schools captured in the latter part of October showed ovaries with nearly spent roes. In mid-November a considerable number of spent adults was taken along the Gulf beaches in the vicinity of the passes by sport fishermen, all fish showing signs of emaciation due, no doubt, to the spawning activity in the previous weeks.

By the middle of November the numbers of larval and very young redfish commenced to decrease, and with the absence of any young under 10 millimeters (0.4 inch) after the 15th of the month it was believed that the spawning season was virtually at an end.

As shown by Tables 4 and 5, the newly hatched redfish in the younger stages were secured in the greatest abundance only in the immediate vicinity of the passes or along the sides of the channels directly supplied with the tidal waters from the Gulf. The distribution of the young apparently resulted from the action of the tidal currents, which, sweeping in from the Gulf, carried the young, nearly helpless fish to shallow areas covered with characteristic heavy aquatic vegetation.

A complicating factor in the ready identification of the redfish larvæ was the presence during late October and throughout November of great numbers of larval croakers (*Micropogon undulatus*), which were spawned in the Gulf and were coming into the bays in such abundance as to clog the nets and to render the separation of the fish from the closely related redfish most difficult. This confusion probably resulted in many larval and young redfish being missed in the tow-net collections conducted in the passes themselves as well as in the open Gulf. With gallons of the larval croakers being secured, little hope was entertained of finding the less abundant redfish. It was only when the young redfish had reached the more shallow waters that a ready separation of the species generally could be made.

There would appear to be no doubt that the redfish spawn in the Gulf of Mexico, near or at the mouths of the passes, and that the young come into the inland waters after hatching, to be distributed over many square miles of bays and lagoons. No other spawning place, save in the Gulf, would be possible to account for the concentrated numbers of young within and about the passes, together with the schools of spawning adults at the mouths of these passes.

Outside of the knowledge gained during the investigation along the Texas coast, very little definite information is available as to the time and place of spawning in other sections of the range of the species. Welsh and Breder stated (1923, p. 184) that "Spawning occurs chiefly in the late fall or early winter, although from the size of some young fish taken in Florida waters in January it is probable that some spawning may take place as early as September."

A series of young-fish collections made by Hildebrand and Schroeder (1928, p. 278) indicates that in Chesapeake Bay spawning occurs slightly earlier in the fall than it does along the Texas coast. The following catches are recorded by Hildebrand and Schroeder from Chesapeake Bay and are presented for comparison with the Texas collections.

TABLE 6.—*Collections of young redfish in Chesapeake Bay in 1921, by Hildebrand and Schroeder*

[Compare with Table 4]

Date	Number of fish	Length range, in millimeters	Date	Number of fish	Length range, in millimeters
Sept. 19	6	24–34	Oct. 15	1	49
Sept. 20	7	20–42	Oct. 26	45	25–49
Oct. 7	6	44–53	Nov. 21	2	48–54
Oct. 11	23	26–46	Nov. 23	28	39–90

GROWTH AND AGE

During the first two years of life the growth of the redfish is very rapid. Spawned about October, 1925, the fish making up the 1925 year class reached a mean total length of 21.5 centimeters (8.4 inches) by the end of May, 1926 (May 30 to June 6). (Consult Table 8 and fig. 9.) Comparably, the succeeding year class, hatched in October or November, 1926, attained approximately the same mean length of 21.5 centimeters by the end of May, 1927 (May 8 to 22). By the 1st of October, 1926 (October 3 to 10), the 1925 year class had grown to a mean length of 33.7 centimeters (13.3 inches). The growth of this class continued rapidly, although becoming reduced during the winter months, and by the end of May, 1927, when about 1½ years of age, the group reached a mean length of 43.6 centimeters (17.1 inches), with a length distribution from 36 to 51 centimeters (14 to 20 inches). This growth during the first year of life may be clearly followed by inspection of Tables 7 and 8 and Figure 9.

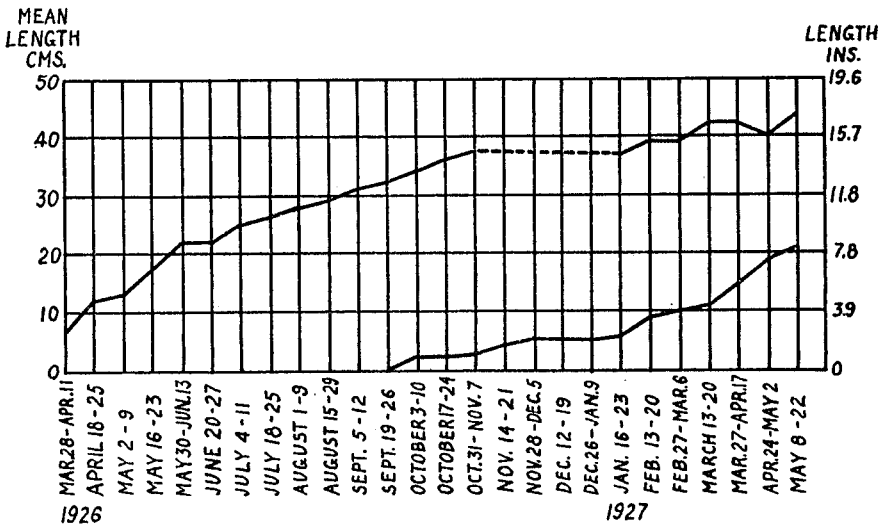

FIG. 9.—Growth of redfish during first 14 months of life. (Based on Table 8)

TABLE 7.—*Length-frequency distribution of redfish taken in Texas, March, 1926, to May, 1927*

[Collections summarized into approximate bimonthly periods]

Centimeters	Mar. 28–Apr. 11	Apr. 18–25	May 2–9	May 16–23	May 30–June 13	June 20–27	July 4–11	July 18–25	Aug. 1–9	Aug. 15–29	Sept. 5–12	Sept. 19–26	Oct. 3–10	Oct. 17–24	Oct. 31–Nov. 7	Nov. 14–Jan. 9	Jan. 16–23	Feb. 13–20	Feb. 27–Mar. 6	Mar. 13–20	Mar. 27–Apr. 17	Apr. 24–May 22
1	----	----	----	----	----	----	----	----	----	----	----	----	26	195	120	8	----	----	----	----	----	----
2	----	----	----	----	----	----	----	----	----	----	----	----	23	140	112	29	----	----	----	----	----	----
3	----	----	----	----	----	----	----	----	----	----	----	----	----	15	70	35	1	----	----	----	----	----
4	13	----	----	----	----	----	----	----	----	----	----	----	----	----	44	52	9	----	----	----	----	----
5	13	----	----	----	----	----	----	----	----	----	----	----	----	----	6	41	15	1	----	----	----	----
6	6	----	----	----	----	----	----	----	----	----	----	----	----	----	----	23	22	7	1	5	----	----
7	1	----	----	----	----	----	----	----	----	----	----	----	----	----	----	8	13	17	----	17	----	----
8	3	1	----	----	----	----	----	----	----	----	----	----	----	----	----	----	20	24	3	13	----	----
9	5	5	3	----	----	----	----	----	----	----	----	----	----	----	----	----	----	40	4	11	----	----
10	10	5	5	----	----	----	----	----	----	----	----	----	----	----	----	----	----	30	3	15	1	----

TABLE 7.—*Length-frequency distribution of redfish taken in Texas, March, 1926, to May, 1927*—Contd.

[Collections summarized into approximate bimonthly periods]

Centimeters	Mar. 28–Apr. 11	Apr. 18–25	May 2–9	May 16–23	May 30–June 13	June 20–27	July 4–11	July 18–25	Aug. 1–9	Aug. 15–29	Sept. 5–12	Sept. 19–26	Oct. 3–10	Oct. 17–24	Oct. 31–Nov. 7	Nov. 14–Jan. 9	Jan. 16–23	Feb. 13–20	Feb. 27–Mar. 6	Mar. 13–20	Mar. 27–Apr. 17	Apr. 24–May 22
11	10	4	7															23	1	14	3	1
12	1	2	8															8	1	21	1	
13	1		12	3														7		8		
14		6	10	4		1														2	2	
15		5	1	4		2												1		2	3	1
16		1	7	2	3																7	4
17		1	3	5	3	3															1	2
18		1	2	5	7																4	11
19			1	2	15	6															2	13
20				4	22	2	2	1														14
21				1	30	10	4	2														19
22					34	12	8	3			1		1									13
23					25	13	15		7	2												5
24					13	15	17	4	9	1												5
25					10	9	13	6	14	5												3
26					2	7	12	13	18	9		3										1
27					1	3	5	8	24	12	5	1										1
28						4	3	8	28	16	7	1	1									
29						2	2	4	21	25	9	4					1					
30						1	2	2	20	25	15	17	2									
31						1		1	7	26	16	16	6	1	1							
32									8	18	15	11	4	1			1					
33								1	9	15	5	10	9	2	3	1	3	1	1			
34									2	10	13	12	10	5	2		7	2	4			
35									1	11	6	8	7	2	1	1	12	5	1			
36									1	6	8	4	7	4	7	1	13	4	11		2	4
37									3	2	4	3	3	1	9	1	14	1	14		2	4
38										2	2	2	1	4	10	2	9	2	16	1	2	3
39			1							1	1	1	1		5	1	7	1	19		1	2
40				1		1				1		1	1	1	1		6	3	8	1		4
41														1	4	1	3	1	8		1	3
42		2													2	1	3	3	8		6	7
43		3	5	1		2											1	2	4	1	2	2
44		1	2	2		2					1	1				1		2	2			2
45			1	1	1				1									2	1			2
46			2	2	2	1			1			1					2		1	1	2	3
47			1		1		1														2	3
48			1		3	2			3	1											1	3
49			4	1	1	3	3		1	1												1
50			1	1	2	3	4		2									1				1
51			1	1	2	1			2	7												1
52			1	1	1	2	2		7	9				2								
53		1		1		1	2		2	4	1											
54						3	1		5	5	1	1										
55		1							3	5		4	1				2					
56						1	1		3	1	1	1	2						1			
57				3			1	1	1	1	1		2				1	1	2			
58		1		2					2	1		3	2				3		1			
59							1			1		1	1					3	2			
60					2				1	3		2					4		2			
61									3	4							3		1			
62		1					1		1	5			1				4		1		1	
63							2	1	2	2							5	2				
64		1		1			1		1	4		4			1		2	1	1			
65							4	1		4							1		2		1	1
66				1			1			1			1						1			
67							2			2							2		2	1		
68								2		1		1		1			1		1			
69				1			2	1				1							1			
70			1				1		1		1	2	1						1			
71							1				1	1							1			
72							2	1		3							1					
73							1	1				1					1					
74							1	9			3	1										
75								5			3											
76							2	2			2	2										
77								7														
78								4			6			1								
79								11			7	1							1			
80								2			5						1		1			

TABLE 7.—*Length-frequency distribution of redfish taken in Texas, March, 1926, to May, 1927*—Contd.

[Collections summarized into approximate bimonthly periods]

Centimeters	Mar. 28–Apr. 11	Apr. 18–25	May 2–9	May 16–23	May 30–June 13	June 20–27	July 4–11	July 18–25	Aug. 1–9	Aug. 15–29	Sept. 5–12	Sept. 19–26	Oct. 3–10	Oct. 17–24	Oct. 31–Nov. 7	Nov. 14–Jan. 9	Jan. 16–23	Feb. 13–20	Feb. 27–Mar. 6	Mar. 13–20	Mar. 27–Apr. 17	Apr. 24–May 22
81											4											
82								4			6								1			
83								2			11											
84							1				9								1			
85								2			10											
86							1	2			3											
87								1			4			1								
88								1			8											
89											2											
90								1			1											
91											1											
92											1											
93											2											
94																						
95								1														
96								1			1											
97																						
98																						
99								1														
100																						
107								1														
108								1														
Total	63	42	80	50	180	113	122	119	214	253	203	122	113	377	398	206	193	195	136	113	47	139

TABLE 8.—*Collections and length measurements of redfish taken in Texas, 1926 and 1927, illustrating growth during first year*

[Periods of collection usually in bimonthly summaries. Fish attain suitable market size at 36 centimeters (14 inches)]

Date	Year class 1925				Year class 1926			
	Number of fish	Length distribution, centimeters			Number of fish	Length distribution, centimeters		
		Minimum	Mean	Maximum		Minimum	Mean	Maximum
Mar. 28–Apr. 11, 1926	63	4	7.4	15				
Apr. 18–25, 1926	31	8	12.3	18				
May 2–9, 1926	59	9	13.2	19				
May 16–23, 1926	30	13	16.7	21				
May 30–June 13, 1926	165	16	21.5	27				
June 20–27, 1926	91	14	22.0	31				
July 4–11, 1926	83	20	24.8	30				
July 18–25, 1926	53	20	26.3	33				
Aug. 1–9, 1926	172	23	28.2	37				
Aug. 15–29, 1926	187	23	29.0	40				
Sept. 5–12, 1926	107	22	31.2	39				
Sept. 19–26, 1926	94	26	32.3	40				
Oct. 3–10, 1926	53	28	33.7	40	49	1	1.9	2
Oct. 17–24, 1926	22	31	35.6	41	350	1	1.5	3
Oct. 31–Nov. 7, 1926	45	31	37.4	42	352	1	2.2	5
Nov. 14–Jan. 9, 1927	10	33	38.3	44	196	1	4.0	7
Jan. 16–23, 1927	82	29	37.1	46	80	3	6.2	8
Feb. 13–20, 1927	29	33	38.6	45	158	5	9.3	15
Feb. 27–Mar. 6, 1927	98	33	38.8	46	13	7	10.2	13
Mar. 13–20, 1927	4	38	41.8	46	108	7	10.9	16
Mar. 27–Apr. 17, 1927	21	36	41.6	48	24	10	15.3	19
Apr. 24–May 2, 1927	19	36	39.9	50	26	11	18.5	23
May 8–22, 1927	25	36	43.6	51	67	15	21.2	27

By a comparison of 1½-year old fish taken during the bimonthly periods of April 18 to 25, May 2 to 9, and May 16 to 23, 1926 (probable length range from 39 to 53 centimeters), and the monthly period of April 24 to May 22, 1927 (probable length range from 36 to 51 centimeters), it is found that the 1926 fish possess a mean total length of 45.8 centimeters (18 inches), while the 1927 group of the same age has a mean total length of 44.1 centimeters (17.3 inches). (See Table 7.)

The May, 1926, 1½-year old redfish, with a length range from 39 to 53 centimeters and a mean total length of 45.8 centimeters (18 inches), appeared to attain an approximate modal length of 52 centimeters (20.5 inches) by September, 1926, on the basis of a collection of fish taken during the period of August 15 to 29, 1926.

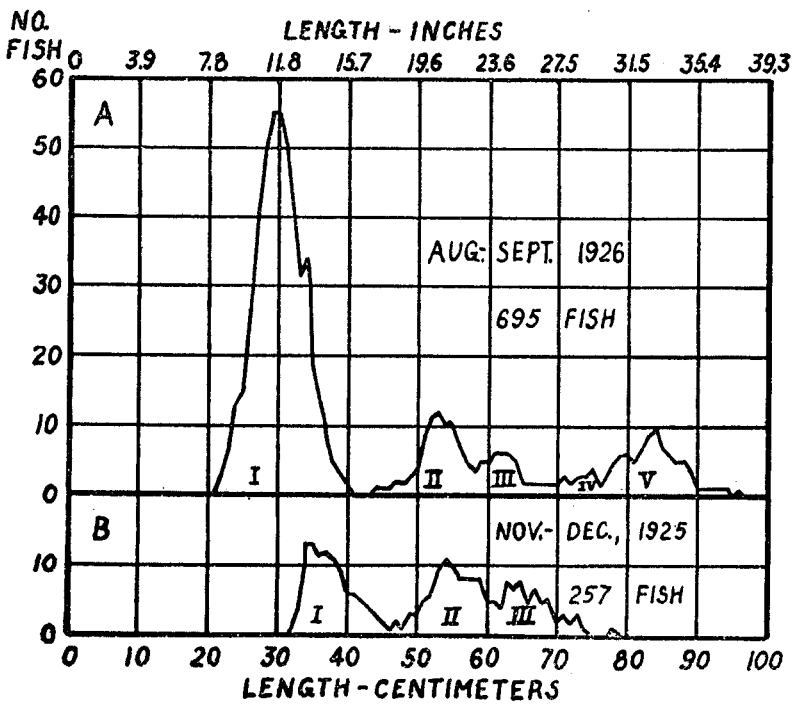

FIG. 10.—**A**—length-frequency distribution of redfish taken in Texas with experimental gear during August and September, 1926. **B**—length-frequency distribution of market redfish taken during November and December, 1925. Actual frequencies in both cases have been smoothed by a moving average of threes. Roman numerals indicate year classes

This collection (Table 7) had a length range from 48 to 68 centimeters, which probably included two year classes, the second with a mode at 52 centimeters and the third with a mode at 62 centimeters.

Collections of redfish above the second year are not numerous, owing mainly to the difficulty experienced in obtaining unselected catches of the larger, more powerful fish. However, by combining all samples of fish secured during August and September, 1926, a fairly well defined series of year groups or classes is discernible by inspection of the modes or humps in the length-frequency distribution. (See Table 9.) An error necessarily is occasioned by this grouping, since fish taken in early August will have grown some by the end of September. This is noticeably true in the case

of the youngest year class by a comparison of the bimonthly samples (Table 7), but for the present purpose of presenting all distinguishable year classes at one time this error may be disregarded.

A smoothed length-frequency distribution of these redfish shows the first three year classes to be marked by modal lengths at 30, 53, and 63 centimeters (11.8, 20.8, and 24.8 inches). (See fig. 10A.) Following these definite year groups, several modes are evident at about 75, 79, and 84 centimeters, and these modes are believed to be composed of fish in the fourth and fifth year classes. The mode at 79 centimeters is probably accidental and made up of fish either in the fourth year and belonging with the 75-centimeter group, or in the fifth year and belonging with the 84-centimeter group. The small number of fish lying within the probable range of the fourth year class magnifies this abnormal or chance mode at 79 centimeters. It must be realized, of course, that a considerable overlapping occurs among the various year classes, particularly as age and size increase.

TABLE 9.—*Length-frequency distribution of redfish collected with experimental gear in August and September, 1926*

Length, centimeters	Frequency	Length, centimeters	Frequency	Length, centimeters	Frequency	Length, centimeters	Frequency	Length, centimeters	Frequency
22	1	38	4	54	12	70	4	86	3
23	9	39	2	55	12	71	2	87	4
24	10	40	1	56	6	72	3	88	8
25	19	41	0	57	3	73	1	89	2
26	27	42	0	58	6	74	4	90	1
27	41	43	0	59	2	75	3	91	1
28	51	44	2	60	6	76	4	92	1
29	55	45	1	61	7	77	0	93	2
30	62	46	2	62	6	78	6	94	0
31	49	47	0	63	4	79	8	95	0
32	41	48	4	64	9	80	5	96	1
33	29	49	2	65	4	81	4		
34	25	50	2	66	1	82	6	Total	695
35	18	51	9	67	2	83	11		
36	15	52	16	68	2	84	9		
37	9	53	7	69	1	85	10		

In a consideration of the reliability of the above age estimates, it should be recognized that the redfish attains an extremely large size. While a length of only 105 centimeters (42.5 inches) was the largest size secured during the past investigation along the Texas coast, many fish reach a much larger size, with the maximum length of the species recorded by Welsh and Breder (1923, p. 184) at 152 centimeters, or about 5 feet. With the increment in length for Texas fish during the first year about 34 cemtimeters (13.4 inches), during the second year about 20 centimeters (7.8 inches), and during the third and fourth years about 10 centimeters each (4 inches), it is most likely that the growth increment during the fifth year would be but little less, causing the fish to have a general average length of about 83 to 85 centimeters (33 inches) at the end of its fifth year of life.

A series of measurements made upon 257 market redfish caught in a commercial seine during November and December, 1925, is presented by Table 10 and illustrated graphically by Figure 10B. A smoothed length-frequency distribution (fig. 10B) shows the presence of the first three year classes (I, II, and III) with length modes existing at 35, 54, and 64 centimeters (13.7, 21.2, and 25.2 inches) and with a slight mode at 74 centimeters (29.1 inches), and probably representing fish

in the IV-year class. The youngest or 0-year class (a few weeks old) is not represented, of course, in the commercial catch. The abrupt curve at about 32 to 33 centimeters (12.6 to 12.9 inches) results from the selection of the gear as well as a legal minimum-size market limit at 36 centimeters (14 inches).

TABLE 10.—*Length-frequency distribution of 257 market redfish taken in Laguna Madre, Tex., November to December, 1925, by commercial seines*

Length, centimeters	Frequency	Length, centimeters	Frequency	Length, centimeters	Frequency	Length, centimeters	Frequency	Length, centimeters	Frequency
33	4	42	4	51	3	60	8	69	3
34	14	43	4	52	6	61	3	70	2
35	17	44	3	53	10	62	3	71	1
36	8	45	1	54	12	63	6	72	5
37	12	46	2	55	11	64	14	73	0
38	15	47	1	56	6	65	2	74	3
39	6	48	2	57	7	66	9	78	1
40	6	49	0	58	12	67	3		
41	7	50	7	59	4	68	10	Total	257

A study of the annual winter growth check, as indicated on the scales of the redfish, afforded verification of the age estimates made from the length frequency. The redfish spawned in the late fall rarely show, on the scale structure, any evidence of a reduced growth rate during the first winter, but after the first winter definite changes occur in the scale pattern during the cold months of the year, which enable the age of the fish to be determined with some degree of accuracy. The scales of the species become heavily calcified and opaque after the second or third year, and it is necessary to treat them with a weak solution of hydrochloric acid in order to make them transparent.

The nature of the redfish scale is similar to that of the black drum, and the winter growth check in both species essentially consists of a break or interruption in the pattern of the circuli on the scale, particularly along the lateral terminals of the circuli. These breaks or irregularities probably are produced by the greatly accelerated growth of the fish and its scale in the early spring after a winter period of retarded growth. Closer approximations of the circuli along the radii during the winter season are evident on the scales from the younger fish, with these approximations forming so-called "bands," ending along the lateral terminals in pronounced breaks in the circuli arrangement.

The abundance of scale material allowed the fact to be proved that these scale checks were formed annually during the winter season, with, however, the first winter's check usually absent or faint, owing probably to the small size of the fish during the first winter. Measurements of these annual checks for the purpose of calculating the average growth were not deemed practical, since the decalcification of the scales caused the latter to change their size.

The ages of 300 unselected redfish were obtained by counting the number of winter scale checks, including any check that may or may not have formed during the first winter, when the fish were but a few months old. Thus, in the case of a collection of fish taken during April and May, 1926 (fig. 11), 35 redfish, ranging from 8 to 21 centimeters in length (3.1 to 8.2 inches), were found to be in their first year (having been spawned the October or November previous and in most cases not showing a winter check on the scales); 22 redfish, ranging from 40 to 51 centimeters (15.7 to 20 inches), were found to be in their second year (possessing, in all cases, one

definite scale check usually near the periphery of the scale and indicating a check in growth during the second winter of life); 6 redfish, ranging from 53 to 57 centimeters (20.8 to 22.4 inches), showed two definite winter checks; and 7 redfish, ranging from

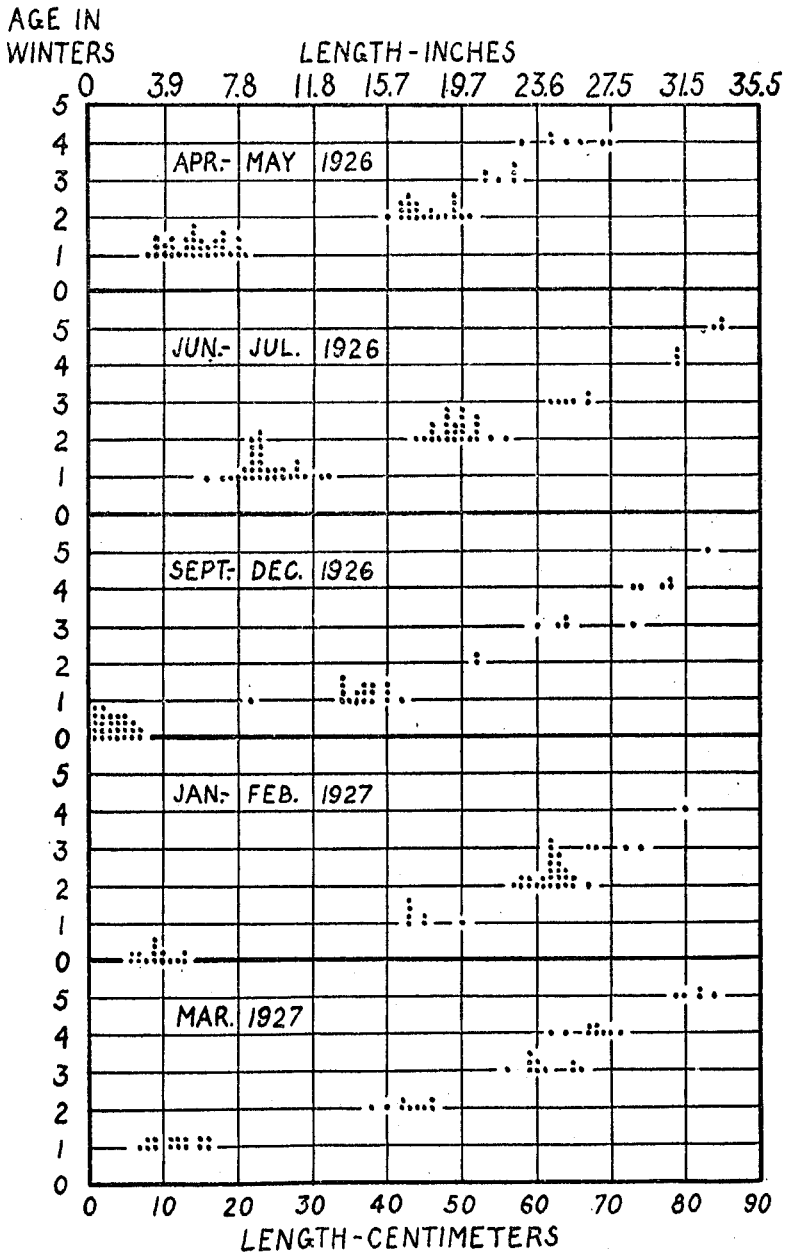

FIG. 11.—Age of redfish according to length, as indicated by winter growth checks on scales

58 to 70 centimeters (22.8 to 27.5 inches), possessed three definite annual scale checks. Hence, the approximate actual age, in years, of the redfish as represented in winters by Figure 11, is one less than the number of winters recorded.

For the first three years little doubt exists as to the verity of these age determinations by the scale method, but it may be said that after the third winter some errors may occur in the age determinations, due both to the extreme difficulty in examining the large scales and to the personal judgment of the writer in counting the annual breaks or "checks" in the annuli of the scales. It would appear, however, on the basis of both scale and length-frequency studies, that the redfish reach a total length of about 80 to 85 centimeters (31.5 to 33.2 inches) by the end of the fourth year or the fifth winter of life.

SEASONAL DISTRIBUTION AND MOVEMENTS

The larval and young redfish, after entering the bays and lagoons from the Gulf spawning grounds, tend to distribute themselves rapidly. While assisted in the early stages of distribution mainly by the tidal currents, the young fish soon is able to use its own power of locomotion to take it to places of safety. By October 27, 1926, several small redfish 25 millimeters long (0.6 inch) were taken along the shores of Corpus Christi Bay near the entrance into Oso Bay, while a collection of young 15 to 29 millimeters long (under 1 inch) was secured in Shamrock Cove, a sheltered indentation of Corpus Christi Bay some 12 miles or more from Corpus Christi Pass.

The young seek the more grassy and quiet coves and lagoons during the early part of life, rarely being found on bare, sandy bottom or in rough water. This preference for shallow tidal flats was most noticeable in the vicinity of the passes. A serious destruction of many small redfish consequently may have resulted in October, 1926, when an extremely low tide occurred in the vicinity of Aransas Pass, which caused large areas of the shallow flats in and about Harbor Island to become dry. Many small mullet and top minnows were observed in a dying or dead condition as a result of being unable to reach the deeper channels when the water drained off from the flats. Many young redfish known to be on such areas were either killed likewise or forced to enter the channels that did not appear suited to the normal requirements of the fish.

With the coming of cold weather during the first winter, the young redfish, ranging in length from 5 to 15 centimeters (2 to 5.9 inches), work into the deeper bayous from the more shallow coves and flats. During the spring following hatching many wander out into the Gulf of Mexico, but apparently they occur only in moderate numbers along the shore lines in the surf, since none ever are caught in the shrimp trawls, which operate from 1 to 10 miles offshore. In less than a year after hatching young redfish may be found within the bays and lagoons, 75 miles or more from the nearest pass, as collections of fish in July, 1926, from Baffin Bay (Laguna Madre) indicate. The absence of young redfish less than 10 to 15 centimeters in length (3.9 to 5.9 inches) from the waters of the Gulf of Mexico is most striking and would indicate that conditions in the Gulf are not suited to the early stages following hatching and that all newly hatched fish come into the bays.

After the first year most of the redfish leave for the deeper bays or Gulf during cold weather. The movement of fish out into the Gulf is gradual and not noticeable to any extent, but in the early spring the movement back into the bays and lagoons is pronounced. This spring movement into the bays, particularly of the younger year

classes (fish from 40 to 60 centimeters), provides hook-and-line fishing about the various passes, especially Corpus Christi.

After a certain maximum length is attained (about 70 centimeters or 27.5 inches) the redfish tend to travel in schools and remain for the most time along the sandy shores of the Gulf of Mexico. According to old fishermen, many of these schools of "bull" redfish frequented the bays and lagoons during the summer months, departing to the Gulf in early fall. At the present time, however, few such schools are noticeable within the bays (two schools taken by the writer in July and September, 1926, in Corpus Christi Bay). This fact has given rise to the opinion that the species is becoming depleted. It is the decided belief of the writer that this absence of larger redfish from the bays is not due to the actual scarcity of the fish (all redfish above 32 inches have been protected by law for some years) but to the marked changes that have resulted from the use of power boats and water traffic, as well as from the activities of sportsmen who congregate about the passes in large numbers. The schools of redfish are known to become easily frightened or "stampeded" at any slight disturbance, and any activities in the vicinity of the passes may be regarded as unfavorable to the entrance of the fish into the bays.

When spawning time approaches (September), the schools of redfish, composed largely of adults above 75 centimeters, travel along the shore lines of the Gulf beaches until they strike the mouths of the passes. This movement or spawning migration is most evident along Mustang and Padre Islands, Tex., during the early fall. Those few schools of ripening adults that have been living within the bays during the summer apparently seek the pass exits to the Gulf. A concentration of spawning schools of redfish at the mouths of the passes undoubtedly results in a condition favorable to natural propagation and distribution of young.

SIZE AND AGE AT MATURITY

One large, unselected collection of sexually matured redfish was captured in late September, 1926, several weeks before the first young of the 1926 year class were taken. The sample consisted of 80 fish, ranging in length from 74 to 96 centimeters (29 to 38 inches), and was part of a large school of fish that apparently was endeavoring to find an exit from the narrow cove into which it had wandered. Several of these fish when examined showed that spawning time was near at hand. A nearly ripe roe taken from a female 90 centimeters long (3 feet) weighed approximately 13 ounces and contained about 3,500,000 eggs. Two methods were used to calculate the total number of eggs, with the results presented below:

Von Bayer method:

D=diameter of known whitefish eggs, in inches	0.127
N=number of whitefish eggs to the quart, by actual count	33,036
d=average diameter of redfish eggs, in inches (0.5 millimeter)	.02
Total volume of redfish eggs, in quarts (400 cubic centimeters)	.4
By use of Von Bayer's formula $D^3:d^3::n:N$, where n is the unknown.	
n, or the number of redfish eggs to the quart, equals	8,457,216
Number of redfish eggs in 0.4 quart	3,382,886
Total number of eggs in 90-centimeter redfish (3 feet)	3,382,886

Actual weight method:

A total weight of 23 milligrams gave an egg count of	176
One milligram, by calculation, equals	7.652
One gram of redfish eggs, by calculation, equals	7,652
Total weight of redfish eggs, in grams	447
Total number of redfish eggs in 90-centimeter fish (3 feet)	3,410,000

Maturity appears to be reached at the end of the fourth or fifth year of life. No redfish under 75 centimeters (29.4 inches) were taken in a mature condition during the field operations, and ripe fish are virtually unknown to the fishermen, who must free all captured fish over the legal size limit of 81 centimeters (32 inches). On the basis of the one collection of nearly ripe fish taken in September, 1926, it would seem most likely that maturity is not reached before the end of the fifth year, certainly not before the end of the fourth.

Figure 12, showing the relation of weight to length in 222 redfish, indicates that a weight of 10 pounds or over is attained before the time of first spawning (70 centimeters, or 27.5 inches in length, at least, being reached by the fish).

FOOD HABITS

The food of the redfish along the Texas coast is made up principally of the crustaceans such as the shrimps and crabs. The commercial shrimps (Peneus) appeared to be the favorite food with some 236 redfish 6 to 72 centimeters long examined for stomach contents. The common blue crab (Callinectes), when small or in a molting condition, ranks second in abundance. (See Table 11.)

TABLE 11.—*Food preference of 236 redfish, presented in percentage of total number of fish in each length group that fed exclusively on the various organisms*

[Mixed food usually a combination of shrimp, fish, and crabs. Fish taken from February to May, 1927]

Length, centimeters	Number of fish	Percentage of fish that had eaten—				
		Shrimp	Fish	Crabs	Mollusks	Mixed
6–16	147	52	20	6	4	18
17–30	42	83	2	10	0	5
31–46	43	79	0	2	0	19
47–68	4	0	25	50	0	25

Fish are eaten to some extent, with the mullet, gobies, and Menidia being identified in the greatest abundance among the food fragments. The larger redfish are able to capture fish of considerable size, as shown by the presence of a 20-centimeter (7.9 inches) mullet (Mugil) in the stomach of a 68-centimeter (26.8 inches) redfish. Surf casting for the larger fish along the Gulf beaches yields the best results when small mullet are used as bait, while shrimp bring the largest catches of the smaller-sized fish.

Curious incidental food may be found in the stomachs of the fish at times. A large marsh rat, squids, annelid worms, and small bivalves have been recorded from redfish stomachs. The species undoubtedly has the ability to pursue its prey, although it can and does adopt a semibottom-feeding habit at times. It may be said to have a feeding habit intermediate between that of the drum, a strictly bottom feeder, and the spotted trout, a pelagic feeder.

COMMERCIAL CONSIDERATIONS

The redfish or red drum occurs in commercial quantities from New Jersey to Texas. Florida leads in the total production, with Texas ranking second. The Gulf States

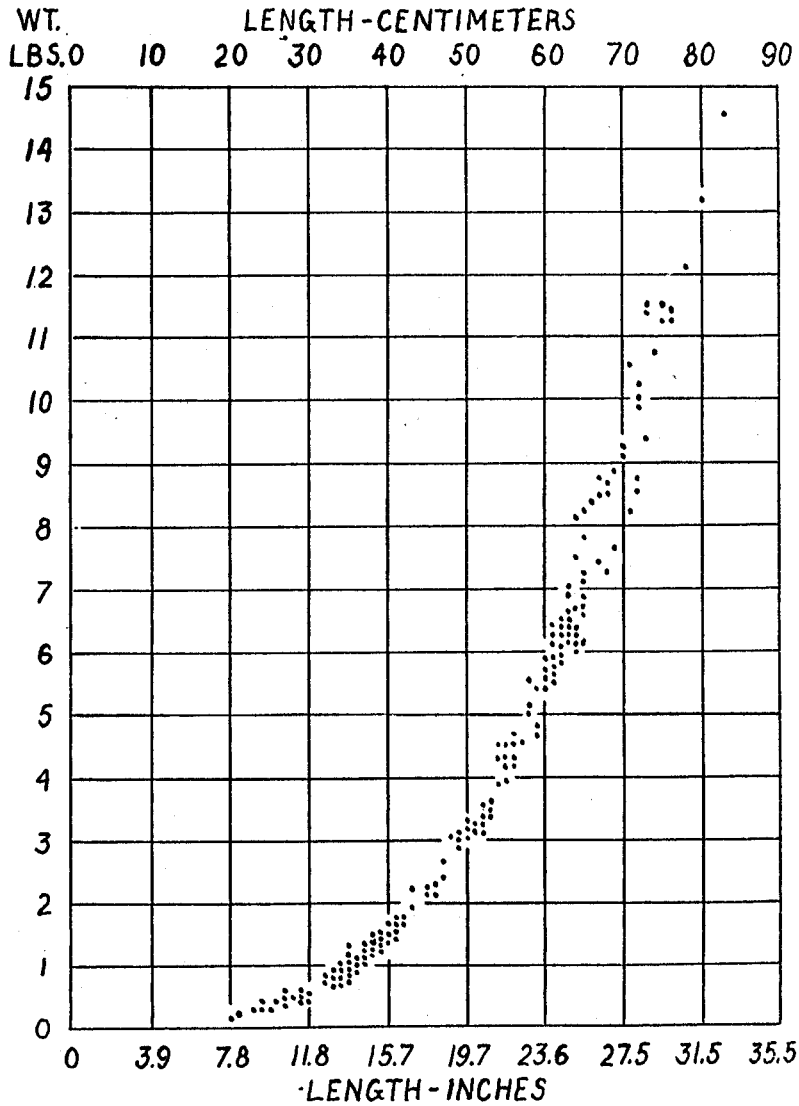

FIG. 12.—Relation of weight to length in 222 redfish

exceed the South Atlantic States in both the quantity and value of the commercial catch. The following table is taken from the reports of the United States Bureau of Fisheries.

TABLE 12.—*Catch of the redfish (Sciænops ocellatus)*

State	Weight, in pounds	Value	Value per pound	Year
Florida:				
West coast	1,398,291	$43,249	$0.030	1923
East coast	121,850	4,434	.036	1923
Texas	877,760	72,299	.082	1923
Louisiana	665,067	55,941	.084	1923
North Carolina	245,443	10,763	.043	1923
Mississippi	176,760	12,979	.073	1923
Virginia	125,390	2,243	.018	1925
South Carolina	31,000	1,730	.056	1923
Alabama	14,765	949	.064	1923
New Jersey	14,300	412	.029	1926
Delaware	3,310	60	.018	1926
Total	3,673,936	205,059	----------	------

The redfish provides both sport and commercial fishing along the coast of Texas. Surf casting along the beaches of the Gulf of Mexico is very popular, and, while such a method of fishing does not account for large quantities of market fish, the income secured by coastal cities and towns from visiting tourists and sportsmen is considerable. Many of the redfish taken along the Gulf beaches by anglers are the larger or "bull" fish (over 32 inches), the sale of which is forbidden by law.

Within the intercoastal bays, extensive commercial fishing operations are conducted to secure the redfish as well as other food fishes. By far the most efficient and practical method of fishing is by means of drag seines. In late years serious opposition has arisen to all forms of net fishing along the Texas coast, with the result that many bays, as well as Gulf waters, have been closed to net fishermen, although commercial hook-and-line fishermen may operate anywhere. Consequently, unrestricted line fishing is conducted within many of the bays, particularly around the passes, for redfish as well as several other species of food fish, although, naturally, more effort and expense is required to catch them in this manner. Simple pole-and-line fishing yields good catches of small redfish (1 to 3 pounds) at certain times of the year, especially in spring, while trot lines or long series of stationary hooks, baited usually with pieces of red rubber, are employed in some of the more shallow lagoons.

As stated by Higgins and Lord (1926, p. 180), the commercial catch of redfish in Texas has shown a virtually horizontal trend since 1890. No signs of depletion could be detected by these investigators on the basis of the rather meager statistical data available. Many fishermen, however, assert that the fishing effort expended to-day is much greater than occurred in former years. While this statement probably is true, for some years past the redfish has been given legal protection in several ways, which tends to reduce the catch to a marked degree.

Omitting from consideration at present the effect of closing many productive redfish fishing grounds, the State of Texas has in operation a minimum and maximum legal size limit for all redfish caught within State waters. No fish under 14 inches (36 centimeters) or over 32 inches (81.2 centimeters) may be offered for sale. From a market standpoint, these size limits appear well worth while, since dealers find it difficult to sell redfish under 14 and over 32 inches. Redfish of over 3 pounds are not especially esteemed for family use, but restaurants and hotels buy the larger

fish, which are served in the form of steaks. By preventing the sale of fish of over 32 inches, virtually all of the mature or spawning redfish are protected. This would seem most desirable from the standpoint of fishery conservation when it is realized that the bulk of the catch is composed of fish in their second and third year, and that the marketability of the species is reduced greatly after the third or fourth years.

The total catch of redfish in Texas undoubtedly could be increased if many of the closed waters were to be opened to net fishing. This applies particularly to a long stretch of Gulf beach along Padre Island, which is an exceedingly fine feeding ground for many of the larger redfish. No way to determine the capacity of any fishery is recognized, except by actual trial by the most efficient commercial methods, and the gradual reduction of the commercial coastal fisheries to a hook-and-line method of fishing will hardly allow such a capacity to be ascertained.

SUMMARY

1. The redfish spawning season occurs mainly in October, and in the Gulf of Mexico actual spawning takes place close to or at the mouths of the various passes.

2. The newly hatched redfish are carried by the tidal currents into the bays and lagoons, where they remain for an indefinite period.

3. The redfish attains a modal total length of about 13.4 inches (34 centimeters) by the end of the first year, 21.3 inches (54 centimeters) by the end of the second, 25.3 inches (64 centimeters) by the end of the third, probably about 29.5 inches (75 centimeters) by the end of the fourth, and 33 inches (84 centimeters) by the end of the fifth year. The species reaches suitable market size soon after the first year.

4. Maturity is reached not before the end of the fourth or fifth year, probably the fifth, with few fish under 30 inches (75 centimeters) in a sexually mature condition.

5. The food of redfish from 2.4 to 23.6 inches (6 to 60 centimeters) in length consists principally of shrimps (Peneus), crabs, and small fish.

NATURAL HISTORY OF THE BLACK DRUM, POGONIAS CROMIS (LINNÆUS)

Black Drum

Labrus cromis Linnæus, Syst. Nat., ed. XII, 1766, p. 479; Carolina.
Pogonias cromis Jordan and Evermann, 1896–1900, p. 1482, Pl. CCXXV, fig. 573; Welsh and Breder, 1923, p. 186; Hildebrand and Schroeder, 1928, p. 287.

DESCRIPTION OF ADULT

The adult black drum has an oblong, compressed body, with the back much elevated. The head is moderately short, with the snout blunt. The lower jaw possesses numerous large barbels along the inner edge of each side, with the series usually reaching back to below middle of eye. The color in life is generally silvery black, with often a brassy luster, and all fins are black or dusky. Variations in color are frequent among drum taken along the Texas coast, depending largely on the particular environment from which the fish is taken. Drum from the Gulf of Mexico are usually uniformly silvery, with the black lateral bars, characteristic of the young fish, becoming indistinct; while adult drum taken in the shallow bays are black or even bronze. (See fig. 19.)

DESCRIPTION OF YOUNG

The smallest larval drum taken in Texas measured 4.5 millimeters (0.2 inch). A small yolk sac is present, and the dorsal and ventral fins are not evident. Two prominent groups of chromatophores are present; both lying ventrally, one slightly

FIG. 13.—Larval black drum. Actual length, 4.5 millimeters

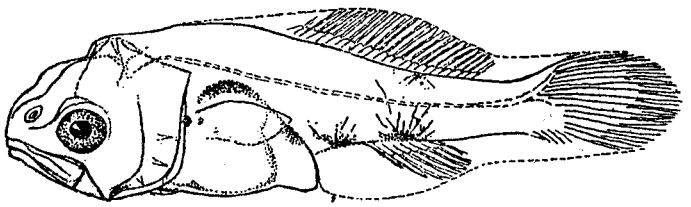

FIG. 14.—Young black drum. Actual length, 6 millimeters

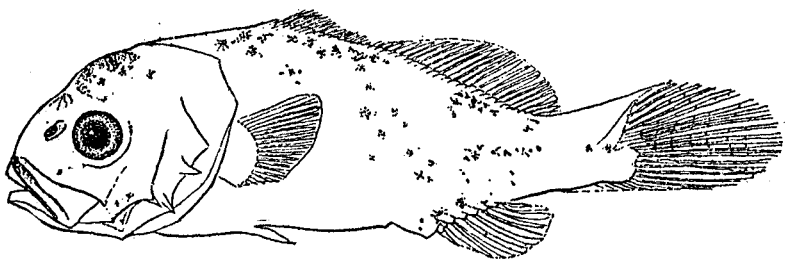

FIG. 15.—Young black drum. Actual length, 8 millimeters

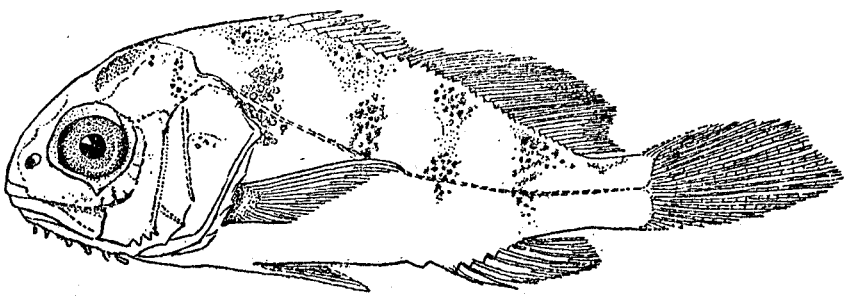

FIG. 16.—Young black drum. Actual length, 18 millimeters

posterior and above the vent, while the other lies approximately at the base of the undifferentiated anal fin. These groups of chromatophores are placed somewhat similarly to the ventral ones observed in the young larval redfish (*Sciænops ocellatus*), but the general absence of any pronounced dorsal markings in the larval drum separate the species distinctly. (See fig. 13.)

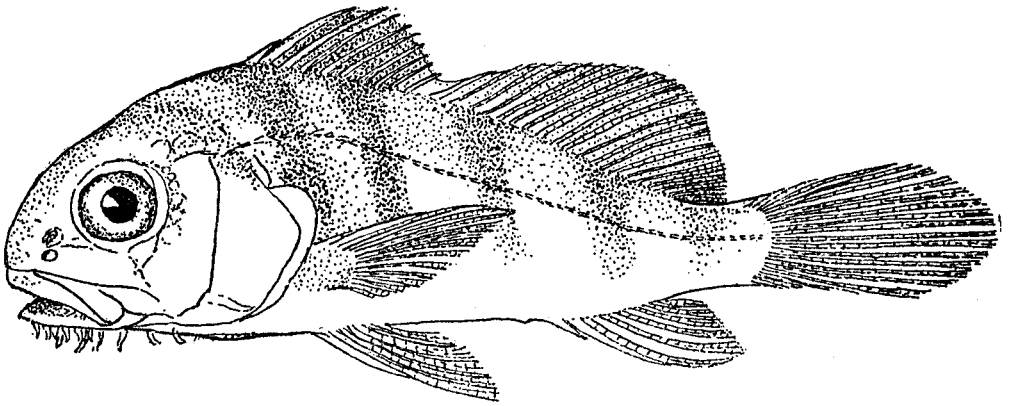

FIG. 17.—Young black drum. Actual length, 35 millimeters

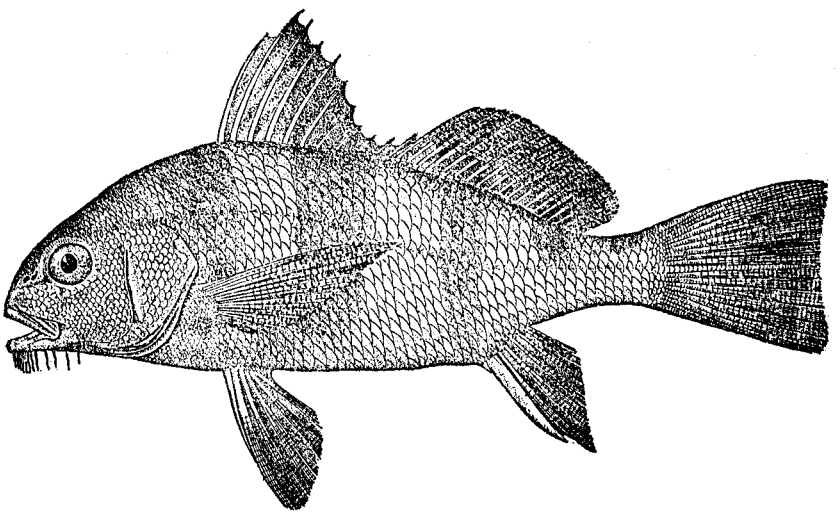

FIG. 18.—Young black drum. Actual length, 23.1 centimeters

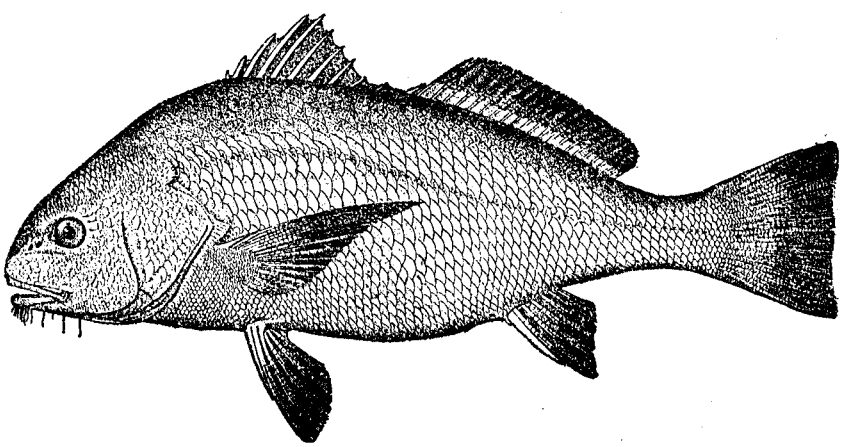

FIG. 19.—Adult black drum

At 6 millimeters the black drum has the vertical fins better developed, with 6 anal rays being discernible usually. This anal-ray count seems most constant and accordingly separates the species from other related ones. The dorsal and ventral fin folds still persist, although now separate from the tail, while the yolk sac is reduced further. The two ventral chromatophores are well marked and weak spines are present on the opercle or gill cover. (See fig. 14.)

A marked change occurs in the general pigment arrangement when the fish has reached a length of about 8 millimeters. Black chromatophores appear in profusion dorsally as well as along the sides and tend to arrange themselves into definite groups extending from the nape to the caudal peduncle. These groups are the forerunners of the six vertical black bars that soon appear, to remain until adult size is reached. On fish of about 8 millimeters, however, all six bars are rarely discernible in one specimen. All vertical fin rays are well formed and easily counted—dorsal, X–I, 21–23; anal, II 6. The ventral chromatophores present in the smaller stages tend to disappear entirely. (See fig. 15.)

When a size of 15 millimeters is attained, the young drum has assumed the general adult shape. The six black bars are pronounced and extend vertically from the back to slightly below the lateral line. All fins, with the exception of the dorsal, are colorless. The dorsal is dotted heavily with black punctulations, particularly along the anterior spines, while the soft rays are marked less heavily. The color of the body above the lateral line is light brown, marked with black vertical bars, while below the lateral line a bright silvery sheen prevails. The series of mandibulary barbels are now evident. (See fig. 16.)

In drum above 25 millimeters the color pattern remains essentially the same, with the exception that the pectorals and anal assume a black cast and the fish tends to become darker with age. (See figs. 17 and 18.)

SPAWNING AND EARLY DISTRIBUTION OF YOUNG

Along the coast of Texas the black drum spawns principally from February to May in the Gulf of Mexico near the mouths of the passes leading into the bays and lagoons. A late or secondary spawning period may also occur from late July to November. Both spawning seasons are preceded by well-defined migrations of the adult fish to the spawning grounds of the Gulf. The newly hatched drum are brought into the bays by the tidal current and soon distribute themselves into more or less definite localities.

The presence of large numbers of ripening adult drum within many of the more shallow bays and lagoons has led to the opinion among many that the species spawns within these bays and lagoons. The drum, well recognized as preferring the shallow and muddy areas of Nueces and Oso Bays and parts of Laguna Madre, is found in the greatest abundance within these particular bodies of water, and the casual observer might easily be led to believe that the entire life of the fish was spent within such localities. It was found, however, during the course of the recent study, that the spawning habits of the black drum were complicated, and that the general supposition of a bay spawning habitat was not tenable in the light of the results obtained by the writer during 1926 and 1927.

The first collection of young drum was taken on May 13, 1926, along the shores of Corpus Christi Bay near the channel entrance leading into Oso Bay. (See Table 13.) The fish, ranging in length from 9 to 37 millimeters (0.4 to 1.5 inches), were secured after a storm from several small, temporary pools along the beach, which had been filled by the abnormal high water resulting from the heavy seas the day previous. A strong current was flowing into Oso Bay from Corpus Christi Bay, and it seemed unlikely that such small drum could have breasted the current and come from Oso Bay to be washed up on the beach later along the shore line of Corpus Christi Bay. It was far more reasonable to expect that the young had come from Corpus Christi Bay and had been thrown into the beach pools accidently while endeavoring to gain the channel leading into Oso Bay.

TABLE 13.—*Collections of larval and young black drum (Pogonias cromis) taken in Texas, 1926 and 1927*

Date	Number of fish	Length range, in millimeters	Locality
May 13, 1926	94	9–37	Corpus Christi Bay by Oso Bay.
May 14, 1926	4	20–29	Nueces Bay.
May 25, 1926	16	25–47	Corpus Christi Bay by Oso Bay.
Feb. 28, 1927	27	4– 6	Harbor Island Lighthouse.
Mar. 11, 1927	140	6– 7	Corpus Christi Pass-Laguna Madre.
Mar. 16, 1927	68	5– 8	Harbor Island, east side.
Mar. 23, 1927	75	6– 8	Corpus Christi Pass-Gulf.
Mar. 24, 1927	3	4– 5	Aransas Pass, in channel.
Mar. 30, 1927	56	5– 8	Corpus Christi Pass-Gulf.
Apr. 6, 1927	8	4– 6	Harbor Island Light.
Apr. 9, 1927	82	8–11	Corpus Christi Bay by Oso Bay.
Apr. 11, 1927	15	5– 9	Harbor Island Light.
Apr. 26, 1927	14	9–15	Nueces Bay.
May 5, 1927	95	13–38	Do.
May 26, 1927	28	28–47	Do.

To substantiate this idea was the fact that on the same day large collections of small drum were secured within Oso Bay proper, and instead of taking smaller fish than were taken in the pools by Corpus Christi Bay, as might be expected had the young been hatched in Oso Bay, much larger and, hence, older fish were caught. Table 14 gives the length distributions of these two collections. All other localities, with the exception of Nueces Bay, failed to yield any young drum until some weeks later, when a considerable size had been attained by all fish. (See Table 14.) It was believed that spawning had terminated by the first of May with the sample of young obtained on the 13th of the month, consisting of a group of fish spawned toward the close of the spawning period.

TABLE 14.—*Collections of black drum illustrating distribution of fish under 25 centimeters (9.8 inches). Fish spawned in 1927 omitted. (See Table 13.) Collections of less than 10 black drum have been omitted also*

Length, centimeters	1926													1927		
	May 13, Corpus Christi Bay	May 13, Oso Bay	June 4, Oso Bay	June 11, Oso Bay	June 21, Oso Bay	June 24, Gulf	July 3, Corpus Christi Bay	July 26, Oso Bay	Aug. 3, Oso Bay	Aug. 16, Oso Bay	Aug. 26, Corpus Christi Bay	Aug. 30, Corpus Christi Bay	Dec. 9, Oso Bay	Jan. 19, Copano Bay	Feb. 1, Oso Bay	Mar. 9, Oso Bay
1	14															
2	74															
3	9															
4		6														
5		20			1											
6		32														
7		33	1	1	1		3									
8		6	2	2	2		11		5							
9			6	22	7		17	3	16	1						
10			17	28	10		20	10	24	6						
11			16	12	3	2	32	21	13	7			2			
12			18	2		13	23	9	1	9	3		10		3	2
13			19	1	1	12	17	6	1	10	32		5		9	2
14			3	2		5	15		2	5	44		3			3
15			1	1	3	1	6		1	5	18	1	13			5
16							2		1	1	1	2	12			2
17							1		2	2		4	7			1
18									3			5	7			
19									1			3	3			
20												4	3			
21									1			1	4	1		
22												1	2	4		
23												1		10		
24														7		
25														4		

Considerable surprise was occasioned on July 26, 1926, when a number of nearly ripe drum, ranging from 31 to 46 centimeters (12.2 to 18.1 inches) in length, were captured in and about the channel leading from Oso Bay into Corpus Christi Bay. Collections of a few ripening fish likewise were made within Oso Bay. All other fished areas, in spite of extensive collections of drum, failed to reveal any ripening fish. It appeared that all maturing fish were centered about Oso Bay, although many unripe adults were taken along with the nearly ripe fish.

Heavy commercial catches of drum were being made during July and August in the open fishing area in Laguna Madre, and it was learned by inspection of the catch that many fish were in a ripening state and apparently were coming into the fishing area from Baffin Bay and other southern points in Laguna Madre that were closed to commercial fishermen. As indicated by Figure 44, the peak of the drum catch, taken almost entirely from a central portion of Laguna Madre and landed at Corpus Christi in 1926, occurred during the months of July and August. While one of the causes for the much larger catch during these months was the general exodus of all fish from the waters of the lower Laguna Madre because of the high salinity that is reached during the late summer months, a spawning migration of many of the adult drum served to increase the catch by bringing the fish from the closed waters, where evidently they had matured, into the restricted open fishing area.

On October 14, 1926, after several months of futile effort in seeking newly hatched drum, together with the capture of small collections of ripening fish at infrequent intervals in and about Oso Bay, a large, nearly ripe female drum, 90 centimeters (35.5 inches) long, was found stranded in Corpus Christi Pass. This was the first indication that spawning drum were to be found near the Gulf of Mexico, and while it could not be determined in which direction the fish was traveling before it accidentally ran up on a shallow sand bar, it was evident that spawning might be looked for in the Gulf as well as within the bays.

In February, 1927, the spring spawning of the drum was indicated to be approaching. About the last week in January fishermen familiar with the movements of the fish in such bays as Nueces and Oso, as well as Laguna Madre, were in the habit of placing large-meshed gill nets near the mouths of the narrow channels leading into such bays to secure the larger migrating adults that generally were supposed to be coming into the bays from some unknown place for spawning. During the winter of 1927, these nets, discussed more fully in another section of this paper, were placed at the mouth of Nueces Bay in Corpus Christi Bay, along the south shore line of Corpus Christi Bay near the entrance to Oso Bay, and in the open fishing area in Laguna Madre. Examination of the larger stand of nets at the mouth of Nueces Bay in early March indicated conclusively that a marked spawning migration of adult drum was occurring. All fish were in a nearly ripe condition, and most of them ranged over 80 centimeters (31.5 inches) in length.

Meanwhile, ripening fish were being captured by commercial gill nets in Laguna Madre and by experimental gear operated by the writer in the closed fishing area of Oso Bay. During the preceding months fishing within Oso Bay had been very difficult and inconclusive on account of the heavy mud bottom and the lack of a landing place for the large seines. Often, nevertheless, large drum (above 60 centimeters, or 23.6 inches) were caught (more generally, only seen) in the shallow recesses of Oso Bay, and it was generally known that a considerable number of large fish were to be found within the bay.

Experimental gill nets were placed in Oso Bay near the channel exit into Corpus Christi Bay during the early part of March with the expectation of determining the direction of this spawning migration of drum. Good catches of large ripening fish soon were obtained, and by the position of the gilled fish in the nets it appeared that the schooling fish were endeavoring to gain their way over the shallow sand bars partly blocking the exit into Corpus Christi Bay. On one occasion large drum were seen deliberately making their way over the shallow bars from Oso into Corpus Christi Bay.

Upon reaching the deeper waters of Corpus Christi Bay, the migrating drum were difficult to catch or to observe. However, fishermen reported that while their boats were lying anchored in the various channels leading to the passes, particularly Aransas Pass, distinct drumming sounds could be heard during the night, presumably caused by the drumfishes on their way to the Gulf. The writer, while not doubting these reports, did not actually hear any such noises, although it is well known that the drum make a loud drumming vibration which is probably employed extensively during the breeding season for the purpose of sexual attraction.

On February 28, 1927, the first collection of larval black drum was secured in Harbor Island Light Bayou in nearly the same spot where the first larval redfish and croakers were taken some months previous. These young drum ranged from 4 to 6 millimeters in length and were not identified definitely as black drum (*Pogonias cromis*) until the second week in March, after the gill nets had indicated the movement of the spawning adults from the bays to the Gulf of Mexico. The fish were helpless and obviously at the mercy of the tidal current, which had swept them into the quiet bayou from the channel leading from Aransas Pass and the Gulf. (See Table 13.)

On March 11 Corpus Christi Pass was visited and large numbers of larval and post-larval drum were taken in the main channel of the pass itself, as well as along the shore lines of the various islands in Laguna Madre adjacent to the pass and reached by the incoming tides. In all cases was it evident that the larval drum were being brought in from the Gulf by the tidal currents. As shown in Table 13, continuous collections of larval and very young drum were made about both Corpus Christi and Aransas Passes during March and April.

It was observed that the young drum left the vicinity of the passes as soon as able, and it was believed, on the basis of the collection of small drum near Oso Bay on May 13, 1926, that the fish were making for definite localities, such as Oso and Nueces Bays. On April 9 a considerable number of young drum had reached the channel leading from Corpus Christi Bay into Oso Bay. These fish ranged in length from 8 to 11 millimeters (under 0.5 inch) and were the approximate size of the smallest of the young drum caught in the beach pools in the same locality on May 13, 1926. On the day these fish were taken, the current was running out from Oso Bay, with the result that the young were forced to remain at the mouth of the channel for some time.

Nueces Bay, similar in most respects to Oso Bay but on a nearly direct line with a recently completed ship channel that connects Aransas Pass with the city of Corpus Christi, was fished at various points during April and May. Many young drum from 9 to 15 millimeters long were taken in late April, while large numbers of young, growing rapidly in size, were secured throughout the month of May.

By the time field operations were discontinued, at the end of May, 1927, the young larval drum had ceased to come into the passes from the Gulf, and those that had gained entrance were concentrated largely within Nueces and Oso Bays and probably Laguna Madre. The young drum preferred the same type of environment as was chosen generally by the older fish.

Several complications in the way of a thorough understanding of the spawning habits of the black drum leave an interesting field for future research along this line. No explanation is offered for the lack of young drum that should have come from the ripening fish taken from July to October, 1926. Whether they escaped observation, owing to their small numbers, or whether there were no fish to be taken are questions unsolved at the present time. The writer expresses the opinion, however, on the basis of the relatively small size of the maturing fish taken in July to September, 1926 (Table 16), that spawning at this time was negligible. The main spawning season of the black drum in the vicinity of Corpus Christi Bay undoubtedly is from late February to May, and the spawning grounds probably are situated at the mouths of the passes in the Gulf of Mexico.

Little information on the spawning habits of the black drum in other sections of its range has been recorded. Welsh and Breder (1923, p. 197) stated that the eggs and larvæ of the drum were unrecorded and that little was known of the life history. Hildebrand and Schroeder (1928, p. 288) recorded a fully ripe male drum, 37 inches long, taken on May 22, 1922, at Cape Charles, Va., in 48 feet of water, but stated that no young drum under 8 centimeters (3 inches) have ever been secured.

GROWTH AND AGE

Study of the age and growth of the black drum brought out the fact that by the method of age determination employed with success in the case of the redfish, croaker, and spot (the Petersen method, whereby the individuals of a large collection are grouped according to their length, and each prominent mode or hump in the

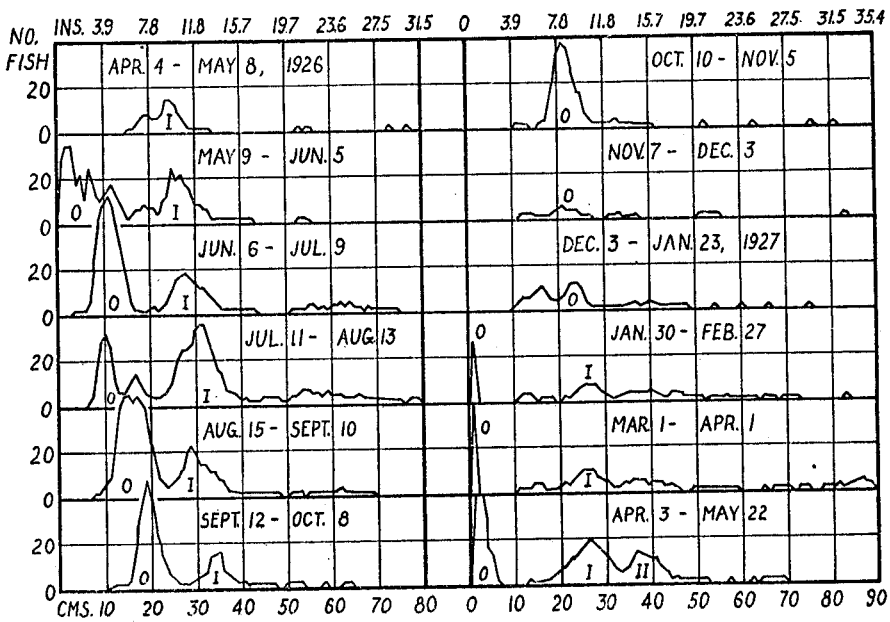

FIG. 20.—Length-frequency distribution of black drum in Texas, 1926–27. Actual frequencies have been smoothed by a moving average of threes. Roman numerals indicate year classes

plotted frequency distribution is assumed to represent an age class), only the first two year classes of drum could be discerned throughout the year with any degree of reliability. After the third year the various year classes overlap to such an extent as to render the Petersen method worthless.

A series of smoothed length-frequency distributions, taken from Table 15, is presented in approximate monthly summaries by Figure 20. Collections from April 4 to May 8, 1926 (following fig. 20), gave a group of drum (I-year class) assumed to be entering their second year with a modal length at about 25 centimeters (9.8 inches). This I-year class grew rapidly during the succeeding months, and by October (September 12 to October 8) had reached a modal length of about 35 centimeters (13.7 inches). While this class held its original identity well during the spring and summer of 1926, it nearly disappeared from the catches during the

winter of 1926–27. In April and May, 1927, the class reappeared in good numbers with a modal length at about 37 centimeters (14.5 inches).

TABLE 15.—*Length-frequency distribution of black drum taken in Texas waters from April, 1926, to May, 1927*

Total length, centimeters	1926								1927				
	Apr. 4–May 2	May 9–30	June 6–July 4	July 11–Aug. 8	Aug. 15–Sept. 5	Sept. 12–Oct. 3	Oct. 10–31	Nov. 7–28	Dec. 5–Jan. 23	Jan. 30–Feb. 27	Mar. 6–27	Apr. 3–24	May 1–22
1		14								27	342	113	1
2		74											94
3		19											26
4		10											20
5		23	1										4
6		32											
7		34	5										
8		8	15	8									
9		6	47	26	1								
10		17	62	45	6								
11		16	57	24	8				2				
12		18	49	10	12		1		10	3	2		
13		19	35	4	46	1		2	5	9	2		
14		3	29	8	60			2	3		3	1	
15		1	12	5	36	2		1	13		7	1	
16		3	2	13	45	8			12		2		
17	2	5	2	14	46	20	5		7	1	4	1	1
18	4	10	1	12	46	53	5	1	7			2	1
19	10	4		4	33	48	17	1	3		1	1	2
20	11	12	3	5	34	47	37	8	3		5	1	6
21	4	4	3	2	12	21	41	2	7		2	5	5
22	2	5	2	7	9	14	35	4	10	1	7	6	4
23	12	3	1	5	6	13	29	6	15	3	4	4	9
24	10	21	9	6	6	6	12	3	12	6	11	4	8
25	19	15	13	13	4	2	6	2	9	5	8	11	10
26	14	26	14	20	11	4	1	1	4	8	14	11	8
27	5	16	18	26	10	1	1			9	9	11	10
28	2	21	18	29	21				2	5	6	8	6
29	4	15	16	22	28	3			1	6	6	8	8
30	1	10	15	31	14	5	1			3	5	8	6
31		3	13	45	19	3	2			2	5	3	6
32	1	10	11	32	13	10	4	1	1	1		3	4
33		2	10	28	11	8	3	2	1		2	4	1
34		2	5	17	9	23	3	2		6	4	4	1
35			3	20	9	12	1		1	4	5	6	6
36		1	4	8	5	9	2	1	5	3	3	5	6
37		1	1	8	4	5	2		2	6	7	12	6
38		1	2	4	1	4	1		1	4	5	7	3
39		1	1	6	3	3	1			6	2	5	7
40				6		3			4	2	2	6	8
41		1		1	1	3			4	6	7	3	3
42			1	1	1	1				3	2	2	10
43				1		1				1	2	1	2
44				2	2	1			1	3	5	1	3
45				2		1				3	2	1	2
46				4	1	1			1	7		1	2
47				3	1				1	1			1
48				3								1	
49				1						1		1	
50			1							1	2	1	
51			1	2		1		1			1	1	
52			1	6	2	1	1						
53	1	1	1	5				1			1		
54		1	3	5				1	1	1	2		
55	1		3	7									
56			3	7	1					3	1		
57			3	2								1	1
58				6	2	1				2	1		
59			3	4	1								
60				4	1				1				

TABLE 15.—*Length-frequency distribution of black drum taken in Texas waters from April, 1926, to May, 1927*—Continued

Total length, centimeters	1926								1927				
	Apr. 4-May 2	May 9-30	June 6-July 4	July 11-Aug. 8	Aug. 15-Sept. 5	Sept. 12-Oct. 3	Oct. 10-31	Nov. 7-28	Dec. 5-Jan. 23	Jan. 30-Feb. 27	Mar. 6-27	Apr. 3-24	May 1-22
61			7	5	1					1			
62			2	3	3	1				1		1	1
63			2	3	1	1	1						
64			3	3									1
65			6	4	1						1		1
66				2					1	1			
67			3	6	1								
68				2	1						1	1	1
69			2	2							1	1	
70			1	3									
71				2						1			
72													
73	1		1	1							1		
74				1									
75									1				
76							1						
77	1												
78				2									
79											1		
80											2		
81							1				1		
82											2		
83								1		1	2		
84											2		
85											6		
86											5		
87											5		
88											2		
89											1		
90											5		
91													
92											4		
93											1		
94											1		
95													
96													
97													
98													
99											1		
100													
105											1		
Total	105	488	526	619	589	341	214	43	151	157	547	268	305

The second summary of drum collections, from May 9 to June 5, 1926, brought the O or youngest year class into consideration, with the fish ranging in length from 1 to 15 centimeters (0.4 to 5.9 inches). Several sharp modes exist within the length distribution of this O class, owing possibly to the various differences in time of hatching. The collections from June 6 to July 9, 1926, however, smoothed out this irregular distribution.

The O year class, positively known to be in its first year, grew rapidly during the summer of 1926, and by November (October 10 to November 5) had attained a modal length of 21 centimeters (8.2 inches), compared with the modal length at 11 centimeters (4.3 inches) shown by the class during June. Collections became much smaller during the winter, but spring catches (April 3 to May 22) showed that the class (I) had attained a modal length of about 26 centimeters (10.2 inches) when a

little more than 1 year old. This modal size in April, 1927, corresponds well with the modal length observed for drum of the same age captured in April, 1926.

In late February, 1927, a newly spawned year class appeared (O year class), which by the end of May, 1927, had attained a modal length of 2 centimeters with a range from 1 to 5 centimeters. It will be observed that during May, 1926, a length range from 1 to 15 centimeters was recorded, while a year later this range was reduced to 1 to 5 centimeters. From the fact that the larger fish included in the O class during May, 1926, possessed no winter scale checks, it must be inferred that spawning occurred earlier in 1926 than in 1927 (the scales of the drum were found to show annual winter growth checks, not including, of course, the first winter during which the fish are hatched). This supposition presumes, however, that the larger fish of the class (10 to 15 centimeters long) actually belonged to the O year class on account of its lack of a winter check, and that any group of fish hatched in the late summer or fall of 1925 would show a growth check during the winter of 1926. The fact that after the period from May 9 to June 5, 1926, all fish in the O year class fell into a more or less regular group would seem in itself to justify the inclusion of these larger fish in the youngest year class.

Some confusion was caused by the capture of a considerable number of drum from December 5, 1926, to January 28, 1927, showing a modal length at about 15 centimeters (5.9 inches), while the modal length of the O year class reached 21 centimeters (8.2 inches) during the preceding October. This small group of drum was reflected in the catches during the next few months, and nearly all fish were taken from Oso Bay. (See table 14.) While it is possible that this undermodal group of the O year class of drum was the result of the suggested spawning in the late summer and fall of 1926, the belief of the writer is that the group merely represented a late season's hatch in the spring of 1926, as indicated by the collection of many young fish around Oso Bay on May 13, 1926. Such differences within a single year class can easily result from the arrival of various schools of adult fish on the spawning grounds at different times. With the existing doubt as to the results obtained from the effort of some fish to spawn in the late summer of 1926, however, the writer suggests the possibility that some young may come from this spawning and be represented by these subnormal modes at about 16 centimeters instead of 23 to 24 centimeters, as appeared typical of the O year class in December, 1926, and January, 1927. Future work could easily clear up the present uncertainty as to the extent and influence of any late summer spawning, which, with the information at hand, appears to be negligible.

It seems reasonable to state, on the basis of an examination of the drum length-frequency distribution composed of about 4,350 fish taken with unselective gear, that a modal length of about 25 centimeters (9.8 inches) is reached by the end of the first year and about 37 centimeters (14.5 inches) is attained by the end of the second year.

The age of the black drum, up to a length of 60 centimeters (23.3 inches), usually may be determined by a count of the annually formed winter-growth checks on the scales. The extremely large size and the heavy calcification that the drum scale undergoes render the determination of age difficult and unreliable after the fish has reached the fourth or fifth year of life and generally has attained a length of 50 to 60 centimeters (19.7 to 23.3 inches). In general, the winter-growth checks of the drum

scales (annuli) have the nature of bilateral breaks or interruptions in the circuli pattern of the scale, most evident at the lateral terminals of the circuli. Many of the younger fish, however, in addition to the lateral terminal checks, show closer approximations of circuli formed during the retarded winter growth. In most respects the scales of the black drum closely resemble those of the redfish, both in size and structure, as well as in the nature of the winter-growth check.

Figure 21 illustrates the relation between age and length, secured by a study of the scales of several hundred drum. No fish over 60 centimeters (23.3 inches) in length has been included in this figure because of the present unreliability of age

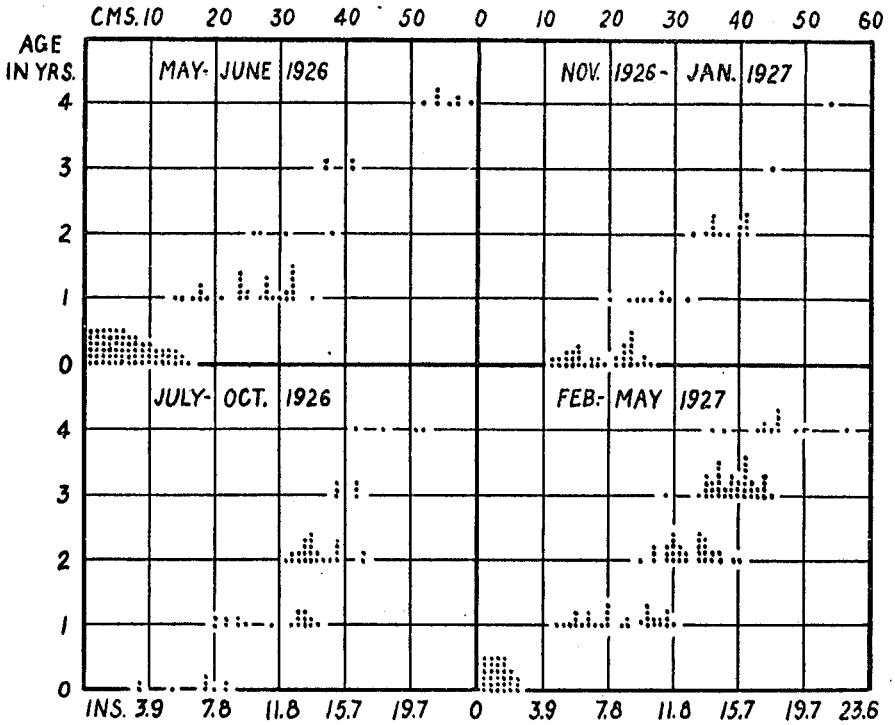

FIG. 21.—Age of black drum according to length, as indicated by winter growth checks on scales

determination as applied to the larger fish. The first four years of age are represented fairly well in the length distribution ranging from 1 to 60 centimeters, although insufficient numbers of fish prevent the discernment of any definite modal lengths at any particular age. The scale collections were small, unfortunately, but the results obtained seem to justify more intensive work in the future on the analysis of age of the drum by means of the scale method.

An incomplete examination of many scales from fish measuring more than 60 centimeters (23.3 inches) indicated that 5 years of age may be attained when the fish reach a length of about 60 centimeters, and that they are 7 to 9 years of age by the time they reach a length of 75 to 85 centimeters (30 to 34 inches).

SIZE AND AGE AT MATURITY

Sexually matured black drum with a total length range from 27 to 105 centimeters (10.5 to 41.6 inches) were taken. Only fish that possessed developing sexual products (granular roe in the females) were sexed, thus obviating personal errors in judging the state of development.

It will be observed, by inspection of Table 16, that the drum found in a ripening or spawning condition during July to October, 1926, were of smaller minimum and

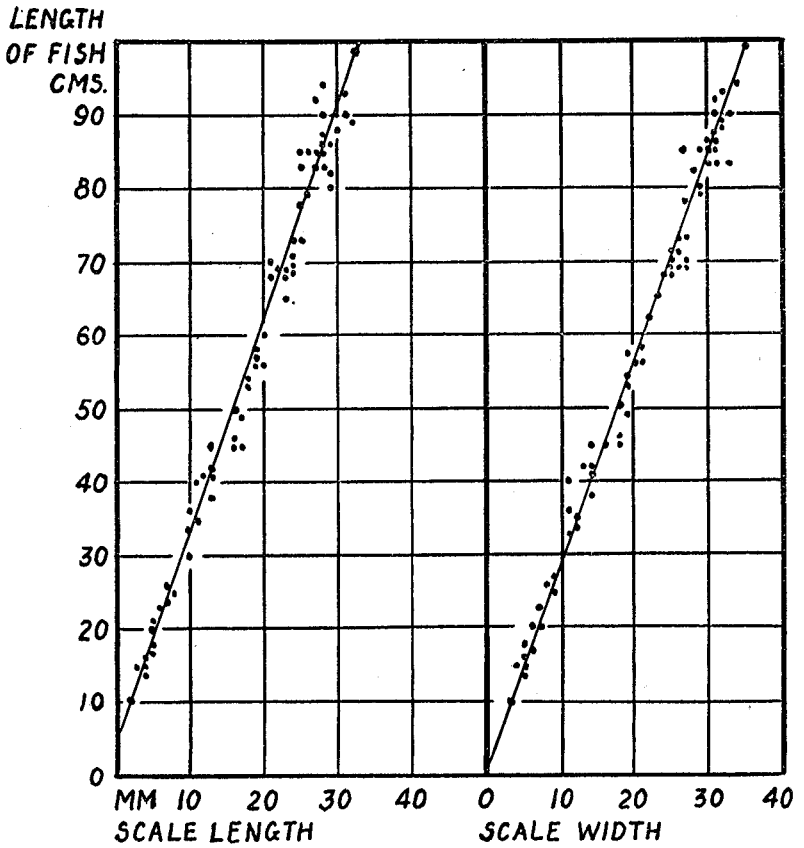

FIG. 22.—Correlation between scale length and width and total body length in the black drum. The average values of the scale lengths and widths corresponding to a succession of body lengths lie nearly upon a straight line, indicating that on the average the growth increment of the scales is a constant proportion of the growth increment of the fish

maximum length than those taken during the main spawning period in the winter and spring of 1927. This difference extends particularly to the older and larger fish, only one drum above 58 centimeters (22.8 inches) being taken during 1926, compared with many secured in 1927 by the writer and by commercial fishermen. This condition is unaccounted for at present. One possibility, however, is that many of the youngest maturing fish (I class) reach sexual maturity either several months prior to or after the older classes spawn.

While not all the drum captured from the adult age groups during 1927 were in a ripening condition (as judged by the writer), a much larger percentage was recorded than during July to October, 1926. From July 11 to October 10, 1926, approximately 490 adult fish were taken (all drum above 29 centimeters considered adult), but only 67 fish, or 13 per cent, were in a ripening condition as indicated by granular roe and running milt. From March 6 to May 1, 1927, 151 adults were secured (all fish above 34 centimeters considered adult), 121 of which, or 80 per cent, were in a ripening state. While these figures are subject to slight error because of the difficulty experienced in determining the state of maturity, the percentages indicate, in a rough way, the seasonal abundance of spawning fish.

TABLE 16.—*Size at maturity of the black drum*

[Only fish with ripening roe or milt were sexed. The 1926 period was from July to October; the 1927 period from February to May]

Length, centimeters	Summer-fall, 1926		Spring, 1927		Length, centimeters	Summer-fall, 1926		Spring, 1927	
	Males	Females	Males	Females		Males	Females	Males	Females
25-29	2	0	0	0	65-69	0	0	1	5
30-34	14	22	0	1	80-84	0	0	3	8
35-39	1	16	7	29	85-89	0	0	8	12
40-44	0	6	8	9	90-94	0	0	5	6
45-49	1	3	2	3	95-99	0	1	1	0
50-54	0	0	3	4					
55-59	0	1	1	2	Total	18	49	39	82
60-64	0	0	0	3					

On the basis of the age estimations secured from scale and length frequency studies it seems evident that the drum reaches sexual maturity by the end of the second year, with annual spawning continuing until death. The larger-sized black drum are very prolific. An approximate count was made of the eggs from a migrating female 110 centimeters long (44 inches) taken at the mouth of Nueces Bay by a commercial gill net on March 6, 1927. Nearly 6,000,000 were counted. (See below.) The average diameter of the eggs was 0.6 millimeter, most of them being equally developed.

Total weight, in grams, of eggs from 110-centimeter black drum	996
Total weight, in milligrams, of 60 unselected eggs	10
Total calculated number of eggs in 1 gram	6, 000
Total calculated number of eggs in 996 grams	5, 976, 000

Figure 23 presents the relation of weight to length in 77 black drum. A fish about 30 centimeters long (11.8 inches) usually is slightly over 1 year of age and weighs about 1 pound. Weight increases rapidly after 70 centimeters in length (27.5 inches) has been reached. A drum measuring 90 centimeters (35.4 inches) weighs close to 22 pounds, while a fish measuring 105 centimeters (41 inches) weighs 37½ pounds.

SEASONAL DISTRIBUTION AND MOVEMENTS

The young drum, usually in a larval or post-larval condition when brought in through the passes from the Gulf spawning areas, make their way soon after entering to a few extremely shallow and muddy bodies of water typified, along the central section of the Texas coast, by Laguna Madre and Oso and Nueces Bays.

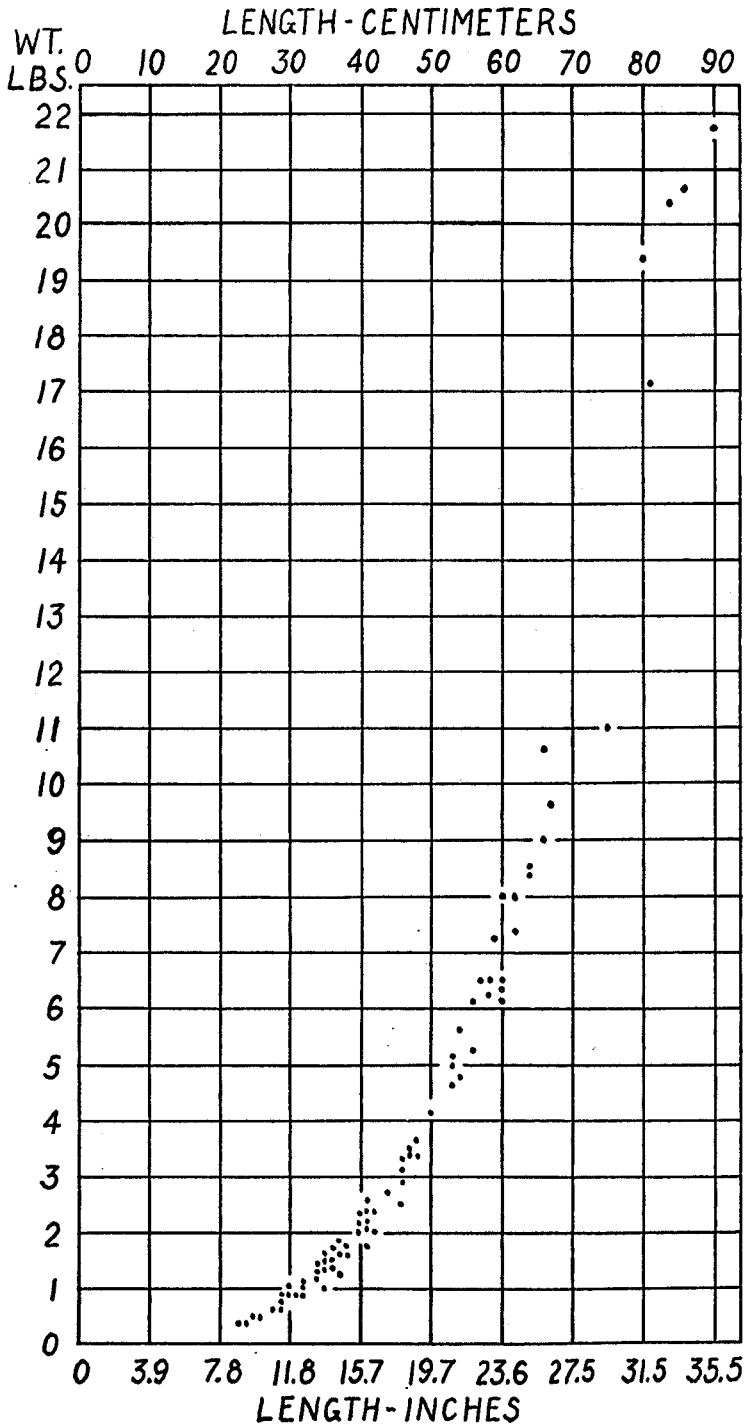

FIG. 23.—Relation of weight to length in 77 black drum

Present knowledge of the exact causes for the voluntary response of young fishes to a certain type of environment is too inadequate to permit a conjecture as to the possible factors that cause the determined effort of the young drum to reach definite isolated bays and lagoons wherein very few species of marine fish dwell. The fact remains, however, that these young drum are attracted to a particular type of aquatic environment soon after coming in from the Gulf of Mexico, to such a degree as to render the absence of the small fish in other types of coastal waters most noticeable.

The young drum generally remain within their favorite bays until they attain a length of at least 10 centimeters (4 inches), when many of them gradually move out into the deeper bays and, to a slight extent, into the Gulf of Mexico. The young drum (fish under 10 centimeters) are more prone than redfish to stay away from the open shores of the Gulf. Most of the drum population, however, appears to reside until maturity (spawning time) within the shallow waters chiefly of Laguna Madre and Oso and Nueces Bays, but relatively few fish roaming into the deeper waters.

The spawning migration of the adult drum from the shallow intercoastal waters to the Gulf of Mexico is most pronounced in the vicinity of Oso and Nueces Bays and Laguna Madre, where, from late January to May, special gill nets are employed to intercept and capture the schools of migrating fish. From personal observations it would seem that the greater part of this movement from the bays takes place at night. The distance to be traveled from such waters as Oso or Nueces Bay to the nearest pass to the Gulf of Mexico may lie, roughly, between 20 and 30 miles. Such a distance might easily be covered by the drum within a few days, which perhaps explains the nearly ripe condition of most drums before they leave the bays.

After spawning outside the passes the spent adults that survive appear to come closer inshore to seek their way back into the bays. Considerable numbers of these spent drum were taken in the late spring of 1927 along the Gulf beaches near the passes as well as immediately within some of the passes. No collections of spent adults were obtained at any time within the confines of either Oso or Nueces Bay, which fact in itself would indicate that spawning does not take place in these bays.

The drums are extremely persistent in remaining within the shallow intercoastal waters, both during the excessive heat and salinity of the water in summer and the sudden-killing cold waves in winter. With the shallow bays preferred by the drum nearly completely isolated from the deeper ones, escape in times of danger is not accomplished readily. Navigation within these shallow waters is difficult, and many of the migrating adults have their bellies badly lacerated from the continual friction in passing over oyster reefs, particularly during the excitement of breeding. It has been said that in past years farmers were accustomed to chase the large 10 to 40 pound drum over the shallow mud flats with pitchforks, such chase, of course, furnishing a considerable amount of thrill as well as fish.

During the summer the waters in the vicinity of Baffin Bay (Laguna Madre) often become extremely saline, with the result that many fish, particularly black drum, die. Cold waves in winter, which chill the shallow water rapidly, are said to work destruction with the species because of the inability of the fish to reach more favorable environments.

The writer feels that future scientific research into the life history of the black drum might take up, with profit, a more intensive study of the various seasonal movements or migrations of the species than was possible during this investigation.

FOOD HABITS

The feeding habits of the black drum bear out the belief that the fish is generally a strictly bottom feeder. Possessing heavily paved pharyngeal teeth, the species has long been known to frequent oyster beds or reefs, the supposition being that the young oysters are crushed and eaten in great quantities. Observations on the stomach contents of many Texas drum, particularly those of a large size, failed to show that oysters of any size make up any considerable percentage of the regular diet.

The main food of the drum after it has attained a length of about 20 centimeters (7.8 inches) is a small mollusk or "clam"—*Mulinia transversa corbuloides*—which abounds in the more muddy and shallow bays, such as Nueces and Oso, in the vicinity of Corpus Christi. Bottoms containing this mollusk invariably are covered with heavy mud, and along such bottoms the drum delights to feed. Certain localities in the more or less grassy-bottomed coves are well known as good "drum hauls" because the drum usually may be found feeding in these localities, which in all cases possess a clear but muddy bottom in which Mulinia may be found in varying abundance. The mollusks lie deeply buried in the mud but are sucked up by the drum, which retains them and proceeds to crush the shells by means of its strong pharyngeal teeth. As much as 2 pounds of broken shell from this small mollusk have been taken from a large fish. Whether or not the fish swallows dead shells can not be stated definitely, but in great numbers of fish examined, the intestines literally were filled with hundreds of fragments of the thin shell of Mulinia. The drum often nearly stand on their heads in feeding, with their tails out of water, so shallow is the water and so intent are the fish on sucking up the mud.

Various other mollusks, such as mussels (Mytilus) and oysters (Ostrea), are eaten in some abundance. Small crabs rank second in quantity to Mulinia, and shrimp also are consumed at times. The smaller-sized drum (under 20 centimeters, or 7.8 inches), with less powerful crushing teeth, tends to prey upon the softer food organisms, such as small fishes, annelid worms, and the smaller crustaceans. Surf fishing along the Gulf beaches, with dead mullet or shrimp for bait, yields catches of drum.

TABLE 17.—*Food preference of 117 black drum, presented in percentages of total number of fish in each length group that feed exclusively on the various organisms, the food named in the parentheses occurring most commonly*

[Forty per cent of the mixed food of the 21 to 50 centimeter group was composed of crustaceans and 60 per cent consisted of mollusks. March to May, 1927]

Length, centimeters	Percentage of first that had eaten—					
	Number of fish	Crustaceans (shrimp, crabs)	Mollusks (Mulinia, Mytilus)	Fish	Annelids (polychæts)	Mixed
8–20	25	8	20	36	32	4
21–50	61	28	33	0	2	37
80–99	31	16	74	0	10	0

Table 17 shows the changing food habits of the drum according to its size. The smaller drum feed largely on fish and annelids, represented by 36 and 32 per cent; the medium-sized drum cease feeding on the softer foods and consume larger amounts of mollusks (33 per cent) and crabs and shrimp (28 per cent), a 37 per cent mixed-food content consisting of mollusks and crabs; and the older drum confine their food largely to the mollusks (74 per cent) and crabs (16 per cent). In general, the food habits of the black drum may be correlated with the environment. In the more shallow, muddy lagoons and bays the greatest numbers of Mulinia are found, and it is in such waters that drum live in the greatest abundance. In an environment where extremely turbid water prevails throughout the year; where the water temperature ranges from 80 to 90° F. in summer and as low as 40° F. in winter; where during the summer salinity often is twice as great as that of ordinary sea water and during the rainy season a brackish condition exists; and where the average depth rarely is more than 4 feet, the black drum attains its greatest abundance along the coast of Texas.

COMMERCIAL CONSIDERATIONS

Texas produces about 70 per cent of the total annual black-drum catch of the United States. The species attains its greatest abundance in the Gulf States, although it occurs in commercial quantities as far north as New York. The trade always has had some aversion for the drum because the larger adults are likely to become infested with parasitic worms, which virtually destroy the marketability of the fish unless the flesh is cut into fillets or steaks. In most sections of Texas the drum is sold under the name of rockfish. The smaller fish (one-half to 3 pounds) are preferred by many people to either the redfish or the spotted sea trout.

The following record of commercial catch, taken from the publications of the United States Bureau of Fisheries, shows the extent of the fishery:

TABLE 18.—*Catch of black drum (Pogonias cromis) in the United States*

State	Weight, in pounds	Value	Value per pound	Year	State	Weight, in pounds	Value	Value per pound	Year
Texas	1,028,451	$36,807	$0.036	1923	South Carolina	13,150	$393	$0.030	1923
Virginia	228,180	3,529	.015	1925	Alabama	9,250	279	.030	1923
Florida	141,994	4,397	.031	1923	Delaware	4,240	73	.017	1926
Louisiana	59,988	2,000	.033	1923	North Carolina	1,794	194	.010	1923
Mississippi	38,989	1,263	.033	1923	New York	200	2	.010	1926
New Jersey	31,100	909	.029	1926					
Maryland	25,150	472	.019	1925	Total	1,582,484	50,318		

Approximately 432,000 pounds of drum were landed from January, 1926, to May, 1927, at Corpus Christi, Tex. (from records of the three leading fish dealers), as compared with 134,000 pounds of redfish and 138,000 pounds of spotted trout (fig. 44).

While the fishermen generally receive but from 3 to 5 cents a pound for drum that retails for 25 cents a pound, spotted trout bring nearly 10 to 12 cents a pound to the fishermen and 35 cents to the retailer. On the basis of the retail value, the drum exceeds in value the redfish and trout combined.

Owing to its relative abundance in Texas coastal waters and its low market value, the drum has not been protected by any special legislative measures. The fact that sport fishermen and commercial hook-and-line fishermen seldom catch this species has caused but little interest to be shown in a rational system of conservation of the fishery. The legal closure in recent years of many of the smaller bays, such as Oso and Nueces, in the vicinity of Corpus Christi has afforded the drum considerable protection because the species spends a greater part of its life in the more shallow, muddy bays and lagoons than elsewhere. At present, however, this attempt at conservation is partly nullified by certain fishing practices that appear to be unduly destructive in proportion to the actual value of the catch.

From late January to May a fishery is operated in Corpus Christi Bay and northern Laguna Madre for the nearly ripe drum that leave their favorite feeding grounds (such as Oso and Nueces Bay and southern Laguna Madre) for the spawning grounds in the Gulf of Mexico. This fishery is conducted largely by means of anchored gill nets with a large mesh (4 to 5 inches square) customarily set as near the entrances into Nueces and Oso Bays (in Corpus Christi Bay) and the deeper channels in northern Laguna Madre as is legally possible. The larger adult drum are secured in abundance, the flesh selling at wholesale at 10 cents a pound and the female roes (weighing about 2 pounds apiece) being supplied to the restaurant trade at 25 cents a pound. The fact that these gill nets secure the drum when they are preparing to spawn and are seeking their way out of restricted areas, together with the fact that most of the drum population congregate in a few small bays and lagoons and are forced to leave them through narrow exits in order to spawn, brings up a serious question as to the desirability in permitting this type of fishery to exist.

On the basis of the relatively slight food value of these large adult drum and the fact that such fish must be of considerable value in replenishing the drum stock, it would seem that their ultimate worth as spawners far surpasses their value as food. The writer, in seeking a way to increase the natural supply of black drum in Texas waters, recommends that suitable protection be afforded to the larger sizes of drum at all times of the year.

The establishment of a maximum legal size limit which operates favorably in the case of the redfish, would appear to be a logical way of protecting these larger drum against possible depletion. Usually all drum above 20 inches in total length (50 centimeters) are released from the drag seines because of the unwillingness of the fish dealers to handle the larger, less profitable sizes. The adoption of a maximum size limit at 20 inches (50 centimeters) would work little hardship to the fishing industry (in fact, it would be a boon to many dealers now forced to accept the nigh worthless large drum) and unquestionably would serve to increase the proportion of spawning adults. Of course, an end would be put to the wasteful gill-net fisheries at the mouths of Oso and Nueces Bays.

While no minimum legal size limit has been set for the drum, as has been done for the redfish and spotted sea trout, it would appear advisable to place some restriction upon the smallest size that might be marketed, since it is highly probable that attempts will be made to market fish of such small size as to be nearly worthless as food. A minimum size limit at 8 inches (20 centimeters) should not meet with any serious objection, at least from the fish dealers who have the task of selling the fish.

The closing of both Oso and Nueces Bays, as well as the southern part of Laguna Madre, to seine fishermen has destroyed the income of the fishing industry, as well as of the entire State of Texas, from some of the best drum-fishing waters along the coast of Texas. While an overflow of drum from these waters into open territory may result in some benefit, it has been shown that the fish prefer to dwell most of the time within such closed areas. Few species of food fish other than drum and croakers frequent Oso or Nueces Bay, and the former fishery in these bays was almost entirely for the black drum. Allowing a suitable area around the entrances to these two bays to permit the fish ingress or egress it would appear desirable to allow a return of seine fishing within the bays. With the larger adult drum protected by reason of a legal size limit, there seems little basis for expecting serious depletion of the drum from the opening of these waters.

Laguna Madre long has been a battle ground for commercial fishing interests and conservation forces, for no apparent reason save that this long, narrow lagoon constitutes a favorite feeding ground for several species of marine food fishes, particularly in summer. The ease with which fish generally may be captured with seines in the shallow waters of the lagoon has alarmed many sport fishermen, who fear the gradual extinction of their favorite game fish. With the sportsmen in the great majority and the general public knowing little of the problems confronting the fishing industry, pressure in legislative circles has resulted in the closure of much of Laguna Madre to any form of net fishing.

The writer, considering the intelligent conservation and utilization of the fish of commercial importance along the coast, sees no legitimate reason for continuing the closure of the southern part of Laguna Madre, particularly in and around the waters of Baffin and Alazan Bays. As mentioned previously, during exceedingly hot and dry summers, when its waters become excessively saline, Laguna Madre becomes the death place of thousands of food fish. To remedy this condition, it has been suggested by many that an artificial channel or pass be cut through Padre Island from the Gulf of Mexico to Laguna Madre in the vicinity of Baffin Bay, and thus allow (at least theoretically) fresh Gulf water to mingle with the excessively salt water within the lagoon. While the construction of such a pass might be possible from an engineering standpoint, there is no evidence that the expense would be warranted under present conditions. In fact, such a pass might bring about a marked biological change in environmental conditions, which would reduce naturally the present supply of some species within the lagoon, particularly the black drum. It would appear to be more practical, from an economic standpoint (perhaps from a biological one as well), to allow unrestricted seine fishing within all of Laguna Madre (except around Corpus Christi Pass) in an attempt to reduce the amount of loss suffered during a period of natural mortality, than to attempt a costly and perhaps futile experiment by making an artificial pass. Removal of restrictions in Laguna Madre would result in the utilization of many of the fish that now perish during the summer months, and it would also result in partly satisfying those who now advocate an artificial pass in the belief that fishery conditions might be benefited.

SUMMARY

1. The black drum spawns in the Gulf of Mexico near the entrances to the bays and lagoons. The young drum enter the inland bays through the various passes soon after hatching and make for definite localities within the inland waters.

2. The spawning period occurs mainly from February to May and is preceded by a marked migration of ripening adults from the bays and lagoons to the waters of the Gulf. A secondary spawning period may occur in late summer and early fall with some of the younger age classes.

3. The black drum reach a total length of about 25 centimeters (9.8 inches) by the end of the first year and about 37 centimeters (14.5 inches) by the end of the second year, with scale study indicating that five years of age may be attained by the time a length of 60 centimeters (23.3 inches) is reached.

4. Sexual maturity is reached at the end of the second year, when the fish generally has attained a total length of 35 centimeters (13.7 inches).

5. The food of the younger drum consists largely of annelids and small fish, while the older fish prefer mollusks and small crabs. A small mollusk, Mulinia, is eaten almost exclusively by the larger-sized drum.

6. The recommendation of a minimum legal size limit at 20 centimeters (8 inches) and a maximum legal size limit at 51 centimeters (20 inches) is made primarily in order to conserve the smaller, less marketable fish as well as the larger, more prolific drum that are caught in great numbers and are of relatively slight market value.

7. The recommendation is made also to allow seine fishermen to fish in the present closed waters of Nueces and Oso Bays, as well as Laguna Madre, after minimum and maximum legal size limits have been adopted.

NATURAL HISTORY OF THE SPOTTED TROUT, CYNOSCION NEBULOSUS CUVIER AND VALENCIENNES

Spotted Sea Trout or Squeteague

Otilithus nebulosus Cuvier and Valenciennes, Hist. Nat. Pois., V, 1830, p. 79.
Cynoscion carolinensis McDonald, 1882, p. 12.
Cynoscion nebulosus Jordan and Evermann, 1896–1900, p. 1409; Welsh and Breder, 1923, p. 164; Hildebrand and Schroeder, 1928, p. 296.

DESCRIPTION OF ADULT

The adult spotted trout has an elongate body, large, oblique mouth, and protruding lower jaw. The teeth are sharp; two enlarged ones occur at the tip of the upper jaw. The color is characteristic and serves generally to identify the species in its adult stage. The upper half of the body is dark gray with sky-blue reflections, while the lower half is pale silvery. The upper sides are marked with many round black spots, which extend to the dorsal and caudal fins. (See fig. 28.)

DESCRIPTION OF YOUNG

The young of the species differ markedly from the adults, both in color and shape of the caudal or tail fin. Young above 3 inches (8 centimeters) in length are recognized easily, however, by the round black spots on the upper parts of the body as well as on the dorsal and caudal fins.

The smallest specimen obtained in Texas waters measures 7.8 millimeters (about 0.25 inch). This fish has the general elongate shape of the species, and the long, acute snout is particularly marked. The vertical fins are well differentiated, the larval fin fold extending from the vent to the spinous anal fin as well as along the caudal peduncle, both dorsally and ventrally. A pronounced series of dark brown chromatophores is placed in the center of the body and extends approximately from the soft dorsal fin to the caudal peduncle. This series of markings is the beginning of the broad, dark, lateral band, characteristic of fish from 15 to 35 millimeters in length. Another smaller group of chromatophores lies along the ventral edge of the caudal peduncle, a distinctive group of darker pigmentations being present on the

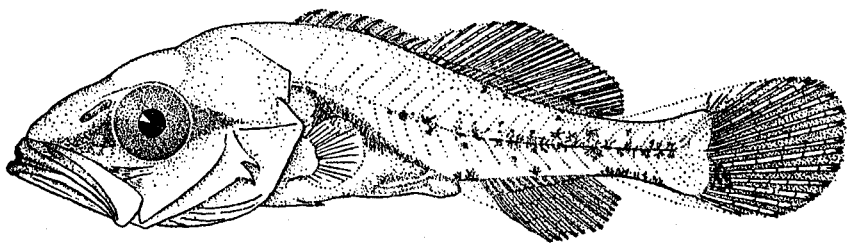

FIG. 24.—Young spotted trout. Actual length, 7.8 millimeters

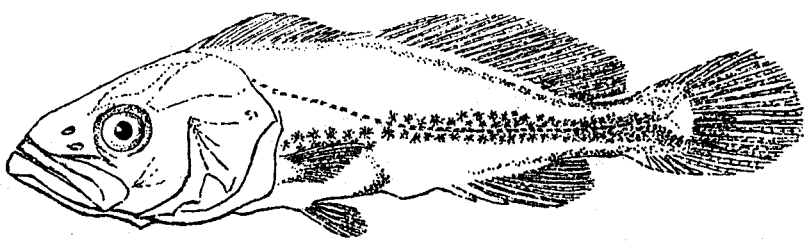

FIG. 25.—Young spotted trout. Actual length, 13 millimeters

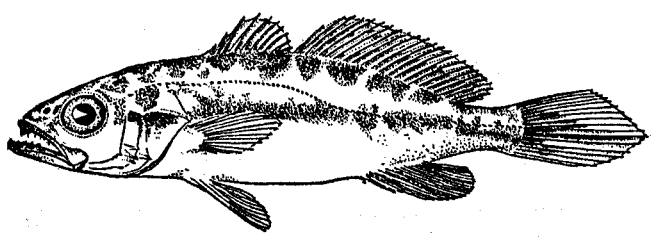

FIG. 26.—Young spotted trout. Actual length, 4.1 centimeters

lower anterior caudal fin. Fine punctulations are apparent behind and above the pectoral fins, as well as from the eye to the snout. (See figs. 24 and 25.)

Young spotted trout from 15 to 30 millimeters have the lateral black stripe most prominent and extending from the snout to the caudal fin in a continuous line. The ground color of the body is light, tinged with yellow and bluish reflections above and with a silvery sheen below. The caudal fin possesses a heavily marked, triangular, blackish area, the apex of which is near the tip of the fin. Fresh specimens have the iris of the eye colored a brilliant golden yellow, which disappears soon after death. The caudal is more sharply pointed in fish under 35 millimeters (1.3 inches). (See figs. 26 and 27.)

SPAWNING AND EARLY DISTRIBUTION OF YOUNG

The spotted trout spawns largely, if not entirely, within the bays and lagoons along the coast of Texas, in contrast to the redfish and black drum, which spawn (probably exclusively) within the Gulf of Mexico. The spawning season of the trout begins in early spring (not before March) and continues as late in the summer as October. The spotted trout do not appear to scatter their eggs within a relatively short period of time, as is the case with the redfish or drum, for individual fish are found in all stages of sexual development throughout the spring and summer and probably spawn for some weeks. The height of the spawning season occurs in April and May, however.

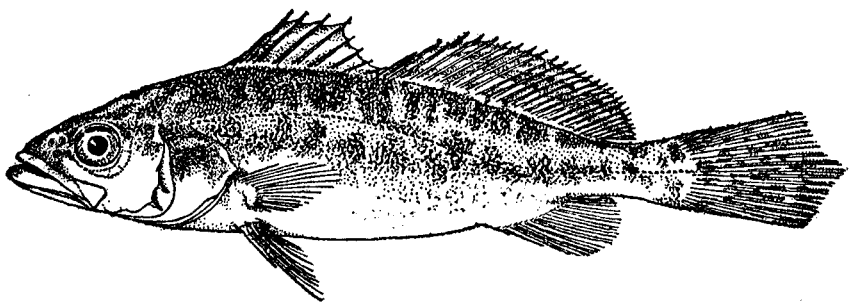

FIG. 27.—Young spotted trout. Actual length, 12 centimeters

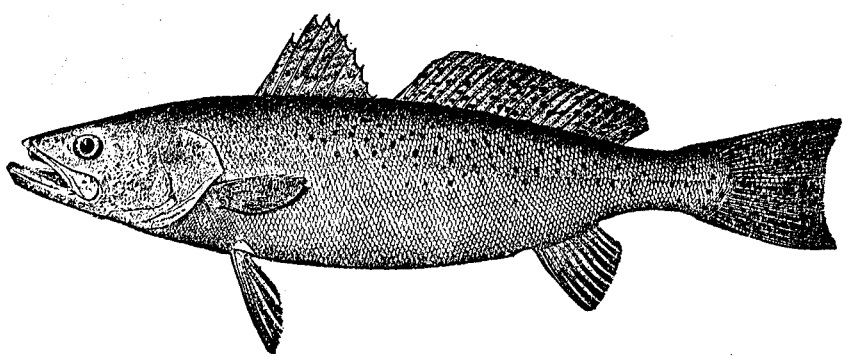

FIG. 28.—Adult spotted trout

The first collection of trout spawned in 1926 was taken on May 13, 1926, along the grassy shore line of Corpus Christi Bay near the channel entrance to Oso Bay. Several young, 10 to 22 millimeters long (under 1 inch), were secured in a few feet of water in the same approximate locality where large numbers of ripe and apparently spawning adult trout were being captured. Four days later another small fish, 18 millimeters long, was seined on the shore of Harbor Island about 1½ miles from Aransas Pass. (See Table 19.) Since Harbor Island was supplied with large numbers of marine organisms brought in from the Gulf of Mexico by the tidal currents, it was thought possible that this fish had been hatched in the Gulf and had entered the intercoastal waters through the pass.

TABLE 19.—*Collections of larval and young spotted sea trout (Cynoscion nebulosus) taken in 1926 and 1927*

Date	Number of fish	Length range, in millimeters	Locality
May 13, 1926	5	10–22	Corpus Christi Bay-Oso Bridge.
May 17, 1926	1	18	Harbor Island Light.
May 25, 1926	1	26	Corpus Christi Bay-Oso Bridge.
June 9, 1926	67	18–50	Corpus Christi Bay-Shamrock Cove.
June 18, 1926	9	30–50	Do.
June 23, 1926	55	18–48	Do.
June 29, 1926	5	37–45	Copano Bay.
July 3, 1926	3	21–22	Harbor Island Light.
Do	6	40–70	Corpus Christi Bay-Ingleside Cove.
July 22, 1926	61	15–27	Grass Island-Espiritu Santo Bay.
Aug. 5, 1926	44	24–61	Corpus Christi Bay-Shamrock Cove.
Sept. 23, 1926	28	28–69	Do.
Oct. 1, 1926	24	9–90	Corpus Christi Bay-Oso Bridge.
Oct. 18, 1926	64	15–68	Harbor Island.
Oct. 20, 1926	1	17	Harbor Island Light.
Oct. 22, 1926	4	22–39	Corpus Christi Bay-Ingleside Cove.
Oct. 28, 1926	3	16–29	Laguna Madre.
Oct. 29, 1926	1	22	Do.
Apr. 20, 1927	1	7	Do.
May 3, 1927	21	9–28	Harbor Island Light.
May 4, 1927	7	21–29	Aransas Bay-Mud Island.
May 11, 1927	2	26–42	Corpus Christi Bay-Shamrock Cove.
May 17, 1927	65	18–50	Copano Bay.
May 26, 1927	4	27–43	Nueces Bay.

Continued observations during 1926, however, soon led to the conclusion that, while considerable spawning of trout occurred along the shore lines of various islands lying inside the passes, no spawning actually occurred in the open Gulf of Mexico. Several definite facts supporting this conclusion were ascertained during the investigation.

As late as October 28, 1926, young spotted trout under 20 millimeters in length were taken within the bays and lagoons, and, together with the presence throughout the bays of ripe and spending adults until late fall, it seemed evident that spawning extended from March or April through September. The spawning season of 1927 contributed more conclusive evidence in support of the bay and lagoon spawning habit of the trout. The first fish, the smallest on record (7.8 millimeters long), was secured in northern Laguna Madre near Corpus Christi Bay on April 27, 1927, on the edge of a deep channel running from the lagoon into the bay by Demid Island–Flour Bluff. For some weeks previous to the capture of this small fish collections had shown the presence of large numbers of ripening trout within most of the bays, following a general movement into the intercoastal waters from the Gulf of Mexico during March and April.

During May, 1927, it was discovered that heavy spawning was occurring in various parts of Copano Bay. Along the grassy shore lines of this remote body of water hundreds of young trout, ranging from 20 to 30 millimeters long (0.8 to 1.1 inches), were procurable, as were also many ripe and spending adults. Small, restricted bayous or creeks that enter the bay proper yielded such abundant collections of very young fish as to preclude any possibility of the young coming into the bay from any considerable distance, certainly not from the Gulf of Mexico, some 50 to 60 miles away. The presence of the young trout with the spawning adults within such

remote bays throughout the spring and summer indicated conclusively that the species spawns within intercoastal waters.

Throughout the period of collection no spotted trout under 10 centimeters long (4 inches) were obtained from the Gulf of Mexico or from the immediate vicinity of any of the passes. This is in strong contrast with the large numbers of young redfish, drum, croakers, and spots spawned in the Gulf and that could be obtained either in the Gulf waters or about the passes. The fact that relatively few larval and post-larval spotted trout were secured by the investigator, compared with the abundant collections of other species, can be accounted for by the nature of the environment in which spawning occurs.

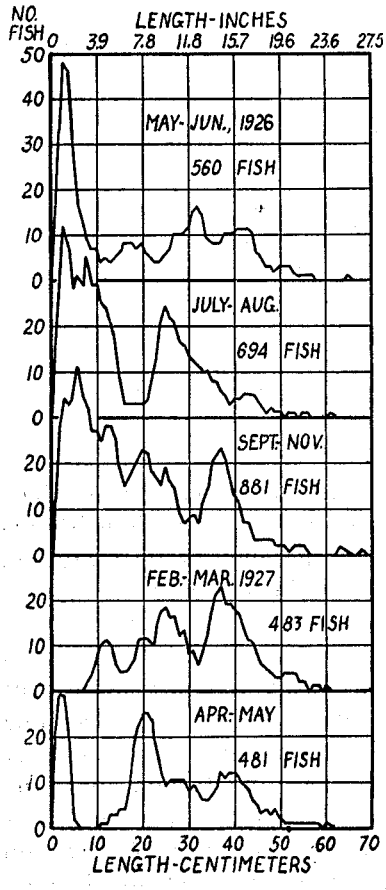

FIG. 29.—Length-frequency distribution of spotted trout in Texas, 1926–27. Actual frequencies have been smoothed by a moving average of threes

Since the eggs of the redfish and black drum were deposited, probably within a short period of time, in a limited area at the mouth of the passes, natural concentration of eggs and larval fish occurred, particularly when the young were carried into the channels of the passes. This concentration made possible large catches of the young fish around the passes. The spawning season of the spotted trout, on the other hand, was observed to be long, and the spawning ground covered wide areas in suitable bays and lagoons. Obviously, no concentration of young fish could result.

Spawning of the spotted trout probably occurs somewhat offshore in the various bays, in water not over 10 to 15 feet deep, although ripe and apparently spawning adults may be taken during the night close to shore. The eggs probably are buoyant and soon drift and hatch over the grassy-bottomed, shallow water, the young seeking protection in the thick aquatic vegetation. The concentration of young in patches of grass was noticeable. Smith (1907, p. 312) stated that the spawning grounds of the spotted trout in North Carolina are in the bays and sounds and that the egg hatches in 40 hours in water with a temperature of 77° F.

GROWTH AND AGE

On the basis of the frequency distribution of the total length measurements of approximately 3,000 spotted trout taken by experimental and commercial collecting gear from May, 1926, to June, 1927, it can be stated that, while size groups appear in the frequency summaries (Table 20 and fig. 29), no one definite year class, save the youngest, can be traced clearly or recognized throughout the entire period of collection. There is a decided tendency for the various age groups to overlap one another to such a great extent as to render any estimations of the growth and age, from length-frequency studies, unreliable. The writer had noted this fact previously with respect

to a series of length measurements made in 1925 upon several hundred spotted trout taken in Pamlico Sound, N. C. (Higgins and Pearson, 1927, p. 56.)

TABLE 20.—*Length-frequency distribution of spotted sea trout (Cynoscion nebulosus) taken in Texas May, 1926, to May, 1927*

Centimeters	1926							1927			
	May	June	July	August	September	October	November	February	March	April	May
1	4					1				1	6
2	10	16	51	1		47					33
3	2	66	29	6	3	22					48
4		50	4	32	15	14					5
5		21	9	21	27	17	1				1
6		22	4	16	12	20	2				
7		9	15	28	22	11	11				
8		7	15	10	12	6	9				
9		10	10	28	10	8	8	5	2		
10	1	4	13	10	7	4	16	5	1		
11	2	3	9	18	8	3	16	6	1		
12	2	1	10	14	4	2	15	11	5	2	
13	6	1	5	15	6	6	24	8	3	2	
14	3		3	17	4	8	14	2	2	3	2
15	6			8	2	4	6	2	2	1	1
16	10				3	1	14		4	2	2
17	6	3		1	4	3	7		4	1	6
18	4	1		7	8	6	5	1	5	6	10
19	8	1		2	14	6	4	2	9	9	20
20	8			1	12	5	4	1	14	11	10
21	4	2	1	5	10	9	5		7	8	18
22	4	1	2	2	8	7	5	3	7	13	16
23	2	3	2	11	9	2		1	12	10	4
24	2	1	7	15	12	6	1	1	18	3	6
25		4	10	15	5	6	3	1	18	5	8
26	2	5	7	17	11	8	4	2	15	2	4
27	1	9	5	12	5	5	2		11	4	6
28	3	9	5	16	3	4		1	18	7	8
29		7	1	13	3	2	2		5	3	1
30	2	8	2	11	4		4	7	8	6	6
31	4	12	2	12	3	2	3		5	2	7
32	2	16	3	8	7	2	1	1	6	2	4
33	5	8	3	8	2	1	1	1	5	5	4
34	4	6	4	5	14	3	2	4	10	1	2
35	1	4	5	4	11	1	6	4	13	2	3
36	3	6	2	5	17	3	3	7	14	11	1
37	3	6	4	3	17	3	5	11	13	6	5
38	2	5	2	2	17	2	3	12	13	9	3
39	5	8	2	2	10		5	7	3	5	6
40	4	7	1	1	9	3	3	10	12	12	1
41	5	2	2	4	3	2	2	9	13	6	6
42	4	10	3	2	6	5		2	6	6	2
43	3	10	3	1	2		1	4	8	6	2
44	1	6	4	3	2	3	1	6	6	4	4
45	5	4	2	1		1		3	3	2	
46	2	1		1	1		2	5	2	5	
47	2	2	2	1	1	1	2	4	1		1
48	3					2		3	1	2	3
49	1	1	3			2		1	1	2	2
50	1	1				2	1	1	2	2	1
51	2	3						3	1		
52	2		1			1	1	2	3	2	1
53	1	1		1				2	1		
54	1				1	3	1	3	1	1	
55	1			1							1
56		1		1		1		1		1	
57		1									3
58								1	1		
59											
60									1		1

TABLE 20.—*Length-frequency distribution of spotted sea trout (Cynoscion nebulosus) taken in Texas May, 1926, to May, 1927*—Continued

Centimeters	1926							1927			
	May	June	July	August	September	October	November	February	March	April	May
61				1				1			
62											
63						1	1				
64							1				
65	1										
66											
67											
68							1				
69											
70											
Total	160	385	267	419	366	287	228	167	316	193	284

From inspection of Table 20 it is evident that during the month of May in 1926 and 1927 the O or youngest year class appeared in the catches at an early age, the

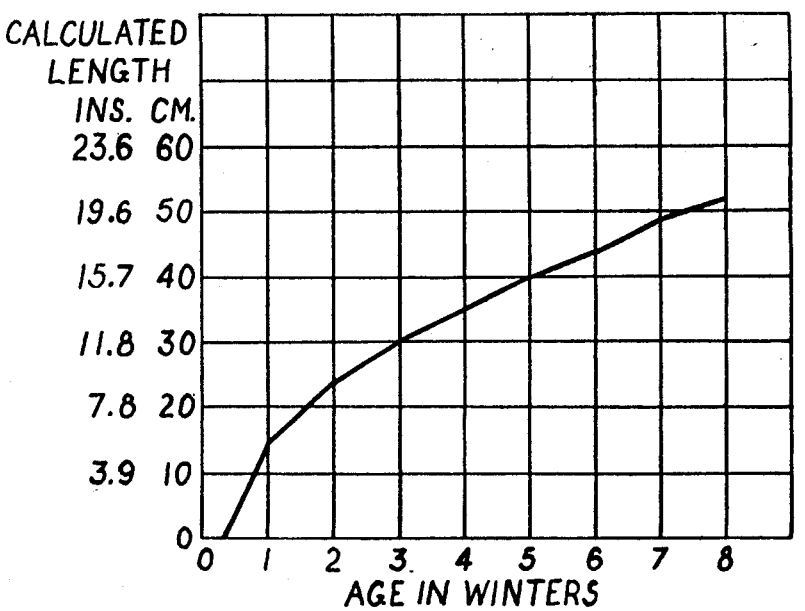

FIG. 30.—Averaged calculated lengths of spotted trout attained at formation of 1 to 8 winter checks. (See Table 23)

length distribution ranging from 1 to 5 centimeters (0.4 to 1.9 inches). The growth during the late spring and summer of 1926 was rapid, but extended spawning occurred from April to October, resulting in a wide length-frequency distribution. By the end of November, 1926, this O class, approaching its first winter, had attained a modal length of about 13 centimeters (5.1 inches), the length distribution being from 5 to 20 centimeters (1.9 to 7.8 inches). There appeared to be little increment in size from November to March, but in early spring growth was resumed, and by the

end of May, 1927, this year class (about 1 year old) reached a modal length of 19 to 20 centimeters (7.4 to 7.8 inches).

Study of the scales of the spotted trout was undertaken in the hope that seasonal-growth checks might be found and from them the annual growth and age of the species determined to a greater degree of accuracy than was possible from inspection of the length frequencies. From annual winter-growth checks (found to have been formed on most of the trout scales examined) it was possible to arrive at a reliable estimate of the age and growth of this species up to the seventh or eighth year of life.

The age of a fish, in years, according to the scale method of age determination, generally is found by counting the annuli or annual winter bands or checks, which supposedly are produced by a slower rate of growth during the cold months of the year. The length of the fish at the end of each year of life is computed from the series of measurements of a scale from a fish of known length. Given the total length of the scale, the length included in its annulus of year X, and the length of the fish from which the scale is taken, the length attained by the fish at the end of year X is determined by the use of the following formula, in which the third term is the unknown.

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

Repeating the above formula for the annulus of each evident year of life, the length attained by the fish at the end of each successive year is computed. From these lengths the annual increment in growth is obtained by simple subtraction.

It is not within the scope of the present paper to discuss in detail the various phases of the scale method of age determination. Most workers have found the scale method to be essentially correct, and it is upon this assumption that the writer presents the results obtained from a study of spotted-trout scales. The scales of the gray trout (*Cynoscion regalis*) provided material for a paper by Taylor (1916), and the reader is referred to Taylor's work for such information as may be of interest pertaining to the more theoretical aspects of scale study applied to the sea trouts (*Cynoscion regalis* and *nebulosus*).

The spotted sea trout is a typical warm-water shore fish, which appears very sensitive to the cold and which customarily departs into deeper and warmer water throughout its range on the coming of winter. Along the Texas coast, even as far south as the Rio Grande, this movement into deeper water is evident in the late fall and winter. A cessation of growth probably accompanies lowering of temperature and is reflected on the scale of the fish by a marked change in pattern and structure. The general character of these annual winter scale-growth checks consists in the formation of incomplete bilateral circuli that tend to become compressed, coalesced, or broken. A certain lack of distinctness is apparent in many of these winter checks (annuli), probably due to the intermittent cold weather that obtains along the Texas coast.

From approximately 2,000 unselected spotted trout taken with experimental fishing gear (excluding about 1,000 fish under 10 centimeters (3.9 inches) in length,

obviously in the O year class and not having reached one winter), 554 fish were examined for age by the scale method. From 4 to 6 individual, unselected scales from each of the 554 fish were mounted on a glass slide, the smooth side of the scales being moistened slightly with a mixture of mucilage and glycerine to cause adhesion to the glass. In all cases the scales were taken from the upper forward left side of the fish. The actual counting of the annuli and measurement of the scale with its annual checks was done by two distinct methods of magnification and measurement. Thus, a reliable check was made upon each method employed, as well as on the personal judgment of the writer. It should be stated, however, that knowledge of the life of the species of fish, particularly the time of spawning, assists greatly in understanding many of the annual checks that might appear confusing to one who knows and sees nothing of the fish save several scales, abstractly presented.

The first method used consisted in examining all scales through a binocular microscope at various magnifications and in selecting one typical scale for measurement by means of an ocular micrometer at a standard magnification of about 30×. Upon examination many scales were found to be useless for accurate age determination, some having broken edges, regenerated centers, or other abnormalities. A scale was judged "typical" by the ease with which it could be read and the support obtained from comparison with the other scales on the slide.

The results of the first method, while appearing reasonable, did not seem to be as accurate as would have been the case if a more refined measurement of the scale and its checks had been made. Two hundred of the original 554 fish had to be omitted from the calculations, either because of the imperfections of the scales or the inability of the writer to distinguish the annuli.

The second method, conducted independent of the results obtained from the first method, gave more accurate readings and measurements, in the writer's opinion, although a comparison of the two showed no serious differences. By means of a projection apparatus the image of the scale was projected on a white wall, and each scale annulus was counted and measured at a magnification of about 100×. The various scale and annuli lengths were recorded on adding-machine tape, and the distances were measured later with a millimeter rule. In many cases two scales from the same fish were read and measured for comparison. (See Table 22.) In both methods of scale measurement the distances usually were measured from the center of the focus, along the radius nearest the periphery of the scale.

Of the 554 trout, 452 were read for age and measured for annual growth by the projection method. Of the 452 individuals, 56 were discarded because of apparent discrepancies in the calculated measurements; and while the inclusion of these doubtful 56 fish did not affect the final results appreciably, it was believed desirable to eliminate obvious errors. In the final calculations 396 trout were analyzed by the second method, while 354 were analyzed by the first. The fact that about 28½ per cent of the original number of fish scales were omitted because the writer was unable to read them can hardly be considered serious, since it was thought better to omit questionable scales rather than obtain doubtful calculations.

The spotted-trout scales were collected from April, 1926, to June, 1927. Consequently, the various age classes of fish passed through one observed winter's growth check. The fish taken from April, 1926, to March 1, 1927, show one less winter

check on the scales than do fish secured from March to June, 1927 (the winter scale check usually is formed by March 1). Obviously, a fish 2 years old in 1926 would be 3 years old in 1927.

Table 21, containing the averaged calculated lengths of 396 trout at the time of the formation of the various winter checks, has two divisions—one presenting the averaged calculated lengths of fish of all ages taken from April, 1926, to March 1, 1927, and the other (bottom of table), the averaged calculated lengths of trout taken from March 1 to June 1, 1927. The latter group naturally show the additional winter check formed during the winter of 1926–27.

TABLE 21.—*Averaged calculated total lengths of 396 spotted trout at formation of winter checks on the scales*

Year of hatching	Age, in winters	Calculated lengths, in centimeters, at formation of winter check									Number of fish
		First	Second	Third	Fourth	Fifth	Sixth	Seventh	Eighth	Ninth	
1925	1	13.5									71
1924	2	14.3	22.9								53
1923	3	14.8	24.2	30.6							54
1922	4	14.6	24.5	30.3	35.2						42
1921	5	15.0	24.5	31.1	36.1	40.5					28
1920	6	15.7	26.1	31.0	35.9	39.2	44.2				16
1919	7	14.6	24.0	29.7	34.4	39.4	44.7	49.1			19
1918	8	14.9	22.6	30.9	36.3	39.6	45.0	48.9	51.8		5
1926	1	13.8									22
1925	2	16.0	22.9								20
1924	3	14.5	24.1	29.6							16
1923	4	16.1	23.9	30.8	36.2						24
1922	5	14.9	22.5	30.5	34.9	41.0					9
1921	6	17.8	23.7	29.1	33.1	38.2	43.6				5
1920	7	16.3	25.0	29.6	33.0	38.6	42.8	48.6			9
1918	9	12.3	26.4	29.9	34.5	39.7	42.6	47.2	50.2	56.8	3
Weighted average		14.7	23.9	30.4	35.2	39.7	44.0	48.7	51.8		
Growth increment		14.7	9.2	7.5	4.8	4.5	4.3	4.7	3.1		

Inspection of this table reveals only slight differences in the various averaged calculated lengths at the same ages for fish ranging from 1 to 8 years of age. The decided absence of any "phenomenon of apparent change of growth rate" (such as observed by Lee (1912) and other workers, in which, with increasing age, the age classes of fish show a decreasing rate of growth in their calculated values for each year of life) is most noticeable. In fact, almost the reverse of Lee's phenomenon appears to be the case, for the youngest fish (those in their second year with one winter check) have the lowest calculated lengths (13.5 to 13.8 centimeters) for the first winter, omitting the calculated length of 12.3 centimeters for three 9-year-old fish.

Table 22, giving a comparison between the averaged calculated lengths of trout derived from measurements of two scales from the same fish, shows in a more distinct manner than does Table 21 the trend of the younger year classes to possess smaller calculated lengths than the older year classes. Averaging the two calculated lengths for fish of the same age, it will be seen that the 1-year-olds have an averaged calculated length of 12.9 centimeters at the formation of the first winter check; the 2-year-olds are 13.6 centimeters; the 3-year-olds are 14.9 centimeters; the 4-year-olds are 15.3 centimeters, and the 5-year-olds are 15.7 centimeters. A similar though much less pronounced progression occurs for the second and fourth years' calculated

lengths. Several natural factors may have caused this phenomenon, directly opposed to Lee's phenomenon of apparent change of growth rate.

TABLE 22.—*Comparison of the averaged calculated lengths of spotted trout, derived from measurements of two scales from the same fish*

[Scales measured by projection method and the total lengths expressed in centimeters. Fish collected from May, 1926, to May, 1927, and selected at random from fish represented in Table 21]

Scale reading	Age, in winters					Number of fish	Scale reading	Age, in winters					Number of fish
	1	2	3	4	5			1	2	3	4	5	
First	13.0					53	Second	14.9	24.3	30.7			28
Second	12.8					53	First	15.6	24.7	30.4	34.8		23
First	14.0	23.0				29	Second	15.1	24.4	29.9	34.5		23
Second	13.3	23.0				29	First	15.1	24.4	32.1	37.0	41.2	8
First	14.9	24.4	31.0			28	Second	16.4	23.9	30.8	36.4	40.3	8

Figure 31, presenting a comparison between matured male and female trout according to size, clearly indicates that a larger percentage of males than females

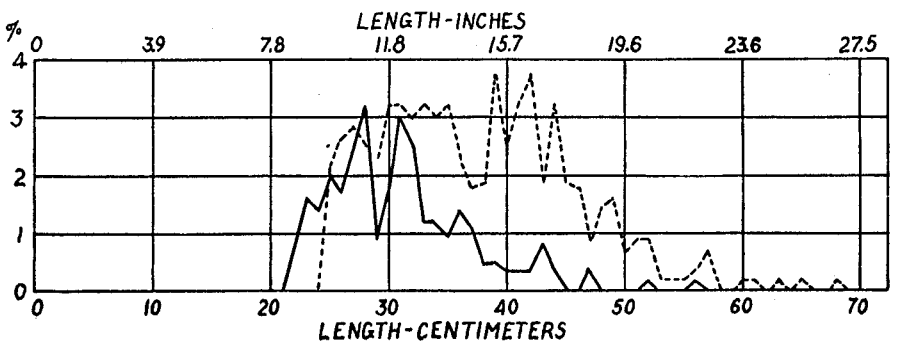

FIG. 31.—Size at maturity of the spotted trout. Males represented by solid line; females by dotted line. Total number of fish, 567

occurs in the smaller sizes than in the larger sizes. Hence, we may assume that in general the younger year classes contain a greater proportion of male fish than do the older year classes. Since the males do not appear to attain the same average mean length as the females (see p. 190), a greater rate of growth might be expected among the latter. Such a condition would result in smaller calculated lengths among the younger year classes with their higher percentage of males and a slightly slower rate of growth than among the older fish composed largely of females. While it is possible to assume that the growth of males and females is identical prior to spawning, and that the females merely reach a greater size (and age) than do the males, the writer hardly believes such an assumption probable, since it is known that in many species of fish the males are smaller than females of the same age.

Another explanation is to assume that the smaller calculated lengths among the younger age groups are the result of the occurrence of greater numbers of "runt" or constitutionally slow-growing fish during the early years of life, but which are eliminated from the fish stock gradually by the natural process of survival of only the largest and fastest-growing fishes. The writer observed often that many spotted trout in their first and second years possessed gill parasites (an isopod, *Livoneca*

ovalis, that generally caused the fish to be undersized, compared with modal lengths for the particular year class) and that older fish were singularly free from them. A greater number of such dwarfed or undersized trout may be expected during the early years, which lowers the averaged calculated lengths for the youngest fish.

While it is impossible at present to attribute any definite cause to this observed difference in calculated lengths according to the age of the fish, aside from the possible error in omitting the first winter's check of more of the older fish than of the younger, the differences among the various calculated lengths at the same age are hardly large enough to vitiate the general conclusions on the age and rate of growth of the species.

TABLE 23.—*Calculated and actual lengths of spotted trout compared*

[Calculated lengths, derived from scale-growth checks generally evident by March, given for fish collected from April, 1926, to February, 1927; actual lengths include only fish taken during March, 1927. The calculated lengths should approximate the actual lengths, but the latter should be slightly larger, since fish taken in March have a newly formed winter scale check plus some additional growth. The calculated lengths for March fish are also presented]

Age in winters	Averaged calculated length, in centimeters, all fish	Total fish	Averaged actual length, in centimeters, March	Number of March fish	Averaged calculated length, in centimeters, March	Age in winters	Averaged calculated length, in centimeters, all fish	Total fish	Averaged actual length, in centimeters, March	Number of March fish	Averaged calculated length, in centimeters, March
1	13.5	71	15.6	14	13.2	4	35.2	42	37.1	16	36.0
2	22.9	53	23.7	8	22.3	5	40.6	28	42.2	4	40.9
3	30.6	54	30.4	10	29.8	6	44.2	16	45.0	1	43.1

The average calculated length of the Texas spotted trout for the first six years approximates that of Florida fish, as indicated by the examination of the scales of 20 spotted trout by Welsh and Breder (1923, p. 165) from Punta Gorda, Fla. Comparison is made between the annual growth of the Texas and Florida fish in Table 24.

TABLE 24

	Calculated average length				Calculated average length		
	Florida fish	Texas fish			Florida fish	Texas fish	
	Cm.	*Cm.*	*In.*		*Cm.*	*Cm.*	*In.*
First winter	11-12	15	5.9	Fifth winter	40	40	15.7
Second winter	23	24	9.4	Sixth winter	43	44	17.3
Third winter	31	30	11.8	Seventh winter	----------	49	19.2
Fourth winter	36	35	13.7	Eighth winter	----------	52	20.4

SIZE AND AGE AT MATURITY

From approximately 1,500 adult trout taken during 1926 and 1927, 567 fish were sexed during the spawning season. The sexed fish were unselected and were either in a ripening, ripe, or spending condition when caught. While it is hardly possible to assume that the relation between sexual maturity and the length of the fish is constant in individuals of the same sex, nevertheless some reliable data concerning size and age at maturity were obtained from the sexing of these fish.

In the case of the spotted trout, as in many marine fishes, the matured male averages smaller than the female, the maximum size being attained by the latter. Of the sexed fish, only 4 males were taken with a length exceeding 45 centimeters

(17.7 inches), while 71 females longer than this were secured. The average mean length of the females exceeded that of the males by 6 centimeters (2.3 inches). The number of females obtained from the sexed 567 fish was 389, a ratio of two females to one male. Many matured fish were under the minimum legal size limit of 12 inches.

Results obtained from the study of the age of the spotted trout would indicate that maturity is attained and spawning occurs for the first time at the end of the second year of life, although it is probable that many fish do not mature and spawn until the end of their third year.

The approximate number of eggs in two nearly ripe trout 48 and 62 centimeters in length (18.9 and 24.4 inches) was 427,819 for the smaller fish and 1,118,000 for the larger one.

Length of fish, in inches (62 centimeters)	24. 4
Total weight of eggs, in grams	238
Total weight of 141 unselected eggs, in milligrams	30
Number of eggs in 1 gram	4, 700
Number of eggs in total of 238 grams	1, 118, 000
Length of fish, in inches (48 centimeters)	18. 9
Total weight of eggs, in grams	87. 3
Total weight of 141 unselected eggs, in milligrams	29
Number of eggs in 1 gram	4, 900
Number of eggs in total of 87.3 grams	427, 819

Figure 32 presents the relation of weight to length in 154 trout. The fish generally reach maturity before a weight of 1 pound is attained. A weight of about 3 pounds is reached by the end of 7 or 8 years.

SEASONAL DISTRIBUTION AND MOVEMENTS

The spotted trout may be taken throughout the year in nearly all of the bays and lagoons along the Texas coast, as well as along the Gulf beaches in proximity to the passes. The species prefers the less turbid, grassy-bottomed areas, and large fish are secured rarely in such muddy waters as Oso and Nueces Bays. Quiet, shallow lagoons and coves, possessing a heavy grass bottom, are the favorite localities for the young trout; while the adult fish generally remain in deeper water, although frequently they come close inshore to feed and possibly to spawn. The young, being spawned within the bays, seldom seek the waters of the Gulf of Mexico until maturity is reached, at about 25 centimeters (9.8 inches), although many adults linger around the entrances to the passes at all times of the year. On the arrival of cold weather most of the trout move off into the deeper waters of the bays or the Gulf. Deep holes or channels that are fished during freezing weather are found to be filled with fish. An example of the movement of trout into deep water during cold waves was afforded during the winter of 1926–27, when a newly completed ship channel near Corpus Christi, at the mouth of the extremely shallow Nueces Bay, became crowded with fish during each cold period. Anglers who fished around the edges of this channel secured heavy catches of trout during the cold weather, but when warm days arrived the fish would scatter over the shallow waters and the fishermen's catches would decrease. Many trout are said to die when caught unawares in shallow lagoons during sudden cold weather, so sensitive are they to the cold.

Many of the larger trout leave for the warm waters of the Gulf of Mexico in winter and in early spring enter the bays in order to spawn and feed. Commercial line fishermen take advantage of this pronounced movement into the bays by fishing in the more shallow passes, such as Corpus Christi, during the early spring months. By May the movement virtually ceases, and the adults distribute themselves through most of the bays. Many trout, both young and old, wander into brackish water, as abundant collections of fish from such localities as Aransas and Copano Creeks show.

In Chesapeake Bay, the northern range of the species, Hildebrand and Schroeder (1928, p. 297) observed two definite periods of abundance—from March to May and from September to November. This fact probably is due to the same general seasonal movements as were observed along the Texas coast—the fish coming into the shallower waters during the spring for spawning and feeding and leaving in the fall for deeper, warmer waters. In the vicinity of Corpus Christi the warm waters of the Gulf are near at hand, and consequently all seasonal movements are less pronounced than in the more northern regions.

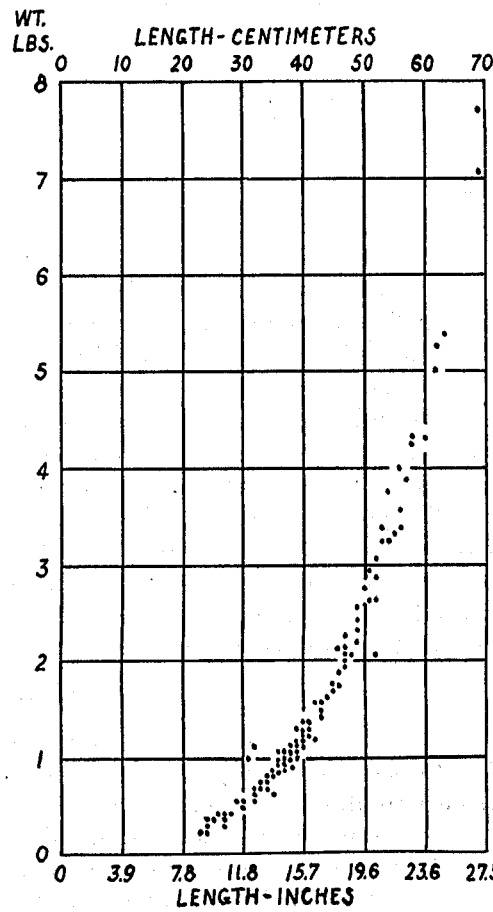

FIG. 32.—Relation of weight to length in 154 spotted trout

Definite schooling prior to and during spawning must occur to some extent, although no very satisfactory evidence could be obtained by the writer. It would appear from collections that small groups of fish make up the spawning units at various localities. This view would seem reasonable for the extended spawning season is hardly in accord with continued schooling of adult fish.

The larger trout travel in small schools, as do the redfish, drum, and croakers, but the movements of these schools are difficult to follow, possibly because of their aimlessness. Young, immature fish usually are well scattered but generally are found in certain localities at all times.

FOOD HABITS

The food of the spotted trout, as indicated by an examination of the stomach contents of 220 fish ranging in length from 6 to 60 centimeters (2.3 to 23.6 inches), is composed largely of various species of marine shrimp and fish. Table 25 presents, in percentages of the total number of fish in various length groupings, the preference for definite organisms and also the percentage of the total number of fish of all sizes

that feed exclusively on these definite forms. Of the 220 trout, 61 per cent had been feeding on shrimp exclusively, usually Peneus, 24 per cent had eaten fish, 1 per cent crabs, and 14 per cent mixed organisms. The mixed food usually was composed of shrimp and fish. The food of the trout, according to the size of the fish (6 to 60 centimeters), appears to be fairly uniform in character.

TABLE 25.—*Food preference of 220 spotted trout*

[Mixed food usually consisted of shrimps and fish. All fish taken February to May, 1927]

Length in centimeters	Number of fish	Percentage of fish that had eaten—			
		Shrimp	Fish	Crabs	Mixed
6–15	86	59	26	0	15
16–30	30	80	7	0	13
31–60	104	57	27	3	13
Total		61	24	1	14

The various species of fish captured and consumed by the spotted trout include principally the young of the croaker, spot, and mullet, besides the young and adult Menidia and Anchovia. Small grass-dwelling fishes, such as the gobies, also are eaten extensively,

The avidity of the trout for its favorite food, the shrimp, is attested by the success fishermen have when they use this crustacean as bait. Often commercial hook-and-line fishing is suspended for lack of shrimp with which to bait the hooks.

The preference of the fish for the clear waters of the more quiet, grassy-bottomed coves and lagoons might justly be attributed to the habit of the trout of selecting its food with some care, taking in little mud and débris, as is customary with such species as the black drum, croaker, and spot, which prefer as feeding grounds areas covered with little or no vegetation.

COMMERCIAL CONSIDERATIONS

The spotted trout (squeteague) has commercial importance from Delaware Bay to the Rio Grande. It is essentially a warm-water, coastal fish, the center of its natural abundance being in Florida and the Gulf States. The maximum recorded size for the species is 16 pounds for a fish from Chesapeake Bay. Individuals weighing over 10 pounds are rare, however, particularly along the Texas coast. The fish is always in market demand and brings a good price to the fishermen at all times of the year. Table 26 gives the catch of spotted trout in certain years as shown by the records of the United States Bureau of Fisheries.

TABLE 26.—*Approximate commercial catch of spotted sea trout (Cynoscion nebulosus) in the United States in certain years*

State	Weight, in pounds	Value	Value per pound	Year	State	Weight, in pounds	Value	Value per pound	Year
Florida:					Virginia	418,797	$41,879	$0.100	1920
West coast	1,590,523	$157,169	$0.099	1923	Mississippi	410,294	37,327	.091	1923
East coast	1,198,400	122,854	.100	1923	Alabama	48,910	4,903	.100	1923
Texas	1,523,965	154,238	.100	1923	Maryland	20,000	2,000	.100	1920
North Carolina	913,910	116,316	.128	1923					
Louisiana	783,214	73,031	.093	1923	Total	6,908,013	709,717		

The spotted trout is the most valuable marine food fish of Texas. Its popularity, both as a game and a market species, has lead to many controversies as to the best method for protecting the fish against overfishing.

The commercial catch is made principally with hook and line in and about the passes and channels (which are closed to net fishing) and with drag seines in the more remote open bays and lagoons. A small amount of gill-net and trammel-net fishing is done during the winter, principally along the northern Texas coast, while a few fish are taken at times with light surf seines along the beaches in the Gulf of Mexico. The drag seines, because of their superior efficiency, account for the greater part of the commercial catch.

Besides by the closing of extensive areas to net fishing, the spotted trout are protected by a minimum legal size limit of 12 inches (30.5 centimeters). This limit, in general, allows the species to reach maturity unmolested, as well as to attain an adequate market length.

While the imposition of a minimum legal size limit appears to be justified, both from an economic and a biologic standpoint, there is some question as to the actual value to be derived from closing extensive marine areas to net fishermen while permitting commercial hook-and-line men to operate anywhere at all times of the year. The closure of most of the inland bays (excepting Oso and Nueces) was prompted by a desire to allow the spotted trout to spawn unmolested. Line fishermen assert that when drag seines are allowed to operate in the bays they destroy young trout as well as other food fishes. No concrete evidence in support of this supposition exists, however, since few impartial observers have witnessed extensive seining operations. The usual method of fishing with drag seines within the Texas bays and lagoons allows the entire net to be in the water until all fish are removed. The gradual hauling of the seine permits most of the illegal fish to escape through the meshes, while any illegal-sized fish that may have gilled are removed and thrown back into the water. Extensive fishing operations conducted by the writer in favorable spotted-trout localities failed to reveal the destruction of any appreciable quantity of young fish (the net used was a standard Texas drag seine, such as is employed in the commercial fisheries). While some young fish (not food species in particular) may be dragged along in the detached bottom vegetation, there is little reason for supposing that these fish die when they come into contact with small quantities of this vegetation. By law, as well as from the needs of the fishery, seines full of fish can not be dragged upon dry land. Since such a practice does not exist, to the writer's knowledge, no great destruction of young, unmarketable trout can be possible.

The small, natural passes should be closed to all fishing operations, whether sport or commercial, for extended movements of trout as well as other food fish necessitate the use of these passes. Commercial and sport hook-and-line fishermen congregate in large numbers about the shallower passes, such as Corpus Christi, to take toll of the ripening or migrating trout on their way to or from the bays and lagoons. Such a condition is not favorable to the fish and consequently is detrimental to the fisheries as a whole.

Higgins and Lord (1926, p. 180) pointed out that no evidence could be found that would indicate that the stock of spotted trout along the Texas coast is undergoing

depletion. As stated before, it is not known how to determine the extent to which a fishery may be prosecuted except by actual trial by unrestricted fishing effort. With the present tendency to discourage the use of the most efficient types of fishing gear in Texas, it can not be expected that the annual catch of trout will be increased to any great degree.

SUMMARY

1. The spawning grounds of the spotted trout in Texas lie within the inland bays and lagoons, often close to the passes and the Gulf of Mexico. The spawning season extends from early April to September, and the height of the season is reached in April and May.

2. The young trout are found in large numbers along the grassy-bottomed shore lines in more or less definite localities prefered by the adults as spawning areas.

3. The species attains an average length of approximately 6, 10, 12, 14, 16, 18, 19, and 20 inches by the end of the first to the eighth winter, as indicated by scale study. The extended spawning season, however, causes a wide overlapping of age classes.

4. Sexual maturity is reached by the end of the second or third year, at a time when the fish generally attain a legal market length of 12 inches.

5. The food of the spotted trout consists largely of shrimp and small fishes.

6. The natural passes, such as Corpus Christi, should be closed to all forms of fishing, since they constitute necessary passageways for the trout, as well as other food fish, from the bays into the Gulf of Mexico, and vice versa.

NATURAL HISTORY OF THE CROAKER, MICROPOGON UNDULATUS (LINNÆUS)

CROAKER, HARDHEAD

Perca undulatus Linnæus, Syst. Nat., ed. XII, 1766, p. 483; South Carolina.
Micropogon undulatus; Jordan and Evermann, 1896–1900, p. 1461, Pl. CCXXIV, fig. 570; Welsh and Breder, 1923, p. 180; Hildebrand and Schroeder, 1928, p. 283.

DESCRIPTION OF ADULT

The adult croaker has a rather robust body with a somewhat elevated and compressed back. The mouth is horizontal and inferior, and the chin has several pores and a row of short, slender barbels on each side. All jaw teeth are small. The color is generally grayish silvery above and silvery white below; the upper part of body is highly irridescent in life. The back and sides have many brassy or brownish spots arranged in irregular, wavy, olique bars on the sides. Both sexes are capable of making a croaking sound, which may be heard when the fish is under the water or after it has been removed from the water. (See fig. 36.)

DESCRIPTION OF YOUNG

The larval croaker of about 6 millimeters length is transparent, and the larval fin fold, or membrane, extends from the vent to the anal fin and along the caudal peduncle, both dorsally and ventrally. The vertical fins are fairly well differentiated, the anal rays being distinct and usually having a count of II–8. The dorsal soft rays are not so well developed, and the spines are not yet visible. The pectorals and

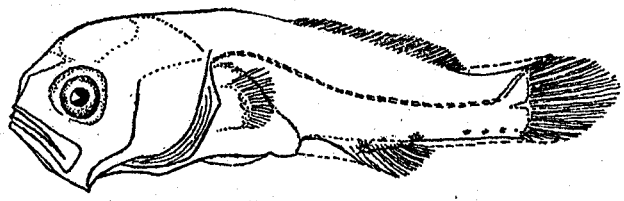

FIG. 33.—Larval croaker. Actual length, 6.5 millimeters

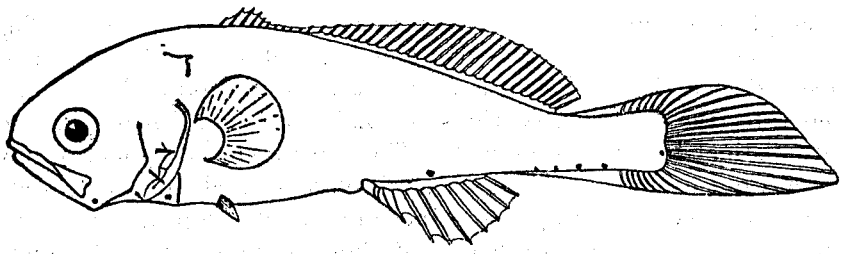

FIG. 34.—Larval croaker. Actual length, 1.225 centimeters

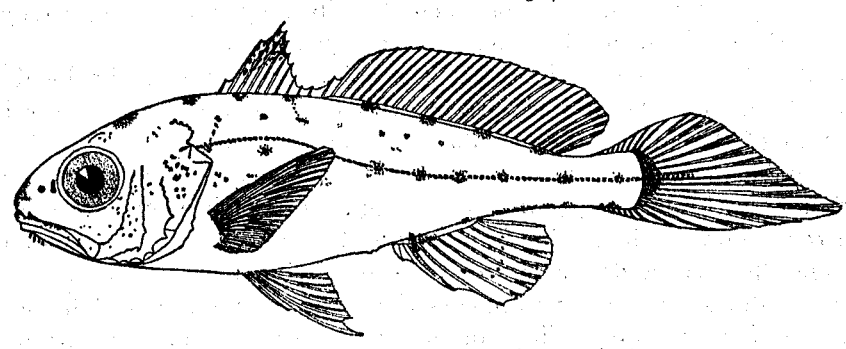

FIG. 35.—Young croaker. Actual length, 3.4 centimeters

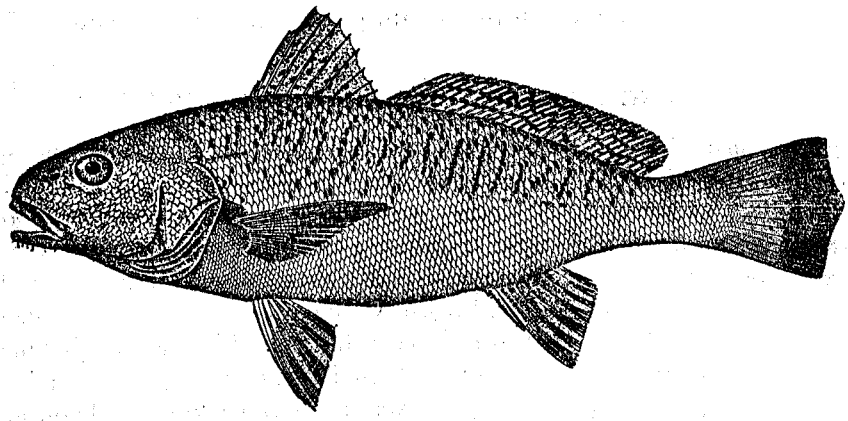

FIG. 36.—Adult croaker

ventrals are inconspicuous. The pigmentation is quite distinctive and helps to identify the larval and post-larval croakers from larval and post-larval redfish and black drum. Two very small chromatophores are at the base of the anal fin—one generally between the first and second soft rays, the other directly posterior to the last ray. The presence of these two markings seems to be constant in all specimens examined, up to a length, at least, at which little doubt exists as to the correct fin-ray count. Three to five small chromatophores lie posterior to the anal fin along the ventral edge of the caudal peduncle. No dorsal chromatophores are evident. (See fig. 33.)

At a length of 11 millimeters a croaker has all rays in the vertical fin distinct, with the usual count of II–8 for the anal and X, I–29 for the dorsal. The fin fold has disappeared, and the caudal fin is now considerably produced, a condition that at once separates the species from the spot (*Leiostomus xanthurus*). Pectorals and ventrals are distinct but not prominent. The ventral chromatophores may or may not be present, but usually are, with the addition of several smaller ones at the base of the caudal fin. Teeth and opercle spines are well developed. (See fig. 34.)

When Texas croakers reach a length of about 30 millimeters (1.1 inches), they closely resemble a 30-millimeter specimen described by Welsh and Breder (1923, p. 182), and their description is given in part. (See fig. 35.)

A croaker 30 millimeters long has the spiny armature of the head strongly developed, the mandibular barbels are in evidence, and the shape of the body approaches that of the adult. The caudal has a flowing extension of the lower rays, the longest ray being about equal to the length of the head. The color (in preserved examples) is pale throughout, punctuated with groups of brownish chromatophores in regular rows, 8 on the dorsal line from head to base of caudal, 8 to 10 on a line from the opercular flap to caudal, a less distinct row lying between these. (In Texas specimens the dorsal row always appears the most pronounced.) The snout, premaxillary, tip of spinous dorsal, base of anal, and base of caudal rays are punctulate with brownish. The adult color pattern is assumed gradually after a length of 3 centimeters is reached, but the fish retains its greatly lengthened caudal fin until a much larger size.

SPAWNING AND EARLY DISTRIBUTION OF YOUNG

Along the coast of Texas the croaker (*Micropogon undulatus*) spawns in the late fall in the open Gulf of Mexico near the mouths of the various passes that lead into the shallow bays and lagoons. Together with the spot (*Leiostomus xanthurus*) this species greatly outnumbers in natural abundance the other members of the Sciænidæ; and, as a result of this abundance, particularly of young, observations on the spawning and distribution of larval and post-larval fish were clear cut and informing.

Soon after the first larval redfish had been discovered in the vicinity of Aransas Pass, Tex., in October, 1926, a deluge of larval croakers filled the pass on each incoming tide. The concentration of the young fish was most remarkable. Thousands were obtained in a short haul with a silk tow net in the deeper waters of the pass itself and thousands more were obtained along the Gulf beach adjoining the pass by means of a small minnow seine hauled along the surf line in a few feet of water. (See Table 27.)

TABLE 27.—*Collections of larval and young croakers (Micropogon undulatus) in Texas 1926 and 1927*

Date	Number of fish	Length range, in millimeters	Locality	Date	Number of fish	Length range, in millimeters	Locality
Mar. 4, 1926	27	30–70	Copano Bay.	Dec. 3, 1926	90	4–9	Aransas Pass-Gulf.
Apr. 3, 1926	3	40–55	Aransas Pass-Gulf.	Dec. 13, 1926	170	8–30	Harbor Island.
May 6, 1926	12	30–70	Harbor Island.	Jan. 4, 1927	29	11–19	Do.
Oct. 18, 1926	12	7–8	Do.	Jan. 10, 1927	500	13–24	Aransas Pass-Gulf.
Oct. 29, 1926	200	6–12	Corpus Christi Pass.		14	21–40	Copano Bay.
Nov. 3, 1926	115	10–14	Aransas Pass-Gulf.	Jan. 25, 1927	98	12–27	Aransas Pass-Gulf.
Nov. 5, 1926	3,000	5–11	Aransas Pass.	Jan. 27, 1927	3	14–37	Corpus Christi Pass.
Nov. 16, 1926	1,500	9–17	Corpus Christi Pass.	Mar. 16, 1927	3	13–26	Do.
	2	14–18	Oso Bay.				

During September and October a noticeable migration of ripe adult croakers from the bays to the Gulf was indicated by the frequent collections around the passes and the lessening numbers of fish in the more remote lagoons and bays. It was not expected, however, that a profusion of young would result from this spawning, since the size of the adult Texas croaker rarely runs over 30 centimeters (11.8 inches)—much smaller than the Atlantic coast fish.

Both Aransas and Corpus Christi Passes were fished in order to find young croakers and young redfish, and the confusion that resulted from the mixture of these two species (which resemble each other closely in larval form) was disconcerting to the investigator, who for a time did not know which fish was being taken in such great numbers. Thousands of larval and post larval croakers were obtained, however, compared with the tens of redfish, as comparison of Tables 4 and 27 shows clearly, although much more time was spent trying to find the young redfish.

The young croakers came into the bays from the Gulf on the incoming tidal currents, to be distributed over the many miles of intercoastal waters. A determined attempt on the part of the post larval and young fish to gain the shelter of the bays was observed on many occasions. Few fish could breast the strong current of the ebb tide, but the young croakers, massed in schools, were seen attempting to enter the passes by hugging the sides of the channels and to take advantage of the slower current in the shallower water as well as the counter wash from the Gulf surf, which tended to offset the outgoing current from the bays and lagoons. Careful fishing around Corpus Christi and Aransas Passes showed beyond any doubt that the young were striving to get through the passes into the quiet bay and lagoon waters. This important fact in the life of the fish was observed in the case of the spot, also, and there is no reason to doubt that the other Gulf-spawned Sciænidæ, particularly the redfish and drum, also make a deliberate attempt to reach the bays from the spawning grounds outside of the passes. That such an attempt was not noticed in the case of the redfish and drum probably was due to the fact that these fish occurred in less abundance.

A marked and interesting concentration of post larval croakers was found to take place during the height of the spawning season in November, 1926, in the angle of the rock jetty at Aransas Pass lying on the north side of the pass. Thousands of young congregated along the Gulf beach in the immediate corner of the jetty, while in the opposite angle, formed by the south jetty, few, if any, young

ever were obtained. This concentration was most noticeable during flood or incoming tide, while the ebb tide had the effect of taking the young fish offshore.

While no definite reason for this curious fact was ascertained, it is believed by the writer (in the light of later observations made on the young spots, as well as observations at the time) that this concentration of young on the north side of the pass only was induced by the heavy northerly winds, which caused a more violent surf along the north beach shore than on the protected south side of the pass. This surf probably caused the young to be thrown farther inshore and out of range of the pass inlet, which lies about 1 mile offshore in the case of Aransas Pass. The incoming tide probably would be felt for some distance around the mouth of the pass and would tend to take in all fish within range of its influence. With the surf, plus the movement of water inshore, being particularly strong along the north side of the pass, many young could not get into the current coming in through the pass perhaps and consequently were caused to drift inshore by the angle of the jetty, where they had to remain until the next outgoing tide, which would carry them offshore and nearer the entrance to the pass.

The capture of larval and post larval croakers from October to February (Table 27) indicates that the spawning season extends over a considerable period of time. The great abundance of fish in November, 1926, however, would place the height of the spawning in this month. Welsh and Breder (1923, p. 180) stated that the spawning season of the species is a long one, extending from August to December and possibly later in southern waters. Hildebrand and Schroeder (1928, p. 284) believe that the early part of November is the principal spawning period in Chesapeake Bay, which estimate agrees with the observations made along the Texas coast by the writer.

GROWTH AND AGE

The growth of the croaker during the first two years of life was determined on the basis of the length-frequency distribution of 3,378 fish collected during the course of the investigation. Following a smoothed length distribution of monthly collections, by means of Figure 37, the first period in April, 1926, gave two distinct groups of fish with modal lengths at 9 and 17 centimeters (3.5 and 6.7 inches). The collections made during May brought these modes up to 11 and 18 centimeters (4.3 and 7.1 inches), with considerable overlapping between these two groups of fish (probably of the first and second year classes.) During July, small numbers of fish of the older year classes appeared in the catches, with faint modes at around 21 and 25 centimeters (8.2 and 9.8 inches). These two larger modes probably represented the third and the fourth year classes. Serious overlapping of size groups during August and September throws little light on the growth of any particular year class. During October, a newly spawned year class of fish entered the catch, with a mode around 1 centimeter; while the third year class was represented strongly by a mode at 22 centimeters (8.6 inches). In the winter months of November, December, and January only fish of the new or O year class were taken, owing largely to the fact that all fish above the second year class had gone to the Gulf of Mexico the previous fall

for spawning purposes. During March, 1927, the second year class, spawned in the late fall of 1925, again appeared, possessing a modal length at about 14 centimeters (5.5 inches), and this class became very abundant during the following spring months.

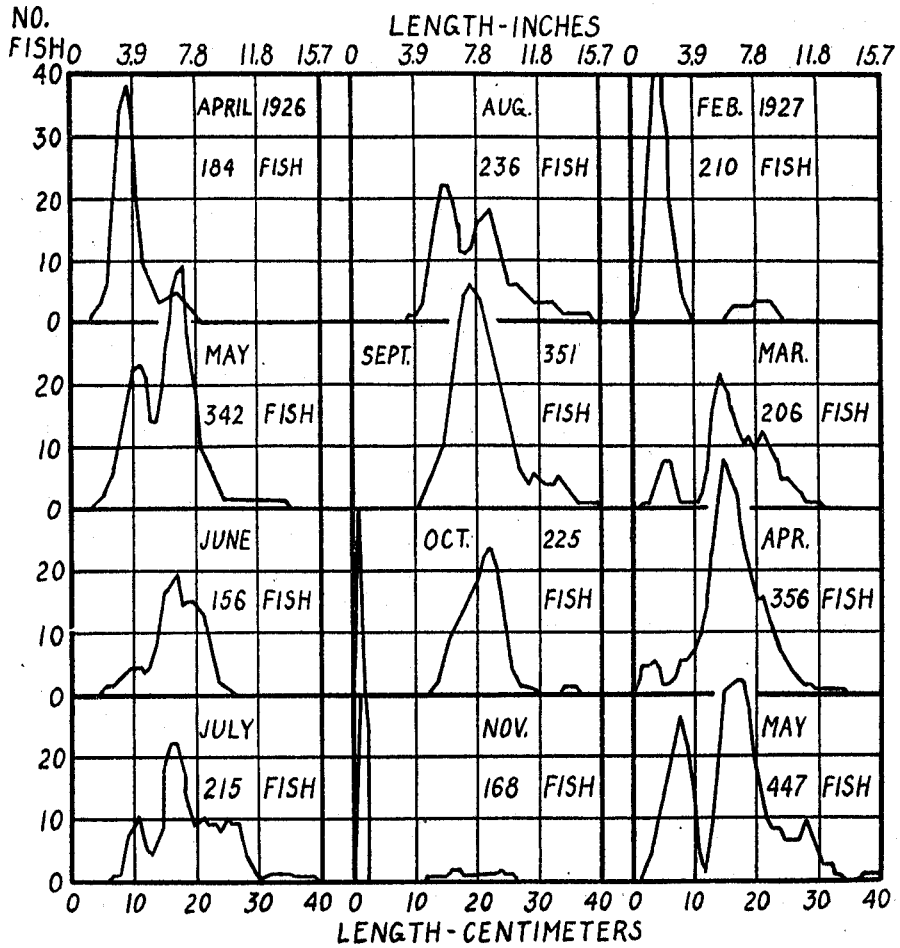

FIG. 37.—Length-frequency distribution of croakers in Texas, 1926–27. Actual frequencies have been smoothed by a moving average of threes

The third year class, with a mode at 22 centimeters in October, 1926, grew little during the winter but apparently attained a length of about 24 centimeters (9.4 inches) by the end of May, 1927. (See table 28.)

TABLE 28.—*Length-frequency distribution of croakers (Micropogon undulatus) taken in Texas, April, 1926, to May, 1927*

Centimeters	1926									1927				
	April	May	June	July	August	September	October	November	December	January	February	March	April	May
1							50	100	50	5	1			
2								50	50	50	7		2	
3									50	50	49	1	12	1
4										6	52	3	4	11
5	5	4								2	35	12	1	16
6	3	3									15	8	1	12
7	16	3	2								10	3	4	28
8	39	13	2	1							8	1	4	25
9	50	20	2	2							1		9	27
10	25	17	5	17	1							1	5	12
11	12	29	4	8	2								8	3
12	9	23	2	4	6	4						3	16	
13	3	15	3	2	15	10		2				16	18	3
14	3	5	9	5	25	3	1	2				27	37	31
15	3	23	15	14	26	10	5			2	3	22	38	33
16	5	36	26	26	16	22	14	3		5	3	12	38	28
17	5	45	10	25	12	32	11	2		10	2	13	30	35
18	5	32	20	16	9	41	12	1		2	3	15	27	36
19	1	29	11	6	13	34	20	1			4	6	14	29
20		12	14	11	15	33	15				3	14	20	24
21		10	16	10	19	37	23	1			5	10	15	14
22		9	9	10	16	23	29	1			5	14	14	8
23		6	4	7	19	19	19	2			1	6	9	7
24			2	10	4	20	14	1			2	4	7	11
25		3		8	6	14	7	2			1	6	7	8
26		1		13	7	8	2					6	4	3
27		1		7	4	3						1	2	9
28				7	4	4	1					1	2	10
29					4	6	1						2	10
30		2			2	7						1	1	3
31				1	2	3							1	5
32				1	4	3							1	
33		1			3	5							2	3
34				2		6							1	
35				1	1	1	1							
36						1								
37					1	1								
38				1										1
39						1								1
Total	184	342	156	215	236	351	225	168	150	132	210	206	356	447

In the last month (May, 1927), during which 447 croakers were measured, the first 4 year classes were present, with all classes save the third marked by distinct modes. At 8, 18, 24, and 28 centimeters (3.1, 7.1, 9.4, and 11 inches), these modes correspond well with the size and age estimates of Welsh and Breder for Atlantic coast croakers, in which they approximate the length attained for the first four winters at 4, 15, 22, and 27 centimeters. A few months of spring growth probably would have brought the Atlantic fish to about the size shown by croakers collected in May, 1926, along the coast of Texas. Length frequencies of 243 croakers taken in Pamlico Sound, N. C., during June, 1925, showed clear modes at 18 and 24 centimeters (Higgins and Pearson, 1927, p. 45), which are identical with the modal lengths of Texas croakers taken in May, 1927.

SIZE AND AGE AT MATURITY

The first collection of croakers with well developed roe and evidently preparing to spawn was taken on September 28, 1926, in Laguna Madre near Corpus Christi Pass, while the last sample of ripe or nearly ripe fish was secured about a month later in the same general locality.

Table 29, giving the length distribution of 230 matured croakers, shows a range in length from 14 to 37 centimeters (5.5 to 14.5 inches) and a modal length for the entire group of 22 centimeters (8.6 inches). This mode corresponds with the actual length-frequency mode for fish caught in October, 1926, and judged to be at the end

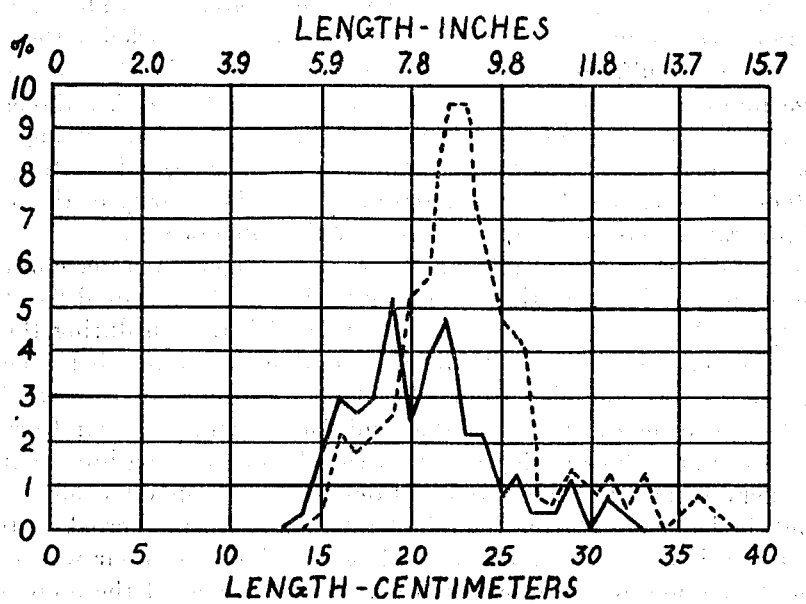

FIG. 38.—Size at maturity of the croaker. Males represented in percentage of total number of fish, by solid line; females, by dotted line. Fish taken at Corpus Christi Pass, Tex., October–November, 1926

of their second year. It appears, therefore, that sexual maturity must be reached and spawning takes place for the first time at the end of the second year of life.

TABLE 29.—*Size at maturity of the croaker (Micropogon undulatus) in Texas, September 28 to October 29, 1926*

Length in centimeters	Males	Females	Total	Length in centimeters	Males	Females	Total
14	1		1	27	1	2	3
15	4	1	5	28	1	1	2
16	7	5	12	29	3	3	6
17	6	4	10	30		2	2
18	7	5	12	31	2	3	5
19	12	6	18	32	1	1	2
20	5	12	17	33		3	3
21	9	13	22	34			
22	11	22	33	35		1	1
23	5	22	27	36		2	2
24	5	15	20	37		1	1
25	2	11	13				
26	3	10	13	Total	85	145	230

Welsh and Breder (1923, p. 183) stated that maturity is reached at the age of 3 or 4 years in the case of the Atlantic-coast fish, but did not explain whether spawning took place at the beginning or at the end of the third or fourth year. Hildebrand and Schroeder (1928, p. 284) estimated the roe of a female croaker, 39 centimeters long (15.3 inches), taken in October, 1921, in Chesapeake Bay, to contain approximately 180,000 eggs of uniform development.

SEASONAL DISTRIBUTION AND MOVEMENTS

After entering the bays and lagoons the young croakers, voluntarily and otherwise, are distributed throughout most of the inland waters. So abundant are they and so hardy are the young that hardly a locality seined or trawled, either within the bays or in the open Gulf, failed to yield large catches. Unlike the redfish and black drum, large numbers of the young croakers remain in the Gulf, although shallow, muddy, brackish-water lagoons and bays hold thousands of the young fish. The young croaker when a year old on the approach of their second winter go into the deeper waters of the bays and Gulf in large numbers, where many of them are caught in the shrimp trawls that operate extensively at this time of year.

By the end of the second year a marked reduction has taken place in the natural abundance of the species. At this time a migration of the matured fish takes place from the bays and lagoons to the Gulf, where the fish remain during the spawning season and the following winter, to return again in small numbers the following spring. Table 29 was compiled from miscellaneous catches of ripe croakers taken from schools of fish on their way to the Gulf for spawning. Near Corpus Christi Pass is situated a large hole or depression in the channel leading into Laguna Madre proper (Packery Channel), which at low tides is almost cut off from the waters of the pass and the lagoon. During the fall of 1925 many ripening croakers temporarily congregated in this hole on coming out of Laguna Madre on their way to the Gulf. Fishing the depression at low tide would give large catches of these croakers, while fishing after the following high tide would reveal that most of them had departed through the pass into the Gulf.

The causes for the probable great mortality after the first and second years of life are unknown, but it is known that the fish seldom reach a desirable market size in Texas waters. It may be that most of the croakers die after spawning, which would explain the sudden decrease in abundance after the second winter. The following quotations from Hubbs (1926, p. 59) may indicate some points to be considered in explaining the smaller size of Texas croakers as compared with fish that dwell farther north.

> The general growth inhibitions often are associated with the ripening of gonads, the attainment of maturity being marked by a cessation of growth in warm-blooded animals, and usually by a sharp decline in the growth rate in the case of fishes and other animals exhibiting indeterminate growth. Accelerating conditions hasten the inception of maturity and the associated decline in growth rate * * * the abrupt and extensive retardation of growth under accelerating conditions of development explains the general observation that fishes of cold or saline waters usually attain a larger size than do individuals or races of the same species inhabiting warm or brackish water, or both.

FOOD HABITS

Of 60 Texas croakers 21 to 35 centimeters (8.2 to 13.7 inches) long, 55 per cent had eaten shrimp; 13 per cent, annelids; 12 per cent, fish; 5 per cent, crabs; 5 per cent, mollusks; and 10 per cent had a mixed diet. Of 19 fish 14 to 20 centimeters (5.5 to 7.8 inches) long, 21 per cent had eaten shrimp; 63 per cent, annelids; 5 per cent, fish; and 11 per cent had a mixed diet. The smaller fish had eaten mainly annelids, particularly polychæt worms, but no crabs or mollusks. Small bottom-dwelling fish, such as gobies and even small croakers, also were found to be the food of some of the fish. Hildebrand and Schroeder (1928, p. 284) stated that the food of croakers in Chesapeake Bay, as shown by 392 stomachs, consists of crustaceans, annelids, mollusks, ascidians, and fish.

COMMERCIAL CONSIDERATIONS

While the croaker is one of the most abundant and valued food fishes of the Middle and South Atlantic States (the average annual catch is about 25,000,000 pounds), the species is hardly represented in the commercial catch in Texas waters. Along the more northern part of the coast a few thousand pounds of small fish are marketed annually, but they are very inferior in size, usually averaging about 22 centimeters in length (8.6 inches) and 3.7 ounces in weight. The lack of any considerable number of croakers above 25 centimeters (9.8 inches) in Texas waters would seem to indicate that the species can never become a leading source of fish supply, in spite of intensive fishing effort. However, the smaller fish, which are marketed to some extent at present, provide a cheap grade of food for those who can not afford the higher prices demanded for the more popular redfish, spotted trout, and Spanish mackerel, and should be utilized whenever possible.

SUMMARY

1. The croaker spawns along the Texas coast from October to February; the height of the season is in November.
2. Spawning takes place in the Gulf of Mexico, and the young fish enter the intercoastal waters or remain along the Gulf beaches in the vicinity of the passes.
3. A total length of about 15 centimeters (6 inches) is reached by the end of the first year, while about 22 centimeters (8.6 inches) is attained by the end of the second year.
4. Maturity is attained at the end of the second year, and few fish appear to live after the first spawning.
5. The croaker is marketed only in small quantities, owing to its inferior size and lack of popularity.

NATURAL HISTORY OF THE SPOT, LEIOSTOMUS XANTHURUS (LACÉPÈDE)

SPOT; FLAT CROAKER; LAFAYETTE

Leiostomus xanthurus Lacépède, Hist. Nat. Poiss., IV, 1803, p. 439; Jordan and Evermann, 1896–1900, p. 1458, Pl. CCXXIII, fig 569; Welsh and Breder, 1923, p. 177; Hildebrand and Schroeder, 1928, p. 271.

DESCRIPTION OF ADULT

The adult spot may be distinguished from other closely related species by its comparatively short compressed body, elevated back, short head, blunt snout, and small horizontal mouth. The color above is bluish gray with golden refections; silvery beneath; the sides have from 12 to 15 oblique yellowish (dusky in preserved specimens) bars in fish above 50 millimeters (2 inches). A large yellowish black spot is found on the shoulder, and the fins generally are pale. (See fig. 42.)

DESCRIPTION OF YOUNG

Young fish, 7 to 15 millimeters long, generally are more slender than the adults and usually are lacking in pronounced pigmentation, which distinguishes them from related species. A specimen measuring 7 millimeters had the larval fin fold extending from the vent to the anal fin, as well as both dorsally and ventrally along the caudal peduncle. The presence of 12 anal rays and the lack of pigmentation on the body separate the fish from other sciænoids. A truncate caudal fin also is a character that serves to distinguish the species in its young stages. (See figs. 39 and 40.) Young spots 20 to 50 millimeters (0.8 to 2 inches) long are quite pale, with the sides of the head silvery and the sides of the body and back with a row of dark blotches composed of dusky punctulations. (See fig. 41.)

SPAWNING AND EARLY DISTRIBUTION OF YOUNG

Along the Texas coast the spot spawns in the Gulf of Mexico in close proximity to the mouths of the passes that lead into the intercoastal waters. The spawning season is extended from late December until the last of March, but the height of the period is reached during January and February. The larval and post larval fish enter the bays and lagoon in great numbers and become distributed over a large extent of territory in a manner comparable to that of the croaker.

The first collection of larval and post larval fish that resulted from the spawning season of 1926–27 was secured on December 23, 1926, in the Gulf of Mexico outside of Aransas Pass by means of a small seine that was swept along the shore north of the rock jetties. A few weeks previous this locality yielded large numbers of larval and post larval croakers, and it was soon learned that the young spots could be taken in the same localities where the croakers were a short time before. The newly hatched spots were extremely abundant around both Aransas and Corpus Christi Passes throughout January and February, and the young spread rapidly throughout all the bays and lagoons. (See Table 30.)

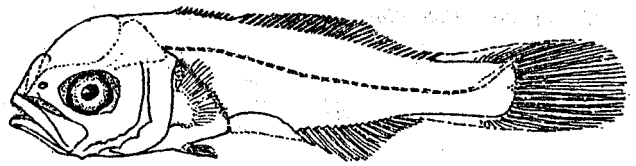

FIG. 39.—Young spot. Actual length, 10.5 millimeters

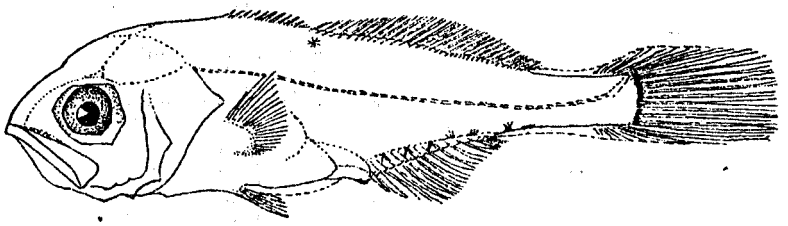

FIG. 40.—Young spot. Actual length, 13.5 millimeters

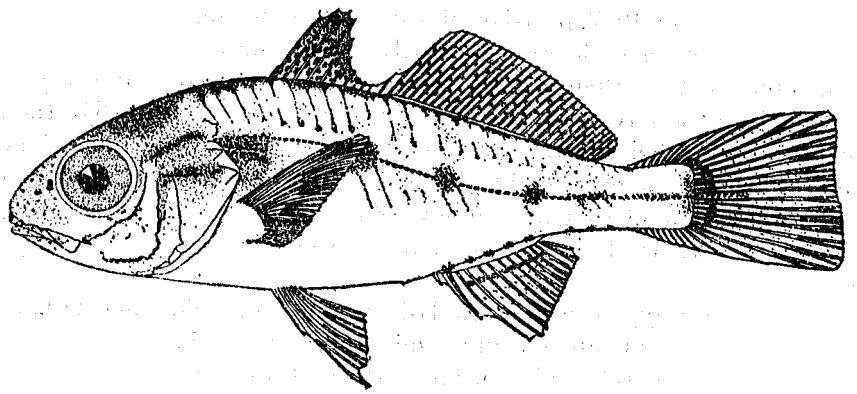

FIG. 41.—Young spot. Actual length, 2.9 centimeters

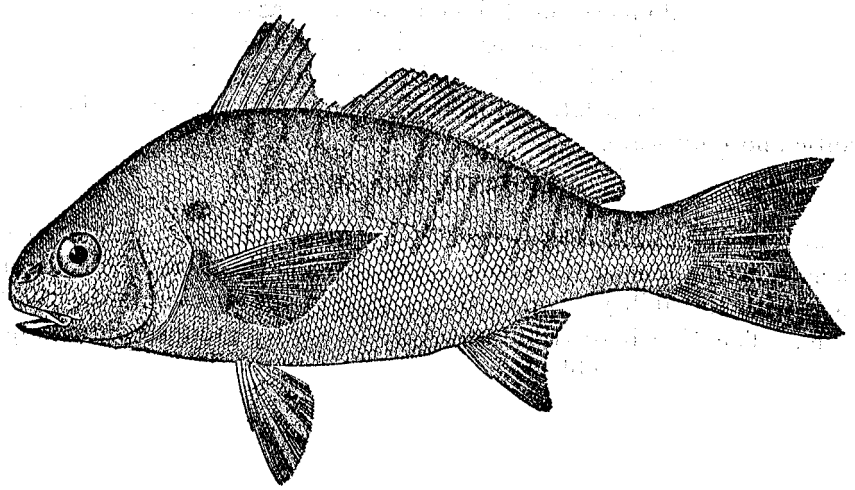

FIG. 42.—Adult spot. Actual length, 16.4 centimeters

TABLE 30.—*Collections of young spots taken in Texas*

Date	Number of fish	Length range, in millimeters	Locality
Feb. 4, 1926	15	11–17	Shamrock Cove.
Mar. 31, 1926	10	13–17	Laguna Madre.
	2	13	Aransas Pass.
Dec. 23, 1926	200	12–15	Aransas Pass-Gulf.
Jan. 4, 1927	14	7–14	Harbor Island.
Jan. 17, 1927	2	18–19	Corpus Christi Bay.
Jan. 20, 1927	160	10–33	Harbor Island.
Jan. 21, 1927	4	11–18	Copano Bay.
Jan. 27, 1927	500	12–22	Corpus Christi Pass.
Feb. 3, 1927	40	9–14	Aransas Pass-Gulf.
Feb. 21, 1927	16	14–29	Oso Bay.
Feb. 28, 1927	500	9–18	Harbor Island.
Mar. 23, 1927	15	11–17	Corpus Christi Pass.
Mar. 24, 1927	3	12–15	Aransas Pass-Gulf.
Mar. 30, 1927	12	12–22	Corpus Christi Pass.

As late as March 30, 1927, post-larval fish were secured on their way into the bays, although the numbers had decreased greatly. The surge of young into the bays made it possible to trace them easily. Observations showed that the young spots not only came into the bays with the incoming tidal currents, but, like the croakers, they sought to gain their way through the passes against the tide. The schools of post-larval fish invariably sought the side of the pass where the velocity of the current was weakest, and a small minnow seine hauled at advantageous points at times secured thousands of the young that were attempting to gain the shelter of the bays.

In Chesapeake Bay, according to Hildebrand and Schroeder (1928, p. 274), "spawning takes place in late autumn and probably in winter and apparently at sea, for in the fall a general exodus of large fish with maturing roe takes place from the bay, the height of this migration occurring during late September and throughout October." This fall migration of ripening adults was observed in Texas, although it was not so pronounced as it appears to be along the Atlantic coast, where the center of abundance is located. Welsh and Breder (1923, p. 177) stated that spawning time for the species is in late fall or early winter and appears to be the same in both Atlantic and Gulf waters.

GROWTH AND AGE

With an extended spawning period, it might be expected that a considerable range in length occurs among the young spots. While this is true in general, it does not interfere with the ability to trace the growth of the species during the first two years of life. The length distribution of 3,471 spots, grouped into approximate 4-week periods, is given in Table 31.

TABLE 31.—*Length-frequency distribution of the spot (Leiostomus xanthurus) taken in Texas from March, 1926, to May, 1927*

Length, centimeters	Mar. 28–Apr. 25	May 2–23	May 30–June 27	July 4–Aug. 8	Aug. 15–Sept. 5	Sept. 12–Oct. 3	Oct. 10–31	Nov. 7–Jan. 9	Jan. 16–Feb. 13	Feb. 20–Mar. 13	Mar. 20–Apr. 10	Apr. 17–May 22
1	4							250	172	48	5	
2	6							30	263	23	15	
3									66	7	22	
4	10	1							77	50	14	
5	36	8							18	12	19	5
6	84	25									27	21
7	53	49	11								35	50
8	28	46	15	1							10	26
9	5	39	6	5							1	20
10		20	5	9								3
11		7	5	10	2	2	2					3
12	1	1	8	9	24	17	27				6	1
13		1	30	10	31	40	39	1	7	1	22	
14	4		26	3	46	40	28		8	3	16	2
15	3	2	9	6	38	12	15	1	8	5	22	13
16	5	1	17	5	18	11	9	3	9	8	25	4
17	17	5	16	24	25	11	6	2	7	6	19	14
18	17	6	6	21	32	25	19	1	5	10	21	22
19	21	5	13	20	49	39	21	1	11	9	22	21
20	25	9	9	18	42	31	13		7	9	4	10
21	9	9	12	6	33	14	7	4	1	5		9
22	3	4	7	8	17	17	5		2	3		3
23	3	1	3	1	8	13	6	2				1
24	1			1		7						1
25	1				4	1	1	1				1
26						1	1					
27					1							
Total	336	239	198	157	370	281	199	296	661	199	305	230

Following Figure 43 (a smoothed frequency graph secured from the data in Table 30), the first period of collection through the weeks of March 28 to April 25, 1926, showed the presence of the first two year classes having modal length at 6 and 19 centimeters (2.3 and 7.4 inches). The youngest or O class grew rapidly during the following summer, reaching a modal length of 13 centimeters (5.1 inches) by October 10 to 31, 1926. Growth of this class during the winter of 1926–27 was not great, but by the end of May, 1927, a modal length of 18 centimeters (7.1 inches) was attained.

The I class, represented by a modal length of 19 centimeters (7.4 inches) in April, 1926, showed very little growth during 1926. At the end of its second year (November to December, 1926) this I class apparently migrated from the bays to the Gulf of Mexico for spawning purposes and did not return to the bays in the spring in any considerable numbers.

The month of December, 1926 (see table 34), brought a new year class of spots into existence. The modal length attained by this youngest or O class by April 17 to May 22, 1927, was about 7 to 8 centimeters (2.7 to 3.1 inches), with a length distribution ranging from 4 to 12 centimeters (1.5 to 4.7 inches). The modal length reached during the period from March 20 to April 10, 1927 (6 centimeters), by this O class was identical with the modal length observed for the O class from March 28 to April 25, 1926.

During the early part of 1926 two distinct modes usually served to distinguish the first two year classes, but after May, 1926, a considerable overlapping between the first and the second year classes resulted, probably owing to the greater rate of

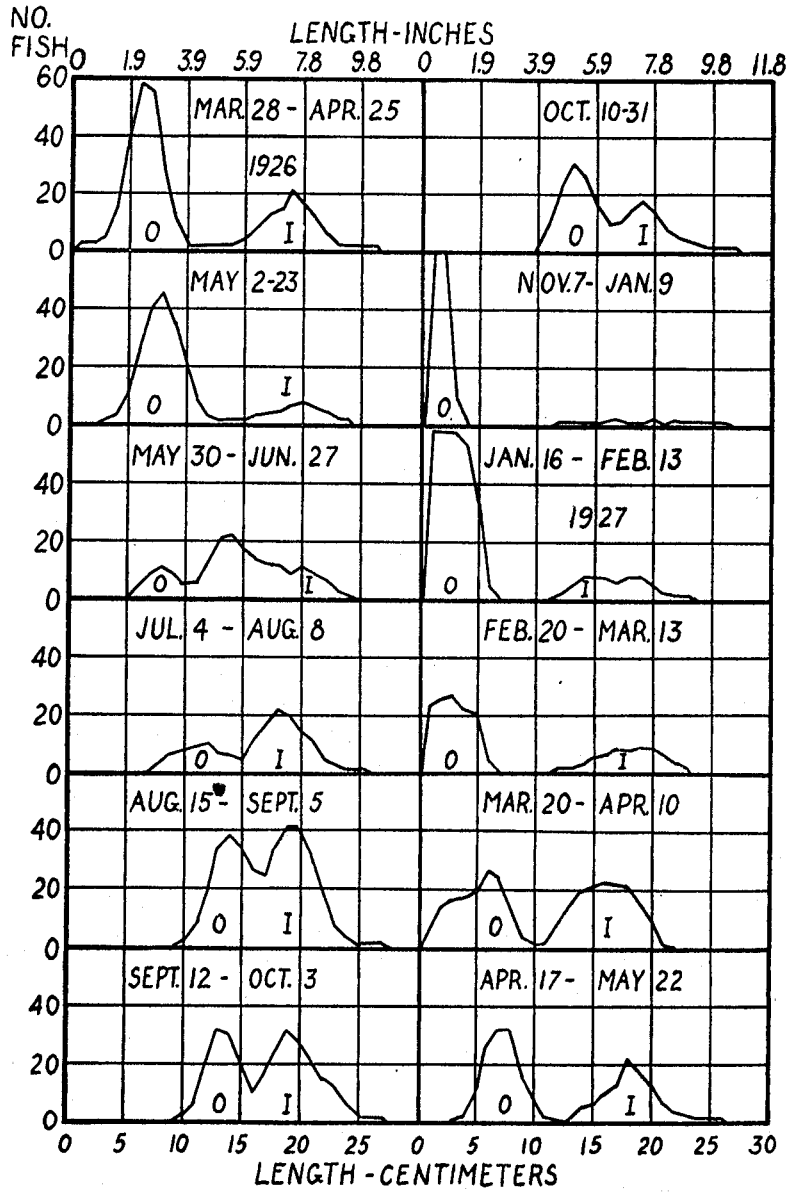

FIG. 43.—Length-frequency distribution of spots in Texas, 1926–27. Actual frequencies have been smoothed by a moving average of threes. Roman numerals indicate year classes

growth of the youngest or O class and the reduced rate of growth of the second or I class. An unusual feature in the length frequencies is the presence in the catch from May 30 to June 27, 1926, of an unusually large number of spots at 13 to 14 centi-

meters (5.1 to 5.5 inches) when the true modes for the two classes would appear, from other collections, to be at 8 and 19 centimeters (3.1 and 7.4 inches). It is assumed that the fish making up this 13 to 14 centimeter mode were composed of rapidly growing fish of the O class or unusually small fish of the I class, or both.

Hildebrand and Schroeder (1928, p. 274) estimated that the spot in Chesapeake Bay attained a length of about 13 centimeters (5.1 inches) at 1 year of age. This is but slightly less than the size reached by the Texas spots, which is about 13 to 14 centimeters (5.1 to 5.5 inches) by the end of the first year and 19 to 21 centimeters (7.4 to 8.2 inches) by the end of the second year. The maximum length attained by the spot is recorded for Chesapeake Bay fish by Hildebrand and Schroeder (1928, p. 276) at about 34 centimeters (13.4 inches). Welsh and Breder (1923, p. 179) stated that fish from 26 to 28 centimeters long, and probably in their third year, were taken abundantly at Atlantic City, N. J., in the summer of 1920. Collections of Texas spots revealed but 3 fish out of 3,471 that were over 25 centimeters (9.8 inches) in length. It must be concluded, therefore, that few fish reach an age of over 2 years in Texas coastal waters.

SIZE AND AGE AT MATURITY

With few Texas spots reaching an age of over 2 years, it seems probable that most of the annual spawning must be done at the end of the second year. Small numbers of ripening adult spots were taken in early December, 1926, near the Passes, and the length distributions of these fish indicated that they belonged to the I class at the approach of the end of the second year. The lengths of the fish ranged from 17 to 21 centimeters (6.7 to 8.2 inches). The migration of the spawning fish out of the bays prevented the taking of large collections of adults.

SEASONAL DISTRIBUTION AND MOVEMENTS

During its first year the spot is extremely abundant in all of the intercoastal waters, as well as in the Gulf of Mexico in the vicinity of the Passes. After entering the bays the larval and young fish tend to remain in the shallower lagoons and coves until the coming of cold weather (the winter following hatching), when many fish move into the deeper waters of the bays and Gulf. Trawls operated in the deeper waters of the bays secure many spots in winter and spring. The young spots, like the young croakers, do not all come into the bays, for many are secured around the Passes throughout most of the year.

A great decrease in natural abundance occurs between the first and second years and particularly at the end of the second year. Along the Atlantic coast the spot has long been known to make a spawning migration in the fall of the year, evidently going out into the deeper waters of the ocean to spawn and for winter protection. This spawning migration takes place along the Texas coast, likewise, and with the general exodus of the 2-year-olds from the bays they disappear forever, for the most part into the Gulf of Mexico.

Hildebrand and Schroeder (1928, p. 274) noticed that spots are very thin and poor in Chesapeake Bay in the spring of the year, indicating that much energy has been spent in the process of reproduction. It may be safe to state that the majority of the spawning 2-year-old Texas spots fail to survive after the first spawning.

FOOD HABITS

No examination was made on the food of the Texas spots. Hildebrand and Schroeder (1928, p. 272) recorded the stomach contents of 157 spots from Chesapeake Bay as consisting mainly of small minute crustaceans and annelids, together with smaller amounts of small mollusks, fish, and vegetable débris. Welsh and Breder (1923, p. 179) mentioned that Florida spots had principally small crustaceans, such as amphipods and ostracods, in their stomachs.

COMMERCIAL CONSIDERATIONS

The spot is not marketed along the coast of Texas to any great extent for the chief reason that few fish of suitable market size are taken in the nets of the fishermen. Occasionally a few fish about 25 centimeters long (9.8 inches) are marketed with mixed catches of fish, but from Corpus Christi to the Rio Grande the species is

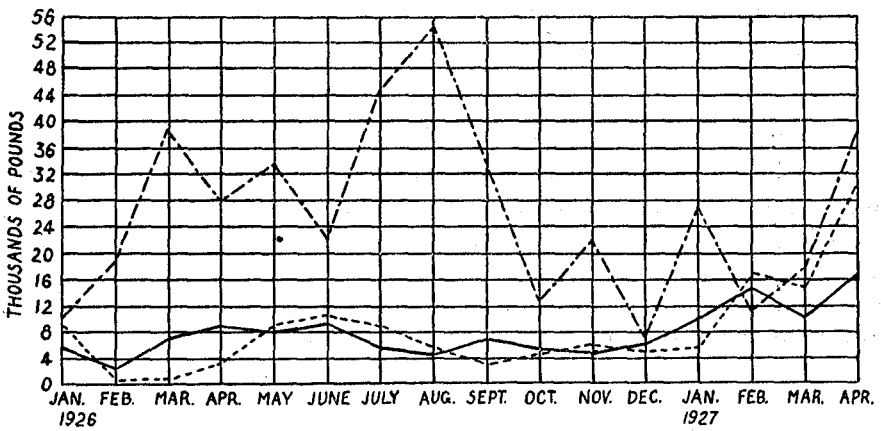

FIG. 44.—Monthly receipts of market redfish (solid line), spotted trout (dotted line), and black drum (dot and dash line) landed at Corpus Christi, Tex., from January, 1926, to April, 1927. Includes only the receipts of the three leading fish dealers

virtually unknown in the market. With the spot, as with the croaker, it would seem that the species does not attain sufficient size to be considered of much value, although it is somewhat of value as a food for other fishes, such as the spotted trout.

SUMMARY

1. The spot spawns in the Gulf of Mexico at the mouths of the passes, and the young come into the bays in great numbers.

2. A length of about 14 centimeters (5.5 inches) is attained by the end of the first year and about 21 centimeters (8.2 inches) by the end of the second year.

3. Spawning occurs at the end of their second year, and after the first spawning most of the 2-year-old fish apparently perish.

4. The species does not attain sufficient size along the coast of Texas for it to be considered a market fish.

SUMMARY OF RECOMMENDATIONS

While certain definite recommendations as to conservation and development of the Texas coastal fisheries have been offered for each species of fish considered in this paper, it seems desirable to present a summarized discussion of them.

At the present time the State of Texas relies upon two major methods of fishery conservation—(1) the imposition of a minimum and maximum legal size limit on certain species of fish and (2) the closing of extensive areas of marine waters to net fishing. The former method, which prohibits the sale or possession of the less valuable redfish under 14 and over 32 inches in length, and the spotted trout under 12 inches, undoubtedly has proved of value both to the fish and to the industry, for it allows the redfish and trout to reach a profitable market size and (in the case of the redfish) protects nearly all of the adult or matured fish.

The black drum never has had the advantage of either a minimum or a maximum size market limit, principally because it has been so abundant in the past and because of its low market value. The day is rapidly approaching, however, when the black-drum stock will be subjected to more intensive fishing than in the past. While several bays that support fish populations consisting largely of drum have been closed to net fishing (Oso and Nueces Bays and Laguna Madre), this protection is offset largely, at the present time, by a fishery operated by a few individuals to capture the large, migrating drum on their way to the spawning grounds. This fishery has been described on page 176. The larger black drum, like the larger redfish, have very little market value but constitute an important element in the annual replenishment of the species. Moreover, many of these larger fish are wasted by the fishery. At the present time sport fishermen and commercial hook-and-line fishermen cast quantities of them upon the beaches to die, and in late winter the local gill-net fishery in Corpus Christi Bay utilizes only the female roes and a small amount of the coarse flesh of the larger fish, which frequently is infested with parasitic worms.

It seems logical, from an economic and biological standpoint, to place a maximum legal size limit on the black drum. This limit should be about 20 inches total length, since few drum larger than this are handled by the more conservative fish dealers, who recognize their general unpopularity and undesirability. As in the case of the redfish, this limit should insure, primarily, a permanent supply of spawning fish. There should be no serious objection to this proposed limit, for it is well known that drum above 20 inches in length are extremely prolific as compared with the younger mature sizes, and that such fish are of slight value to the industry. The further imposition of a minimum legal size limit at 8 inches total length is suggested in order to save the young fish until a time when an adequate market value can be realized.

Along with the imposition of these legal size limits for black drum, it is recommended that Oso and Nueces Bays and Laguna Madre be opened so that the fishing industry may utilize more of the black drum before they attain an undesirably large size. Oso and Nueces Bays yielded fairly large quantities of drum in the past, and the writer believes that if the recommended legal size limits are adopted, commercial seining in these bays can be resumed. The presence in these waters of large areas in which fishing operations can not be conducted (owing to mud bottom, oyster reefs, and débris) will give all the fish a certain amount of protection. While it will cause the fishermen a little trouble to liberate all drum under 8 inches and over

20 inches, it is believed that they would be willing to go to this trouble to secure market catches of the more valuable sizes. Gill nets, or forms of gear that generally cause the quick death of the fish, should be forbidden in both Oso and Nueces Bays and similar waters. Likewise, the opening of Laguna Madre south to and including Baffin and Alazan Bays is recommended. The excessive salinity that occurs at times within the closed section of this lagoon destroys great quantities of fish with no benefit whatsoever to the State of Texas, and better utilization of those fish within the lagoon (mainly black drum) undoubtedly could result from more intensive fishing than is permitted at the present time.

The closing of many inland bays to net fishing has afforded considerable protection to the spotted trout throughout the year. The greater part of the closed territory is considered spawning ground for the trout, although it is known that the closing of such territory throughout the year prevents the taking not only of nonspawning trout but of all other species of fish that come into the closed areas. The assertion has been made (usually by commercial line fishermen, who are allowed to operate in all closed waters) that the bays were closed to net fishing primarily on account of the destructiveness of the drag seines. This view, as stated on page 193, seems to have little foundation, for from extensive tests with commercial seines and from examination of commercial catches the writer found no evidence of serious waste of fish from the use of the drag seines.

The closing of marine waters to the most efficient types of gear brings up the question of whether such a method is the most valuable for properly conserving the spotted trout or whether some better means can be devised, whereby the closed bays may be opened for part of the year. At present large numbers of ripening and ripe trout are captured in open territory by seines and about the passes and in closed waters by hook-and-line fishermen. A closed season during the summer was in effect at one time in Texas, but such a method has the serious disadvantage in a mixed fishery of not only stopping the capture of trout but of all other species of fish as well. The virtual abolition of the entire bay and lagoon fishery during the period of the closed season renders this method decidedly impractical. It is probable that the continued closure of the present closed areas (with the exception of Oso and Nueces Bays, Laguna Madre, and Padre Island Beach) is a better means of conserving the trout, with least harm to the industry as a whole, than any other.

In addition to the continued closure of certain bays, it is urged that the immediate vicinity of all the natural passes, particularly Corpus Christi, be closed to all methods of fishing. It has been pointed out in previous chapters that it is necessary for the redfish, black drum, and spotted trout to use the passes during spawning or seasonal migrations. The passes are the key to the inland waters, and disturbances caused by fishermen and tourists about the smaller, shallower natural passes produce conditions unfavorable to the movement of these fish into or out of the bays and lagoons.

The complete closure of Padre Island beach is believed to be unwarranted, and the opening of this 180-mile stretch of nearly virgin fishing territory to all forms of gear is strongly recommended. Large quantities of food fish of species seldom found elsewhere along the Texas coast occur along this shore line. Robalo or Gulf "pike," pompano, Spanish mackerel, redfish, and spotted trout are found here in considerable numbers. Pound for pound, the most valuable Texas fish, the pompano, occurs in commercial quantities only along the Gulf beaches. Large schools of these fish often

are seen by fishermen along Padre Island, and abundant collections of young made by the writer in 1926 and 1927 near the passes indicate the presence of many adults in the Gulf surf. With the opening of Padre Island, modern surf-fishing gear should be employed by the fishing industry to secure the largest catches of fish. While it is recognized that hordes of sharks and other predaceous fish render fishing here more difficult than in the inland bays, such gear as that used along the coast of Florida certainly would make profitable catches at certain times of the year.

In the above discussion the writer has attempted to present a few recommendations as to practices that he believes will benefit the Texas coastal fishes and fisheries. The proper regulation and development of any fishery, however simple, is a difficult matter, particularly when the many biological and economic factors affecting the fishery change constantly. Some sort of an indicator is necessary to show the trend of abundance of any particular fish stock. Such an indicator is provided in adequate fishery statistics. Should the redfish stock be overfished, this condition would be reflected in the decline of catch per unit of gear, with the result that effort could be made to rehabilitate the stock.

The writer urges the passage of a law requiring the collection of statistical data in Texas, so that the future trends in abundance of the various species of food fishes may be discerned more easily than is possible at the present time. There is no way at present to determine the actual annual catch of any particular species of fish along the Texas coast in any locality, except from statistics collected by the United States Bureau of Fisheries every five years.

For some time several States have successfully operated systems of collecting fishery statistics, which in their general features might be used advantageously by the State of Texas. The most suitable of these consists essentially in securing original records of the daily catch of each species of fish made by each individual fishing boat or unit of gear. Such a record could be collected easily by providing each dealer with manifolding receipt books, in which the landings or original sales of fish should be recorded. A duplicate copy of the receipt should be the property of the State, to be collected and filed for compilation and analysis.

The various facts in the life histories of the redfish, black drum, and spotted trout, as presented in this paper, suggest many new lines for biological investigation of the fisheries. The need for scientific research to determine the exact biological relationship between the Gulf of Mexico and the inland waters, the distribution of fish eggs and young prior to their entrance into the bays and lagoons, and the possibilities in developing a practical method of artificial propagation of the leading marine food fishes offers an abundant field for study. In conclusion, a condensed summary of the above recommendations is given.

1. The establishment of minimum and maximum legal size limits for black drum (the minimum length at 8 inches, the maximum at 20 inches).

2. The opening of Oso and Nueces Bays and Laguna Madre to seine fishing in order to utilize black drum of the more valuable sizes and to prevent the economic waste (in the case of Laguna Madre) of many food fish that now perish as a result of occasional cold weather and excessive salinity.

3. The opening to all forms of fishing gear of Padre Island Beach along the shores of the Gulf of Mexico in order to utilize the large quantity of food fish occurring in this territory.

4. The closing of the immediate vicinity of the smaller natural passes (particularly Corpus Christi Pass) to all methods of fishing, since most of the shore fishes utilize these passes during spawning or seasonal migrations.

5. The adoption of an adequate system of collecting fishery statistics to provide means for learning the trend of abundance of the various species of marine food fishes and to indicate the possible need for modifying existing regulations.

6. The continuing of biological research along the Texas coast to determine the practicability of artificial propagation of the leading food fishes and devising better methods for conserving and utilizing the marine resources of the State.

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EXPERIMENTS IN MARKING YOUNG CHINOOK SALMON ON THE COLUMBIA RIVER, 1916 TO 1927

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INTRODUCTION

As one of the most important means of studying the life histories of salmon, the Bureau of Fisheries, in cooperation with the Oregon Fish Commission, has conducted an extensive series of marking experiments during the past 11 years. In these experiments young, artificially reared salmon were marked by removing certain of the fins and then were liberated in the streams on which the various hatcheries are situated. The experiments that were begun during 1916 and 1917 were described in United States Bureau of Fisheries Economic Circular No. 45. Other experiments have been initiated since then and are described here for the first time.

In this report are presented the data collected up to and including the season of 1927 as the result of marking young chinook salmon. Additional returns are to be expected during the next two or three years from some of the experiments described herein, and a number of experiments have been started from which no returns are yet due.

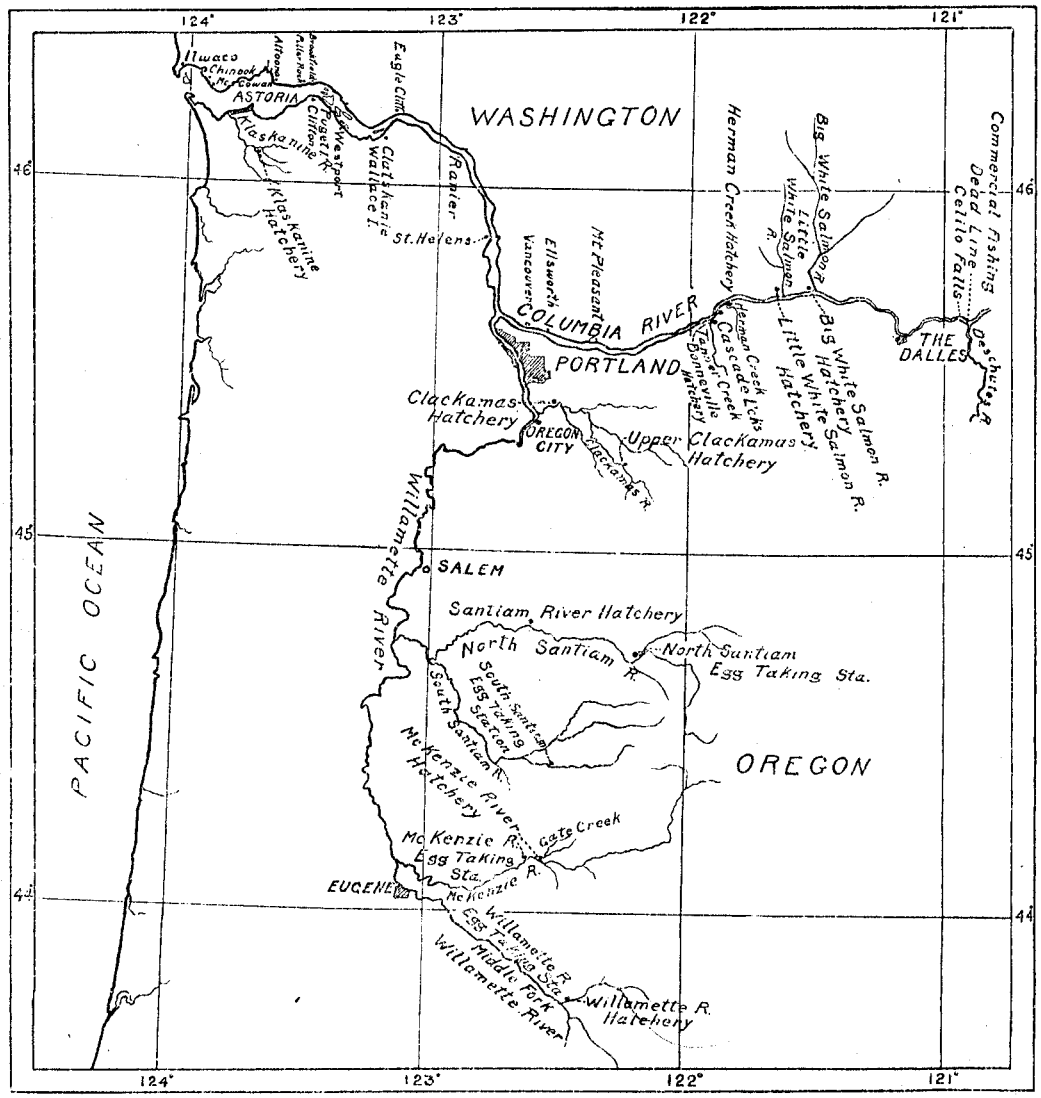

FIG. 1.—A portion of the Columbia River and its tributaries, showing the location of hatcheries and the localities in which marked salmon were recovered

The experiments have been planned with the advice and cooperation of Dr. C. H. Gilbert, Commissioner of Fisheries Henry O'Malley, and R. E. Clanton, formerly director of hatcheries for the State of Oregon, and the success of the work has depended largely upon the aid received from these officials. The actual marking of the young fish was under the direct supervision of the writers, who were assisted ably by numerous hatchery operatives.

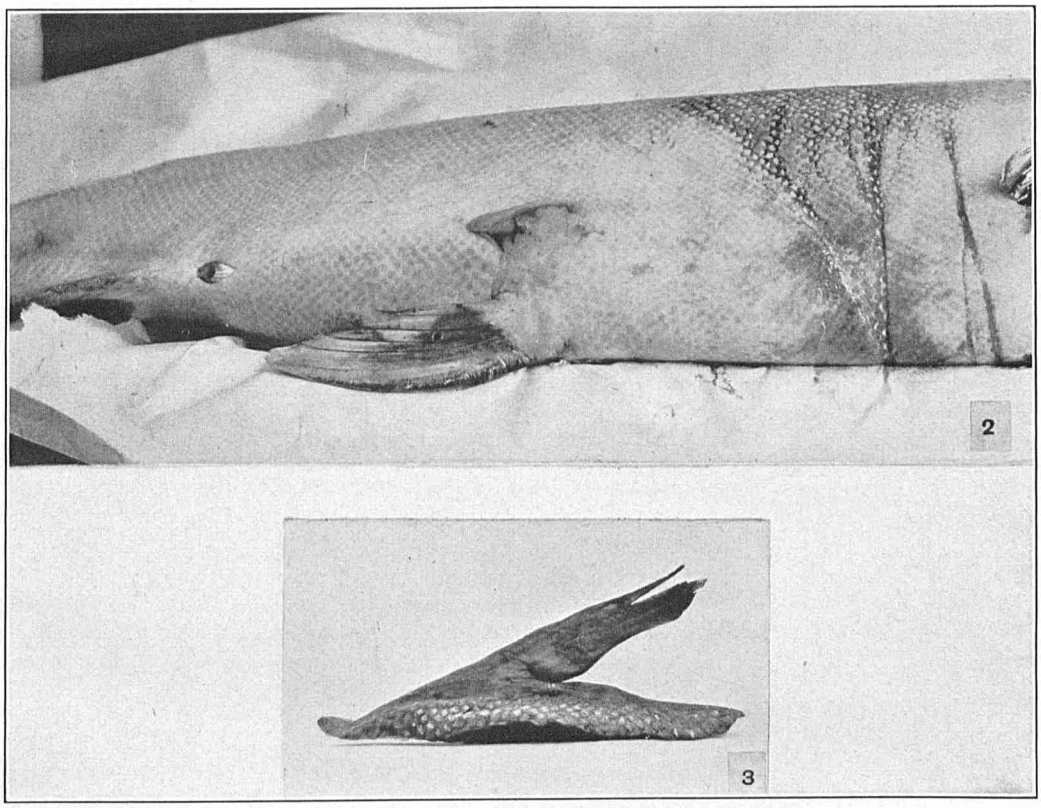

FIG. 2.—Chinook salmon marked by the removal of the adipose fin and the right ventral fin. Illustrating a typical scar resulting from the removal of a ventral fin

FIG. 3.—A typical scar resulting from the removal of the posterior half of the dorsal fin

It had previously been determined that the rayed fins regenerated if not removed very close to the body of the fish, regeneration being most complete when only a part of the distal portion of a fin was removed. When the fins were carefully removed without leaving any stubs of the rays, there was slight regeneration of a soft, fleshy tissue but no indication of regeneration of fin rays. The appearance of the scars on the adult fish recovered gives further evidence of the slight amount of regeneration. In these the point where the removed fins were inserted is typically represented by a slight growth of flat or slightly projecting, soft scar tissue, the surface of which is invariably smooth and bears no scales. In some cases, fin rays have partly regenerated, but even in extreme cases the regenerated stub consists of only three or four rays less than one third the length of those of a normal fin. A typical scar resulting from the removal of one ventral fin is shown in Figure 2. The appearance of the dorsal fin when the posterior half has been removed, as in experiment No. 4, is shown in Figure 3.

In order to test the immediate effects of the marking some of the marked fish in each case and as a matter of routine were retained in the hatchery until they had recovered fully. It was necessary to take this precaution in order that the percentage of return might not be affected by an unusually high mortality resulting from the operation and the handling incidental to marking. In two instances experiments were begun that had to be abandoned on account of the high mortality. These two, however, presented unusual conditions, for in all other instances there was no serious mortality; in fact, in most cases the fish showed no signs of injury from the operation.

The removal of fins from young salmon as a means of marking them for identification when they return to fresh water to spawn has been practiced for many years. The earlier investigators who employed this method used marks that were duplicated easily in nature or that did not persist throughout the life of the fish. As a result, the reported returns from their experiments seem to have consisted, for the greater part, of fish whose fins had been mutilated accidentally. The conclusions based upon this erroneous evidence have since been shown to be incorrect, and the reliability of this method of marking has been questioned. It therefore seems advisable to point out the causes of error in the earlier experiments and to emphasize the precautions taken in this series of experiments to assure positive identification of the marked fish and thus to prevent similar confusion.

The greatest cause of error in the earlier experiments was the failure of the investigators to realize that salmon occasionally lose one or more of their fins in other ways, and that as a result, if only one fin is removed experimentally, the mark may be duplicated accidentally. For example, Hubbard removed the adipose fin from chinook fingerlings at the Clackamas hatchery in Oregon in 1895.[1] The reported returns from this marking are so greatly opposed to the known facts of the life history and growth of chinook salmon that they are obviously in error, and there can be no question that they included fish not marked by Hubbard. In 1903 Chamberlain marked sockeye salmon at Naha River, Alaska, by removing the two ventral fins.[2] Returns from this marking were reported as late as 1911, when the

[1] For a description of the experiment and returns, see Oregon Fisheries Department (1898 and 1900) and Gilbert (1913).

[2] For a description of the experiment and returns, see Marsh and Cobb (1908, 1909, 1910, and 1911); and Chamberlain and Bower (1913).

fish would have been in their ninth year, an age greater than the maximum attained by sockeye salmon. Chamberlain later observed fish with both ventrals lacking and concluded that they were not of his marking.[3]

Another unsatisfactory mark, which has been used on several occasions on the Columbia River, is the removal of a small piece of the caudal fin. In some cases the tip of the dorsal lobe of the fin was removed, but more frequently a small U-shaped piece was clipped out of the posterior margin of the fin. These marks are unsatisfactory for two reasons: First, because the caudal fin frequently is mutilated in nature; and second, because, as mentioned above, fin rays regenerate rapidly unless they are removed at their base. Supposed marks of this nature are brought to the attention of the authors every season. They have been found on all species of salmon and on the steelhead and cutthroat trout, although no such marks have been applied to any but chinook salmon. The condition observed most frequently is a U or V shaped notch in the posterior margin of the fin. The rays that form the margin of the notch generally are bent and distorted. Occasionally the distortion extends for a considerable distance back into the fin, indicating that the notch was much larger originally and that it was reduced by regeneration. Some of these supposed marks obviously are the results of attacks by seals or sea lions. In some cases this is indicated clearly by tooth marks, which can be traced across the side of the fish and across the caudal fin to the apex of the notch.

By marking two or more widely separated fins in the present series of experiments we believe we have obviated, as nearly as may be, the possiblity of having our marks duplicated by accidental means. The validity of every record of recovery of marked fish has been checked by careful examination of the scars resulting from the removal of the fins. Where there has been any question as to the validity of the marks the records have been excluded. The scars, particularly those resulting from the removal of the ventral fins, have been found to be so uniform and characteristic in appearance as to make it seem almost impossible for them to be produced by other means than amputation with a clean-cutting instrument. It is not hard to conceive that an occasional fish might lose one or more of its fins as the result of attack by enemies, or that among the many thousands of salmon there might be a few that would fail to have the full quota of fins at birth; but it is difficult to imagine how such loss could result in scars that indicate the removal of the fins at their very insertion and leave the surrounding tissue and pelvic bones normal. It is inconceivable, also, that such improbable accidental loss could occur to hundreds of salmon at the same time and in just such a manner as to confound the results of our experiments. Furthermore, the evidence of scale readings entirely corroborates the evidence of our marks—a most unlikely occurrence if the scars were the result of accidental mutilation.

Marsh and Cobb (1908), in discussing the returns from Chamberlain's experiments, describe the "scars" of the two ventral fins as follows: "In most cases there was scarcely a trace of the missing fins, the skin at the site of the base of this pair of fins being overgrown with scales." In no case in the present series of experiments have the scars resulting from the removal of the ventral fins been overgrown with

[3] Chamberlain and Bower, 1913, pp. 29-31.

scales, and the locations of the fins are indicated clearly by an abrupt change in the contour of the body at that point and by a slight growth of scar tissue. Fish lacking the ventral fins and appearing as those described by Marsh and Cobb have been observed by the present authors, but invariably these fish have had all other fins present and normal, indicating that they were not marked fish of this series. Furthermore, the pelvic bones invariably were absent, which would indicate further that the scars were not the result of amputation but probably were caused by abnormal development. During the marking of many hundreds of thousands of young salmon we have observed fish occasionally with one or both ventral fins missing. Possibly one fish in ten thousand will show this abnormality. It has been noted also that the adipose fin is missing in about the same number of fish, but we have never observed a case in which both the adipose and the ventrals were affected. The theoretical probability of finding such a case in nature would be about one in one hundred million, a contingency so remote as to be of no practical importance whatsoever.

During the years that the Columbia River marking experiments have been in progress, Dr. J. O. Snyder, of Stanford University, has conducted a similar but less extensive series of experiments in California.[4] His method of marking and other details of his experiments have been nearly identical with ours, and his results also have been approximately the same. The outstanding features of his results are as follows: Salmon marked on the Klamath River were found in the ocean as far south as Monterey Bay; those marked on the Sacramento River were found in the ocean both north and south of the mouth of that river. Notwithstanding this extensive migration, all returned at maturity to the river system in which they were liberated. The proportion of marked fish recovered was approximately the same as in the Columbia River experiments. The scales of the adult fish have been found to be a correct and reliable record of the age and life history of the fish.

Snyder recently conducted an experiment designated to determine the more minute details of the homing instinct of salmon. Satisfactory returns were obtained from this experiment during the seasons of 1926 and 1927, but the results have not been published.

The collection of data from returning adults has proved difficult. One of the authors or some other representative of the Bureau of Fisheries has spent the greater part of each season in the commercial fishing district searching for marked salmon; however, the one or two persons could observe only a small proportion of the salmon taken from the river, as the fish are divided between about 20 canneries distributed along 200 miles of the river. It has been necessary, therefore, to depend largely upon assistance from fishermen, cannery employees, and hatchery men. Theodore F. Rich and W. H. Spaulding aided materially in this work during the seasons of 1919 and 1920. The greatest assistance was rendered by the Oregon Fish Commission, which since 1920 has paid rewards for records of the recovery of marked fish. During 1920 and 1921 a reward of 50 cents for each record was offered. From that time until about the middle of the season of 1926 the reward was $1, but because of the many records of marked sockeye salmon recovered during 1926 it became necessary to reduce the rewards to 50 cents during the latter half of the season. A reward of 50

[4] See Snyder, 1921, 1922, 1923, and 1924.

cents was paid during the season of 1927. Most of the returns have come as a result of these rewards.

On account of the manner in which the data were collected it is necessary to accept the measurements of the fish with some reservation. In all probability the data as to sex are reliable, but those as to length, weight, and time of capture are less dependable. Measurements of length and weight were made by persons usually untrained, and it is more than likely that instruments for taking accurate measurements were not available to them. It is also possible that the length was measured differently; for example, the rays of the caudal fin may have been included in some measurements and excluded from others.

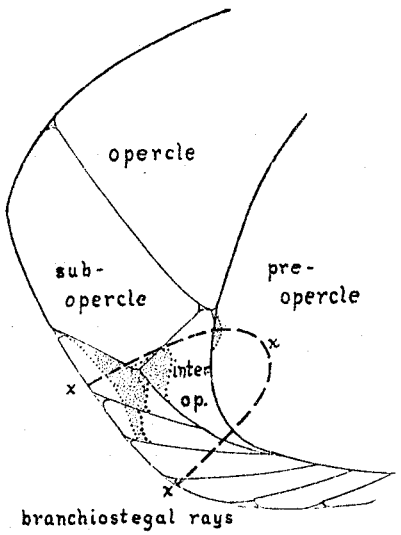

FIG. 4.—Diagram of the gill cover of a salmon, showing extent of injury and regeneration in the case of yearlings marked with a clip in the gill cover at Bonneville hatchery during the spring of 1916. Experiment 1. Broken line, X—X, indicates approximately the original mark as placed on the young fish. The dotted lines indicate the edges of the bones, and the stippled areas the parts filled in with soft tissue on the gill cover of the returned adult fish

These experiments were planned with several purposes in mind. First and foremost they were designed for the very practical purpose of testing the relative efficiency of various procedures in artificial propagation. It is believed that this method of investigation, more than any other, promises information of vital importance in the upbuilding and improvement of current hatchery practices. The experiments also bear upon important problems in the life history of the salmon, such as the home-stream theory both as applied to entire river systems and to the tributaries of a single system, the factors affecting the age at maturity, the time of entering the river, and the hereditary character of the quality of the flesh. And finally, an examination of the scales of marked fish, the history of which is known aids materially in the interpretation of various difficult types of scales frequently encountered in general collections from the regular runs. On this account special attention has been paid to the scales and detailed measurements and ring counts are given in the accounts of the several experiments.

EXPERIMENT NO. 1. BONNEVILLE HATCHERY, FEBRUARY-APRIL, 1916

Eggs from: Willamette River, 1914.
Reared and marked at: Bonneville hatchery.[5]
Mark used: Removal of adipose fin and U-shaped clip in right gill cover.
Number marked: 4,000.
Liberated: In Tanner Creek during February, March, and April, 1916.
Age: Approximately 18 months.[6]

These fish had been reared in the ponds at the hatchery with a much larger number of sockeyes of the same age. It was during the course of the marking of 50,000 of the sockeyes that these few yearling chinooks were marked incidentally. As no special attempt was made to select chinooks, comparatively few were handled.

[5] For location of hatcheries and fishery locations, see fig. 1.

[6] The ages given are counted from the time the eggs were taken and include the period of incubation. This is done on account of the confusion arising in counting the age from the time of hatching, due to the variable length of the incubation period, which is dependent upon temperature.

For the same reason the mark adopted was not the best. It was felt that the clip in the gill cover would not prove satisfactory and that nearly complete regeneration might be expected. The results have shown this to be the case. In order to reduce the possibility of complete regeneration the clip was placed low on the opercle, so as to cut through the branchiostegal rays, the interopercle, and into the preopercle. The line *X——X* on the diagram (fig. 4) indicates the approximate extent of this clip.

A number of specimens were held in a tank at the hatchery for several months and the process of regeneration noted. At the end of about four months the clipped section was regenerated almost completely, so that but a slight indentation of the margin of the gill cover remained. This regenerated tissue seemed to be mainly soft, however, while the bones apparently were regenerated more slowly.

Fifty specimens were preserved for reference during the course of the marking. These average 134.6 millimeters (5.3 inches) in length. The scales show a more or less well-defined growth of the first year, followed by a band of wider rings representing the second year's growth. Figure 5 illustrates a scale showing a well-defined winter band terminating the first year's growth, and Figure 6 a more typical scale in which the boundary between the first and second years is not shown so definitely. The average number of rings in the first year's growth is 15.2 and in the second 6.6. The average length of the anterior radius of the scale is $\frac{46.5}{120}$ millimeter to the end of the first year and $\frac{68.9}{120}$ millimeter to the periphery.[7] The complete data for this collection are given in Table 1.

TABLE 1.—*Chinook-salmon yearlings marked at Bonneville hatchery March 2 and 11, 1916*

Length in millimeters (mid-value of class)	Scale record																								
	Number of rings																								
	First year's growth											Second year's growth													
	11	12	13	14	15	16	17	18	19	20	23	1	2	3	4	5	6	7	8	9	10	11	13	14
105					1										1									
115			2	2	1	(1)		1						1	2	2	1							
125		3	2		2	2	1		2				1	2	2	3	2	1	1					
135			1	3	2	2		1	1		(1)			1	3	2	1	2			1			
145			2	2	2	1		1								1	4				2	1		
150	1		1	1			2													2		1		1
160		1																				1		
175			1		1																	1	1	
195							1	1		1											2			
Total	1	4	9	8	9	6	4	4	3	1	1		1	4	8	8	8	3	2	2	5	4	1	1
Average	15.2											6.6												

[7] In practice the image of the scale, as projected by a camera lucida to the level of the base of the microscope, is measured by means of a millimeter scale. The magnification of this projected image used in making this study is 120 diameters. For the sake of convenience the measurement is given as a fraction, the numerator of which is the measurement of the image and the denominator the magnification used.

TABLE 1.—*Chinook-salmon yearlings marked at Bonneville hatchery March 2 and 11, 1916*—Contd.

Length, in millimeters (mid-value of class)	Scale record																		Males	Females	Total
	Length of anterior radius, in millimeters×120																				
	First year's growth (mid-value of class)							Second year's growth (mid-value of class)													
	32.5	37.5	42.5	47.5	52.5	57.5	62.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	82.5	87.5	97.5	117.5			
105				1					1										1		1
115		1	(4)	1				1		4									4	2	6
125		2	4	5			1		2	4	3	3							7	5	12
135		1	2	3	(2)	3				2	1	3	4						7	4	11
145			3	4	2					1	1	2	3	1	1				7	2	9
150	1		2	1		1							1	1	1	1	1		4	1	5
160			1													1			1		1
175		1	1												2					2	2
195					2		1							1		1		1	3		3
Total	1	5	17	15	6	4	2	1	3	11	5	8	8	3	4	3	1	1	34	16	50
Average	46.5							68.9											[1] 135.2	133.4	134.6

[1] In this and subsequent tables the averages given at the foot of the columns of frequencies represent the average length in millimeters.

NOTE.—Groups in parentheses each contain 1 individual whose scales show no second year's growth.

A slight narrowing of the rings about midway in the first year's growth is apparent in some of the scales. (See fig. 6.) This narrowing or check is comparable to that which the senior author (Rich, 1920) observed in the scales of many seaward migrants and has termed "primary check." In this connection the term "primary" was intended to be descriptive from the standpoint of time, but to some readers it has given the impression of first in the order of importance. In view of this confusion of meaning it seems advisable to discontinue its use and to introduce the more general term "incidental check," to be applied to all checks other than annuli, which represent a winter in the life of the fish. The significance of this check, formed during the first year's residence in fresh water, is not always clear, but it has been shown in some cases to have resulted from some abrupt change in the environmental conditions. (Rich, 1920.)

Only one adult fish has been recovered that unquestionably shows the mark used in this experiment. This fish was a male weighing 48 pounds (21.8 kilograms) and was taken in one of the wheels near The Dalles, Oreg., on May 4, 1920. The adipose fin was entirely lacking and the right opercle showed unmistakably the scar resulting from the clipping. Figure 4 shows the approximate extent of the scar. One other specimen was obtained that probably is of this series. This doubtful specimen was taken on May 28, 1920, near Warrendale, Oreg., and was sent by the finder to the Oregon fish commission. The data, including scars, were forwarded to the writers, together with data from several other marked fish. En route the package was damaged badly, and from this specimen only the scar of the adipose fin remained. It is not known whether the gill cover was included in the original shipment or not.

The scales of these fish are similar and show that they were in their sixth year. The central portions of the scales, the "nuclei" (representing the growth of the first year), are typical of the stream type described by Gilbert (1913) and correspond

closely to the scales of the young fish preserved at the time of marking. Figure 7 shows a scale from the one undoubted marked fish, and Figure 8 shows the nuclear area enlarged. The margins of the scale are rather badly absorbed, and the winter band of the fifth year and the beginning of the sixth year's growth do not show. The width of the outer (fifth) summer band is conclusive evidence, however, that the fish was actually in the sixth year and not in the fifth, as might appear to be the case. In the majority of fish taken at this time of year, whose scales are complete, the new growth of the current year has seldom more than three or four rings. Frequently the marginal rings are those of the preceding winter. The marginal band of summer rings shown on the scales of this fish is virtually as wide as the summer band of the preceding (fourth) year and particularly in view of the fact that serious absorption of the scale had taken place, could not possibly be interpreted as being the new growth of the current year. The remainder of the scale offers no difficulty whatever to interpretation.

EXPERIMENT NO. 2. KLASKANINE HATCHERY, JULY AND AUGUST, 1916

Eggs from: Willamette River, 1915.
Reared and marked at: Klaskanine hatchery.
Mark used: Removal of right ventral fin and anterior half of dorsal fin.
Number marked: 50,000.
Liberated: In Klaskanine River during July and August, 1916.
Age: Approximately 11 months.

A collection of 50 specimens was preserved on July 16, 1916. The average length is 81.8 millimeters (3.2 inches). Their scales vary but slightly in general appearance. In general the rings are strong and well spaced, indicating that a vigorous and uniform growth had been maintained. In this respect these scales resemble closely those of wild fish, although as a rule the scales of hatchery fish show a more irregular growth. An occasional incidental check is found (see fig. 10), and in many the narrower marginal rings indicate that the slower growth of the fall and winter had begun. Figure 9 shows a typical scale. The average number of rings is 9.3, and the average length of the anterior radius is $\frac{36.2}{120}$ millimeters. The detailed data are given in Table 2.

TABLE 2.—*Chinook-salmon fingerlings marked at Klaskanine hatchery July 16, 1916*

Length in millimeters (mid-value of class)	Scale record															Males	Females	Total
	Number of rings						Length of anterior radius in millimeters×120 (mid-value of class)											
	7	8	9	10	11	12	29	31	33	35	37	39	41	43	45			
67.5	1	1	1				1	2								2	1	3
72.5		1		1					1	1						1	1	2
77.5		2	12	4				2	6	6	3	1				9	9	18
82.5		2	4	5	1				2	3	3	3	1			7	5	12
87.5		1	5	2	1			1			4		4			7	2	9
92.5			1		1	1						1	1		1	1	2	3
97.5				2	1							1	1	1		3		3
Total	1	7	23	14	4	1	1	5	9	10	10	6	7	1	1	30	20	50
Average	9.3						36.2									82.6	80.5	81.8

Only one individual with this mark was recovered. This fish was found by a Chinese butcher at one of the canneries in Astoria, who preserved the scars but no other data. The mark is perfectly clear, although it is worthy of note that the posterior half of the dorsal fin had not grown normally. The rays were short, and their tips bent backward as though the resistance of the water had modified the growth as the growth of trees is modified by the prevailing winds. The exact date of capture is not known, but it was some time between May 25 and June 21, 1920.

The scales of the adult fish (fig. 11) show clearly the four complete years of growth and a narrow marginal band of wide "summer" rings, which represent the beginning of the fifth year's growth. Scales from the skin attached to the scars were the only ones available for study, as a sample of scales taken from the central portion of the body was not preserved. While the details of the life history may be as readily obtained from perfect scales taken from unusual regions of the body as from the more typical ones taken from the central portion, they are not as satisfactory for comparative studies. In this case, for instance, it is not as easy to compare the nuclear portion of the adult scale with the scales taken from the young fish preserved at the time of marking. Taking this into consideration, the nuclear portion of the adult scale (fig. 12) does, however, correspond fairly well with the typical scales of the young fish (figs. 9 and 10).

EXPERIMENT NO. 3.—LITTLE WHITE SALMON RIVER HATCHERY, JULY AND AUGUST, 1916

Eggs from: Little White Salmon River, 1915.
Reared and marked at: Little White Salmon River hatchery.
Mark used: Removal of left ventral fin and the posterior half of dorsal fin.
Number marked: 50,000.
Liberated: In Little White Salmon River during July and August, 1916.
Age: Approximately 10 months.

The average length of 50 unselected specimens preserved on July 28, 1916, is 54.4 millimeters (2.1 inches). The scales have an average of 4.8 rings and an average anterior radius of $\frac{20.2}{120}$ millimeters. Table 3 gives in detail the data relative to these fish. Figure 13 shows a typical scale from an individual 60 millimeters in length.

TABLE 3.—*Chinook-salmon fingerlings marked at Little White Salmon River hatchery July 28, 1916*

Length in millimeters (mid-value of class)	Scale record												Males	Females	Total
	Number of rings					Length of anterior radius, in millimeters×120 (midvalue of class)									
	3	4	5	6	7	15	17	19	21	23	25	27			
42.5		1					1						1		1
47.5	3	4	3			1	2	6		1			4	6	10
52.5	2	3	10	2		1	1	6	5	2	1	1	13	4	17
57.5		4	5	5				3	4	4	2	1	7	7	14
62.5			1	5	1					2	4	1	4	3	7
67.5					1						1		1		1
Total	5	12	19	12	2	2	4	15	9	9	8	3	30	20	50
Average	4.8					20.2							54.5	54.2	54.4

Adults developing from these marked fish were found among the spawning fish taken for purposes of artificial propagation in the Little White Salmon River in 1918, 1919, and 1920, when the fish were in their third to fifth years. One 3-year-old, four 4-year-olds, and one 5-year-old were recovered in this way. In addition to those taken in the parent tributary, one was taken in the lower Columbia in 1919 and another was taken by purse seine in the ocean near the mouth of the Columbia in 1920. Table 4 gives the detailed data regarding the adult fish.

TABLE 4.—*Chinook salmon marked at Little White Salmon River hatchery during the summer of 1916, when approximately 10 months old, and recovered during the seasons of 1918, 1919, and 1920*

Date of capture	Place of capture	Sex	Length, in inches	Weight, in pounds	Scale of record			
					Number of rings		Length of anterior radius, in millimeters ×120	
					To first incidental check	Total stream growth	To first incidental check	Total stream growth
1918 [1]	Little White Salmon River hatchery	Male	19.5	9	5	12	16	31
Aug. 25, 1919	Astoria	Female			6	16	23	46
Oct. 3, 1919	Little White Salmon River hatchery	do	33.5		6	16	20	45
1919 [1]	do				7	20	20	52
Do.[1]	do				6	16	21	47
Do.[1]	do				5	18	14.5	41
Aug. 21, 1920	Ocean	Female	39	27	7	15	23	42
Sept. 27, 1920	Little White Salmon River hatchery	do	36.75		7	17	27	60

[1] Date not reported.

The scales of the fish recaptured at the hatchery were absorbed to such an extent that no part of the original margins remained. As there is no criterion by which the amount of absorption may be determined, it is impossible to determine the age from such scales. A scale from the 3-year-old fish recovered at the hatchery is illustrated in Figure 14. The two fish taken before they reached the spawning grounds have complete scales marked by the expected number of summer and winter bands. Scales from these fish (4 and 5 years old, respectively) are shown in Figures 15 and 17.

The nuclei of the scales of these fish present peculiarities that may be discussed more conveniently in connection with the scales of the adult fish in experiment No. 8. The discussion of them therefore will be deferred until the latter have been considered.

EXPERIMENT NO. 4.—BONNEVILLE HATCHERY, SEPTEMBER, 1916

Eggs from: Umpqua River, 1915.
Reared and marked at: Bonneville hatchery.
Mark used: Removal of right ventral fin and posterior half of dorsal fin.
Number marked: 25,000.
Liberated: In Tanner Creek during September, 1916.
Age: Approximately 12 months.

Fifty specimens were preserved on September 13, 1916. These average 67.6 millimeters (2.7 inches) in length. The average number of rings on the scales is 9.2, and the average length of the anterior radius is $\frac{31.8}{120}$ millimeters. (See Table 5.) In

a large proportion of cases the scales are characterized by a distinct narrowing, an incidental check, some five or six rings from the center. A narrowing of the marginal rings is typically present also, indicating the beginning of the slower winter growth. Figure 21 shows a typical scale with a distinct incidental check five rings from the center and the narrower winter rings at the margin. Figure 20 shows a scale from the smallest fish of the collection. This fish was only 47 millimeters (a little less than 2 inches) in length, and the scale shows only five rings, with no indication of either the incidental check or the marginal winter rings.

TABLE 5.—*Chinook-salmon fingerlings marked at Bonneville hatchery September 13, 1916*

Length, in millimeters (mid-value of class)	Scale record																		Males	Females	Total
	Number of rings							Length of anterior radius, in millimeters×120 (mid-value of class)													
	5	7	8	9	10	11	12	23	25	27	29	31	33	35	37	39	41	43			
47.5	1								1										1		1
57.5		1	2					2	1										2	1	3
62.5			5	7	4					3	3	4	4	1	1				8	8	16
67.5			3	5	5				1	1	2	1	2	2	2	2			7	6	13
72.5			1	2	4	1						1	2	2	3				4	4	8
77.5				3	3	2								2	1	3	1	1	5	3	8
82.5							1						1							1	1
Total	1	1	11	17	16	3	1	2	3	4	5	6	9	7	7	5	1	1	27	23	50
Average	9.2							31.8											67.3	67.8	67.6

Thirty-six adult fish from this experiment were reported from the commercial fishery during the season of 1920, when the fish were in their fifth year. Table 6 gives the data regarding these recaptures. The males average 33.8 inches (85.8 centimeters) in length and 22.5 pounds (10.2 kilograms) in weight. The females average 35.3 inches (89.7 centimeters) in length and 20.7 pounds (9.4 kilograms) in weight. One record of 40 pounds in weight, which is obviously in error, has not been considered in the average. No significance can be attached to the lower average length for males than for females, as the average for the former is based on only four specimens and, as previously mentioned, the measurements are subject to considerable error. With reliable data, males usually are found to average greater than females in both length and weight.

TABLE 6.—*Chinook salmon marked at Bonneville hatchery during the fall of 1916, when approximately 12 months old, and recovered during the season of 1920*

Date of capture	Place of capture	Sex	Length, in inches	Weight, in pounds	Scale record: Number of rings: Stream growth	Number of rings: Intermediates	Length of anterior radius, in millimeters×120: Stream growth	Length of anterior radius: Stream growth plus intermediates
May 13	Astoria	Female	40	31	10	9	29	50
May 17	Ilwaco	do	35.4	21.5	11	6	35	52
May 18	Astoria	do		[1] 16 or 21	9	11	23	52
Do	do	do		[1] 16 or 21	8	0	20	0
May 21	do	do	31	[2] 18	12	11	39	65
May 22	Sand Island	Male		[3] 40	9	11	30	70
May 25	Astoria	Female	35.5	20	12	15	36	74
May 28	Warrendale				11	9	33	55
May 31	Altoona	Male	33	23	12	4	35	46
June 1	Sand Island		34.5	17	8	4	24	35
June 3-5	Warrendale	Female	37.25	20	13	6	31	46
Do	do	do	38	21.5	12	9	34	64
Do	do	Male	38	25	10	11	30	60
June 5	Wallace Island	Female	36.25	28	10	8	29	50
Do	Altoona	do	32	21	10	3	35	45
June 7	do	Male	32	23	9	11	31	64
June 11	Sand Island		36.25	30	9	9	29	53
Prior to June 21	Found in canneries at Astoria				6	9	20	44
					8	7	30	45
					15	8	35	55
					10	8	33	54
					15	7	30	48
					19	0	56	0
					9	13	29	68
					7	12	23	57
					11	9	33	55
May or June	Ilwaco	Male	32	19	10	17	30	46
	do	Female	32	19	12	12	38	72
	do	do	32	16	11	9	38	70
	35 miles above Astoria	do	37	17	14	9	58	90
	do	do	37	17	15	10	40	72
No date					12	7	38	56
					11	11	35	68
					14	10	46	70
					12	11	38	66
					11	13	35	73

[1] The records accompanying these two specimens were confused, so that it was impossible to tell which specimen weighed 16 pounds and which 21 pounds.
[2] The data here are not exact, as the fish had been cleaned before the data were taken.
[3] The excessive weight given for this individual is undoubtedly an error.

The examination of the scales of these marked adults has shown, as would be expected from their known history, that the nuclei are all of the "stream" type, and that there are invariably three complete years of ocean growth and usually a marginal band of wider rings representing the beginning of the fourth year in the ocean—the fifth in the life of the fish. (See figs. 22, 24, 26, and 28.)

Particular interest attaches to the examination of the nuclear portions of the scales of these fish on account of the light they throw on the interpretation of scales from unmarked fish. The chief difficulties in the interpretation of the scales of chinook salmon are those associated with the growth of the first year, and positive information as to the significance of various phenomena, such as is obtainable from marked fish, is especially desirable. The nuclei of the scales of these fish consist in a central portion of true stream growth, which is usually surrounded by a more

or less distinct band of intermediate rings, which in turn is surrounded by the wider rings of ocean growth formed during the second year. Although the scales are all similar, there is considerable variation, which it is important to consider in some detail.

The true stream growth is relatively small, as compared with the usual size of stream nuclei, and is often poorly defined with marginal winter rings that are not as typical as those on the scales of wild fish. An incidental check was found on the scales of 13 individuals. The number of rings within the incidental check ranges from 4 to 9 and averages 5.8. The general appearance of the stream growth in these adult scales corresponds exactly with that of typical scales from the young fish preserved at the time of marking. (Compare figs. 20 and 21 with the stream growths in figs. 23, 25, 27, 29, 30, and 31.) The average number of rings in the stream growth of the adult scales (see Table 6) is 11, as compared with an average of 9.2 on the scales of the young fish. The average length of the anterior radius to the edge of the true stream growth is $\frac{34.1}{120}$ millimeters, as compared with $\frac{31.8}{120}$ millimeters for the young fish. It is apparent from these figures that the check considered here as terminating the true stream growth was formed at approximately the time when the fish were liberated at the hatchery. Immediately outside of this true stream growth is usually found a band of distinctly wider rings forming the intermediate growth. The term "intermediate" has been applied by Gilbert and others to the band of rings frequently encountered between the true stream and the undoubted ocean growth, the rings of which are intermediate in width between the stream and ocean rings. It frequently, though not always, is developed during the time spent in the brackish water of the estuaries during the seaward migration. The intermediate growth shown on the scales of the marked fish of this lot is usually fairly wide, averaging 9 rings and ranging from none (fig. 29) to 15 rings (fig: 27). Not infrequently the outer rings of the intermediate band widen gradually and merge into the ocean growth, so that it is difficult to set a definite boundary between the two (fig. 23). In extreme cases, where both the stream and the intermediate bands are poorly defined, the true character of the nucleus is so obscured that were the scales presented without additional data the nuclei might be mistaken for the ocean type. Figures 29 and 31 show such nuclei. These scales show considerable gradation from a pure stream type of nucleus to what we have designated a "composite nucleus." This type will be discussed in more detail later in this report in connection with another experiment, which throws light on the interpretation of these scales.

EXPERIMENT NO. 5. LITTLE WHITE SALMON RIVER HATCHERY, JUNE AND JULY, 1917

Eggs from: McKenzie River, 1916.
Reared and marked at: Little White Salmon River hatchery.
Mark used: Removal of adipose fin and dorsal fin.
Number marked: 44,500.
Liberated: In Little White Salmon River during June and July, 1917.
Age: Approximately 10 months.

The average length of 45 unselected specimens of young fish preserved on July 18, 1917, is 47.4 millimeters (1. 9 inches). The scales have an average of 4.4 rings,

and the average length of their anterior radii is $\frac{16.0}{120}$ millimeters. No peculiarities are noticeable in the scale growth. A typical scale is shown in Figure 32. The detailed data for these 45 specimens are given in Table 7.

TABLE 7.—*Chinook-salmon fingerlings marked at Little White Salmon River hatchery July 18, 1917*

Length in millimeters (mid-value of class)	Scale record																Males	Females	Total
	Number of rings							Length of anterior radius, in millimeters ×120 (mid-value of class)											
	0	1	2	3	4	5	6	7	9	11	13	15	17	19	21	25			
37.5	1	1	1	1	1			1		4							4	1	5
42.5		1	2	3	6	1			1	2	5	3	2				7	6	13
47.5				1	3	4	1				1	3	4	1			7	2	9
52.5						3	11					1	3	6	3	1	8	6	14
57.5						1	3							1	3		1	3	4
Total	1	2	3	5	10	9	15	1	1	6	6	7	9	8	6	1	27	18	45
Average	4.4							16.0									46.9	47.9	47.4

One adult specimen, a female 27 inches (69 centimeters) in length and weighing 10.5 pounds (4.8 kilograms), was recovered. It was taken during spawning operations in the Little White Salmon River on October 13, 1920. The anterior half of the dorsal fin was somewhat regenerated, but there was little question of the reliability of the mark.

The scales show such an extreme amount of absorption (fig. 33) that they are useless for determining the age. Only one complete year of the ocean growth remains. The nucleus is usually large and poorly differentiated and probably represents the composite type to be discussed later. A slight check may be seen about four rings from the center, which possibly was formed at or just before the time when the fish was marked and liberated. It is impossible to determine the exact boundary of the first year's growth, but apparently there is an unusually wide band of intermediate rings, including perhaps as many as 16 of the rings immediately within the undoubted ocean growth.

The fish that spawn in the McKenzie River, from which the fish marked in this experiment originated, enter the mouth of the Columbia in the spring and therefore constitute part of the so-called "spring" run, which is of the highest quality and the maintenance of which is especially to be desired. The primary object of this experiment was to test the effect of liberating young fish belonging to a race that normally enters the river during the spring into a stream such as the Little White Salmon (which is populated mainly by a race of fish that normally enters the river during late summer or fall). The great amount of absorption exhibited by the scales of the one specimen recaptured would indicate that it had spent considerable time in fresh water. The absorption is noticeably greater than that of the scales of other fish taken during the spawning season in the Little White Salmon. (See fig. 14, showing a scale from a fish only 3 years old.) If the amount of absorption of the scales can be taken as indicating the length of time spent in fresh water, it would follow that this individual had entered much earlier than the usual run that populates the Little

White Salmon River. Apparently there has been a tendency for the fish hatched from eggs taken from early-running fish to enter the fresh water early, even though planted in a stream typically inhabited by a late-running race. A more complete discussion of this question is given in connection with later experiments, which offer more conclusive evidence.

EXPERIMENT NO. 6.—HERMAN CREEK HATCHERY, MARCH, 1920

Eggs from: Willamette and McKenzie Rivers, 1918.
Reared and marked at: Herman Creek hatchery.
Mark used: Removal of both ventral fins and the adipose fin.
Number marked: 20,000.
Liberated: In Herman Creek during March, 1920.
Age: Approximately 18 months.

The eggs from which these fish developed were hatched at Bonneville and the fry were transferred to Herman Creek soon after hatching. During June, 1919, the greater number of the fish in the ponds were liberated, but those marked in this experiment lingered in the pond and became mixed with sockeyes of the same age, which had been placed in the ponds a few days after the chinooks were liberated. It was in the course of the marking of the sockeyes that the chinooks were segregated and marked.

Twenty-nine specimens preserved during the course of the marking average 107.5 millimeters (4.2 inches) in length. Their scales have an average of 13.8 rings and an average anterior radius of $\frac{42.2}{120}$ millimeters. (See Table 8.) Scales from 26 of the 29 individuals have an incidental check inclosing an average of 8.4 rings (radius $\frac{30.1}{120}$ millimeters). The winter check usually is absent but is represented on a few scales by one or two broken rings at the margin of the scale. Two specimens have a fairly distinct winter check followed by a couple of rings of the rapid growth of the second year. (See fig. 35.) Figure 34 illustrates a scale in which both the incidental check and the winter check are lacking.

TABLE 8.—*Chinook-salmon yearlings marked at Herman Creek hatchery during March, 1920*

Length in millimeters (mid-value of class)	Scale record																											Males	Females	Total
	Number of rings										Length of anterior radius in millimeters×120 (mid-value of class)																			
	9	10	12	13	14	15	16	17	18	19	27	29	33	35	37	39	41	43	45	47	49	51	53	55	59	63				
77.5		1										1																1		1
82.5			1								1																	1		1
92.5			1			1										1		1										1	1	2
97.5				1	1	1										1		1	1									2	1	3
102.5	1	2		2	1	1							1	1	2	1	1		1									5	2	7
107.5			1	1		1													1			1		1				2	1	3
112.5		1		1	1	2								2					2			1						3	2	5
117.5								1		1											1		1					2		2
122.5				1			1									2												2		2
127.5										1																1		1		1
137.5							1													1								1		1
147.5									1																1			1		1
Total	1	4	3	6	3	6	2	1	1	2	1	1	1	3	2	5	1	2	5	1	1	2	1	1	1	1		22	7	29
Average	13.8										42.2																	109.3	103.1	107.

One adult fish that returned to spawn in its fourth year was taken during the season of 1922; 29 five-year-olds were reported during the season of 1923, and 18 were taken during the season of 1924, when they were in their sixth year. Tables 9 and 10 give the data regarding these captures.

TABLE 9.—*Chinook salmon marked at Herman Creek hatchery during the spring of 1920, when approximately 18 months old, and recovered during the seasons of 1922, 1923, and 1924*

Date of capture	Place of capture	Sex	Length, in inches	Weight, in pounds	Scale record, first year	
					Number of rings	Length of anterior radius, in millimeters×120
1922: Sept. 10–19	Cascade Locks					
1923:						
May 1–5	Lower Columbia	Female	36	18		
May 1–5	do	Male	30	11		
May 1–5	do	do	36	17		
May 1–5	do	Female	25	11		
May 1–5	do	do	36	19		
May 3	do	do	36	17	17	52
May 3	Westport		33	13.5	15	52
May 4	do	Male	34	14	13	44
May 4	Lower Columbia	Female	35	22	16	44
May 6	Tongue Point	Male	26.5	19	16	44
May 7	Astoria	do	34.75	20	13	33
May 8	Rainier	do	36.5	21	16	44
May 8	Bonneville	do		18	14	39
May 9	Rainier	do	35.5	21.5	17	37
May 9	Sand Island	Female	38	20	16	52
May 10	Westport	do	41	28.5	17	62
May 13	Cascade Locks	Male	26	10	16	41
May 14	Altoona	Female	35	19	19	67
May 17	Smith Point	do	35	17	17	47
May 17	do		36	18	17	52
May 20	Ellsworth	Male	36	15	14	41
May 22	Bonneville	do	26.5	8	21	60
May 25	Sand Island	Female	35	15.5	13	45
May 26	do	do	38.5	23		
May 26	Tongue Point	do	31	13		
May 28	Lower Columbia	Male	26.75	7	15	36
June 17	Mouth Herman Creek	Female	35	16	23	65
July 31	Cascade Locks		32	15	15	41
Oct. 1	Herman Creek					
1924:						
May 3	Ranier		38	20	13	32
May 4	The Dalles	Female	35	16	10	41
May 6	Warrendale	do	36.75	21	17	45
May 6	The Dalles	do	39.25	22.5	19	54
May 6	Corbett	Male	35.5	17.75	14	42
May 6	Lower Columbia		28	34	19	60
May 7	Clatskanie		38	22	15	54
May 9	The Dalles	Female	39.5	23		
May 10	Warrendale	Male	36	19.75	20	54
May 10	The Dalles	Female	36.5	21	18	50
May 20	Bonneville		26	16	16	44
May 23	do	Male	39.5	25		
May 26	do	Female	32	13		
May 15–31	The Dalles	do			16	45
June 7	Warrendale	Male	43.5	30.5		
June 28	Bonneville	Female	34.75	15	18	51
June 29	The Dalles	do	40	25	15	41
July 15	Chinook	do	29	18.25		

TABLE 10.—*Chinook salmon marked at Herman Creek hatchery during the spring of 1920, when approximately 18 months old, and recovered during the seasons of 1923 and 1924*

Age	Average length		Average weight	
	Inches	*Centimeters*	*Pounds*	*Kilograms*
Fifth year, 1923:				
Males	31.7	80.5	15.1	6.9
Females	35.1	89.1	18.4	8.4
Sixth year, 1924:				
Males	38.6	98.0	23.2	10.5
Females	35.9	91.1	19.6	8.9

This experiment adds more conclusive evidence to that given by experiment No 5 regarding the influence of heredity on the time when the adult salmon return to fresh water. In this experiment, as in experiment No. 5, the progeny of salmon that enter the river in the spring were liberated in a tributary normally inhabited by fall-running chinooks. Of the 47 recaptures reported from the commercial fishery, 40 were taken during May, and two-thirds of these were taken during the first 10 days of the month. In other words, the run seems to have been well under way when the season opened on May 1. With the exception of the one fish taken on July 15, 1924, even those caught during June and July probably entered the river during May, as their scales were greatly absorbed and the fish themselves were reported to be dull, soft, and thin rather than plump and bright, as are fish that have recently left the ocean. The condition of the fish taken on July 15 was not reported, but judging from its scales, which were less absorbed than those of many of the fish taken during May, there is no reason to believe that it had been in the river for any length of time. The scales of the fish taken during September, 1922, were absorbed to an extent indicating that the fish had entered the river some time before being caught; but this alone is not sufficient evidence to justify the conclusion that it left the ocean as early as the majority of the fish returning from this marking. In view of the fact that such a large proportion of the fish are known to have entered the river during a very short period in the spring, the two possible exceptions need not affect the general conclusion that the factors determining the time of entering fresh water are hereditary and are not altered by conditions of early environment. Additional data regarding this important question are furnished by later experiments.

The fact that salmon return to spawn in the river system from which they migrated as fry or fingerlings, even though the eggs from which they developed may have been taken from another river, has been demonstrated in many instances. Gilbert (1919) has shown that sockeye salmon, of the Frazer River at least, return to the particular spawning district in which they spent their early life. The authors have numerous unpublished data that indicate that the same is true in general of the chinook salmon of the Columbia. This series of experiments offers an unusual opportunity to observe this tendency, both as regards natural and transplanted runs. In this particular experiment fish were transplanted from one tributary to another of the same system. The absence of heredity as a factor in determining which tributary the resulting adult fish chose to enter is shown by the fact that a constant search at the Willamette and McKenzie egg-taking stations (where the eggs from which these fish developed were taken) revealed no marked fish. Their failure to enter the Willamette is shown further by the fact that the majority of those recaptured were taken in the main Columbia River above the mouth of the Willamette. Not only did they fail to return to the tributary in which they originated, but the majority also failed to return to the tributary in which they were reared and liberated. Only one entered Herman Creek. This one, a female, was found about 1 mile above the mouth of the creek on October 1, 1923.

Herman Creek was observed on several occasions during the season of 1923, but prior to the visit of October 1 it had not seemed necessary to look for fish above the hatchery station, because a small dam used to divert water into the rearing ponds had been impassable since late in May. The appearance of at least a dozen

adult fish in the rearing ponds (which they had entered with the intake water) prompted a more thorough investigation of the creek. Between the hatchery station and a small power dam, about 1 mile above, 5 living and 14 dead fish were found. All were inspected carefully for the absence of fins, but only one marked fish was found. Unquestionably these fish entered the creek early in the spring, because not only was the dam impassable, but the creek became so low early in the summer that nearly all of the water was diverted through the ponds, leaving the creek virtually dry for a distance of several hundred feet.

The appearance of an occasional adult chinook salmon in Herman Creek during the spring is not an unusual occurrence, but this was the first time that any number of spring chinooks had been reported from there. A second run was reported in 1926, when 130 spring chinooks ran into the creek.

Additional data regarding the tendency of salmon to return to a particular tributary to spawn were secured from later experiments.

The scales of the adult fish present nothing unusual. Their nuclei are typical of the stream type and are identical with the scales of the young fish at the time of liberation. (See figs. 37 and 39.) The majority of those having perfect scales show an incidental check inclosing an area marked by an average of 8 rings and having an average anterior radius of $\frac{28.4}{120}$ millimeters. As mentioned above, the scales of the young fish showed an incidental check inclosing an average of 8.4 rings and with a radius of $\frac{30.1}{120}$ millimeters—a remarkably close correspondence. The average total number of nuclear rings is 16.2, and the average total radius is $\frac{47.5}{120}$ millimeters. (See Table 9.) The scales of the adult fish are characterized further by a comparatively small growth during the first year in the ocean. Figures 36 and 38 illustrate typical scales from mature fish in their fifth and sixth years, respectively.

EXPERIMENT NO. 7.—BONNEVILLE HATCHERY, OCTOBER, 1920

Eggs from: Willamette, McKenzie, and Santiam Rivers, 1919.
Reared and marked at: Bonneville hatchery.
Mark used: Removal of adipose fin and right ventral fin.
Number marked: 65,000.
Liberated: In Tanner Creek during October, 1920.
Age: Approximately 13 months.

A sample of 50 fingerlings preserved on October 14, 1920, averages 96.6 centimeters (3.8 inches) in length. The rings of the scales are regular in shape and evenly spaced, giving evidence of comparatively rapid and uninterrupted growth. The average number of rings is 15.3, and the average length of the anterior radius is $\frac{46.6}{120}$ millimeters. A typical scale is shown in Figure 40. The complete scale and length records are given in Table 11.

TABLE 11.—*Chinook-salmon fingerlings marked at Bonneville hatchery October 14, 1920*

Length, in millimeters (mid-value of class)	Scale record																						Males	Females	Total
	Number of rings								Length of anterior radius, in millimeters ×120 (mid-value of class)																
	11	12	13	14	15	16	17	18	33	35	41	43	45	47	49	51	53	55	57	59	61	67			
82.5		1	1	1						2	1													3	3
87.5	1		1		1	2	1		1		3		1					1					2	4	6
92.5				6	1	2	1	2				2	6	2		1			1				6	6	12
97.5			2	2	2	2	3	2	1	1		2	1	2	1	2	1	1		1			5	8	13
102.5				2	3	3	3				1		2	1	1	2	1	1	1	1			3	8	11
107.5			1				1						1						1				2		2
112.5					1								1										1		1
122.5								1														1	1		1
132.5							1														1			1	1
Total	1	1	5	11	8	9	10	5	2	3	5	4	12	5	2	5	2	3	3	2	1	1	20	30	50
Average	15.3								46.6														98.0	95.6	96.6

From the standpoint of adult fish recovered this has been one of the most successful experiments with chinook salmon, 252 having been taken. One 3-year-old was taken by troll in the ocean near the mouth of the Columbia River, and the rest were taken in the Columbia River, 8 of them during 1923, 215 during 1924, and 28 during 1925. Records of the time and place of capture are given in Tables 12 and 13.

TABLE 12.—*Chinook salmon marked at Bonneville hatchery during the fall of 1920, when approximately 13 months old, and recovered during the seasons of 1922, 1923, and 1925*

Date of capture	Place of capture	Sex	Length, in inches	Weight, in pounds	Scale record, first year	
					Number of rings	Length of anterior radius, in millimeters ×120
1922: August 9	Ocean	Male	23.25	5.5	15	42
1923:						
May 1-5	Lower Columbia	Female	32	16		
May 1-5	do	Male	31	13		
May 1-5	do	Female	28	14	18	49
May 1-24	do			11	24	78
May 7	Ocean	Female	30	12.5	14	42
May 9	Astoria	do	32	18	24	70
May 16	Lower Columbia	Male	26	9	16	47
May 22	Mount Pleasant	do	25.5	8	19	68
1925:						
May 1	The Dalles	do	37.75	22	22	66
May 2	Bonneville	do	45.25	39.75	17	48
May 3	Warrendale cannery		42	27	17	47
May 4	Ellsworth cannery	Male	27	18	18	51
May 4	Bonneville	Female	34.75	13	18	51
May 4	Cascade Locks	Male	41	28.25	25	81
May 5	Rainier	Female	32	13	24	63
May 5	Bonneville	Male	46.5	42.5	20	69
May 5	Warrendale cannery		36	20		
May 5	Dodson cannery		47	50	17	57
May 7	Bonneville	Male	40.5	27	17	48
May 8	Dodson cannery	do	43	37	26	69
May 8	do	Female	38.5	22	21	65
May 9	Warrendale cannery	Male	24	25	19	47
May 11	Dodson cannery	do	38	23	14	35
May 14	Ellsworth cannery	Female	34	21	18	51
May 14	do	do	37.5	25	14	62
May 20	Warrendale cannery	do	38	20	24	57
May 16	Cascade Locks	Male	48	40	23	74
May 29	Bonneville	Female	37.5	21.5	20	51
June 3	Warrendale	Male	36.5	18	19	53
June 10	Warrendale cannery	Female	37.5	21	22	62
During May, exact date not recorded.	Pillar Rock	Male	35	19	17	48
	do	Female	40	35	15	45
	Dodson cannery	do	34	21	16	45
	do			26	15	38
	do				18	48

TABLE 13.—*Chinook salmon marked at Bonneville hatchery during the fall of 1920, when approximately 13 months old, and recovered during the season of 1924*

Place of capture [1]	Date of capture								Total
	May				May 29–June 4	June		Date unknown [2]	
	1–7	8–14	15–21	22–28		5–11	12–18		
Mouth of Columbia-Vancouver	15	5	5	1	1			1	28
Vancouver-Cascade Locks	24	29	8	6	4	2	1	4	78
Cascade Locks-Celilo Falls	40	47		5				1	93
Unknown (above Vancouver)	9	3		2		1			15
Total	88	84	13	14	5	3	1	6	214

[1] One fish taken near Astoria during February is not included in this table.
[2] All during May.

The detailed length and weight data are given in Tables 12, 14, and 15. The average sizes appear in Table 16. These averages can not be relied upon as accurately representing the size of the fish at the three ages, because, as has been mentioned, the individual records are not dependable. The figures for the 5-year-olds (as a result of the large number of data comprising them) probably are quite accurate. The small number of records for the 4-year-olds makes the averages for that age group least dependable.

TABLE 14.—*Chinook salmon marked at Bonneville hatchery during the fall of 1920, when approximately 13 months old, and recovered during the season of 1924*

Length, in inches (mid-value of class)	Males	Females	Length, in inches (mid-value of class)	Males	Females
23.5	1	2	38.5	7	11
26.5	1		39.5	8	7
27.5	1	2	40.5	9	
28.5	1	1	41.5	4	
29.5	2	3	42.5	4	
30.5	2	4	43.5	3	
31.5	3	2	47.5	1	
32.5	7	5			
33.5	5	5	Total	91	91
34.5	6	11			
35.5	8	10	Average, inches	36.7	35.2
36.5	9	13	Average, centimeters	93.2	89.4
37.5	9	15			

TABLE 15.—*Chinook salmon marked at Bonneville hatchery during the fall of 1920, when approximately 13 months old, and recovered during the season of 1924*

Weight, in pounds (mid-value of class)	Males	Females	Weight, in pounds (mid-value of class)	Males	Females
10.5	2	1	27.5	1	1
11.5	2	2	28.5	6	1
12.5	2	1	29.5	1	2
13.5	2	5	30.5	3	
14.5	1	3	31.5	3	
15.5	4	2	32.5	3	
16.5	5	9	33.5	1	
17.5	3	6	34.5	2	1
18.5	9	5	35.5	2	
19.5	3	9	36.5	1	
20.5	5	13	41.5	1	
21.5	2	7	42.5	1	
22.5	6	9			
23.5	6	4	Total	90	91
24.5	4	2			
25.5	3	4	Average, pounds	23.0	20.1
26.5	6	4	Average, kilograms	10.5	9.1

TABLE 16.—*Chinook salmon marked at Bonneville hatchery during the fall of 1920, when approximately 13 months old, and recovered during the seasons of 1923, 1924, and 1925*

Age	Average length		Average weight	
	Inches	*Centimeters*	*Pounds*	*Kilograms*
Fourth year, 1923:				
Males	30.8	78.2	10.0	4.5
Females	30.5	77.5	15.1	6.9
Fifth year, 1924:				
Males	36.7	93.2	23.0	10.5
Females	35.2	89.4	20.1	9.1
Sixth year, 1925:				
Males	38.6	98.0	28.3	12.9
Females	36.4	92.5	21.2	9.6

The consistency with which these fish entered fresh water during the early part of the season greatly outweighs the few doubtful cases in other experiments in showing that the time at which the adults enter fresh water is determined by heredity and is not affected by early environment. The parents of the fish marked in this experiment were of the early spring run that spawns in the headwaters of the Willamette River. The fingerlings marked were reared at Tanner Creek, where only salmon of the fall run are found normally; but the time when the adult marked fish returned to fresh water to spawn was not altered by this change in their early life. This is shown most clearly by the records of the 1924 recoveries. (See Table 13.) Of the 208 recoveries for which the date of capture is known, 82 per cent were taken during the first two weeks after the season opened on May 1. The largest catches were made during the first four days of the season. The date of the latest recovery from this experiment was June 13.

The evidence from this experiment, regarding the factors that influence the adult salmon to return to a particular tributary to spawn, is in complete agreement with that derived from experiment No. 6. As in experiment No. 6, none returned to the tributaries in which the eggs were taken. Approximately one-half of the reported recaptures were made in the Columbia several miles above the mouth of Tanner Creek, where the fingerlings were liberated, whereas only three ran into Tanner Creek. From these facts it is evident that heredity has no effect on the tendency in question and that early environment is an influencing but by no means controlling factor.

Scales from all of the recaptured adult fish were examined microscopically in the usual manner. Evidence of absorption, which normally sets in soon after the fish enter fresh water, was found in nearly all cases. In the majority the original margin was removed entirely, but there remained at least a part of the last winter band, which in fish that leave the ocean in the spring lies just within the margin of the complete scale. In a few of the 5-year-olds and most of the 6-year-olds the last winter band was entirely lacking, but a wide band of well-spaced rings following the preceding winter check is ample assurance that the fish were in their fifth and sixth years, respectively. Typical scales from fish recovered during their third, fourth, fifth, and sixth years are shown in Figures 41, 42, 43, and 45.

The nuclei of the scales of 50 of the 5-year-olds and of all of the other age groups were measured for comparison with the scales of the fingerlings. All were distinctly of the stream type. The range of variation in size and number of rings was shown most clearly by the measurements of the 50 unselected 5-year-olds, which are tabu-

lated in Table 17. The average number of rings was 18.4; the average length of the anterior radius was $\frac{51.8}{120}$ millimeters. These measurements are slightly greater than those for the fingerling scales, which averaged 15.3 rings and a radius of $\frac{46.6}{120}$ millimeters. As a rule the rings were very regularly spaced and unbroken, but there was an occasional incidental check, which probably was formed at the time of planting. In a few cases the typical stream and ocean growths were separated by a few rings of intermediates. Nuclei of average, large, and small size are illustrated in Figures 44, 46, and 47, respectively.

TABLE 17.—*Chinook salmon marked at Bonneville hatchery during the fall of 1920, when approximately 13 months old, and recovered during the season of 1924*

Length of anterior radius, in millimeters × 120	Scale record, first year: Number of rings																
	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	27	Total
32–33									1								1
34–35		3	1	1													5
36–37	1	1															2
38–39		1															1
40–41							1										1
42–43					1	2		1									4
44–45					1	1	1				1						4
46–47						1		2									3
48–49							1		2								3
50–51							1		2	1	1						5
52–53									1		2						3
54–55											1						1
56–57							1	1									2
58–59										1	3			1			5
62–63									1	2	1						4
64–65													1				1
68–69															1		1
70–71												1					1
76–77													1				1
82–83														1			1
90–91																1	1
Total	1	5	1	1	2	4	5	4	7	4	9	1	2	2	1	1	50

EXPERIMENT NO. 8.—LITTLE WHITE SALMON RIVER HATCHERY, JULY AND AUGUST, 1920

Eggs from: Little White Salmon River, 1919.
Reared and marked at: Little White Salmon River hatchery.
Mark used: Removal of adipose fin and left ventral fin.
Number marked: 24,000.
Liberated: In Little White Salmon River during July and August, 1920.
Age: Approximately 10 months.

A sample of 40 specimens preserved during the course of the marking averages 49.6 millimeters (2 inches) in length. Their scales average $\frac{16.2}{120}$ millimeters in radius and have an average of 3.5 rings. (See Table 18.) A typical scale is illustrated in Figure 48. This sample is represented by an unusually large proportion of males, the males exceeding the females nearly 3 to 1. This uneven representation of sexes

could not be due to error in recognition of the sexes, as the gonads, though small, are distinctly differentiated and independent determinations by the two authors agree in every case.

TABLE 18—*Chinook-salmon fingerlings marked at Little White Salmon River hatchery during July and August, 1920*

Length, in millimeters (mid-value of class)	Scale record											Males	Females	Total
	Number of rings				Length of anterior radius, in millimeters × 120 (mid-value of class)									
	2	3	4	5	11	13	15	17	19	21	23			
42.5	1	1	----	----	1	1	----	----	----	----	----	1	1	2
47.5	----	5	7	----	----	----	4	5	2	1	----	10	2	12
52.5	2	11	9	4	----	3	4	6	8	4	1	18	8	26
Total	3	17	16	4	1	4	8	12	10	5	1	29	11	40
Average	3.5				16.2							49.6	49.6	49.6

The first returns from this experiment were reported during the season of 1923 when the fish were in their fourth year; 17 were reported from the commercial fishery and 4 were secured in the parent tributary. During the season of 1924, 22 were reported—14 from the commercial fishery, 7 from the parent tributary, and 1 from the Big White Salmon River egg-taking station. The detailed data are given in Table 19. The average lengths and weights are given in Table 20.

TABLE 19.—*Chinook salmon marked at Little White Salmon River hatchery during the summer of 1920, when approximately 10 months old, and recovered during the seasons of 1923 and 1924*

Date of capture	Place of capture	Sex	Length in inches	Weight in pounds	Scale record, first year			
					Number of rings		Length of anterior radius, in millimeters×120	
					To first incidental check	Total first year	To first incidental check	Total first year
1923:								
July 3 [1]	Lower Columbia	Male	34	15.5	10	23	32	70
July 14 [1]	do	do	34.5	15	10	19	28	49
July 19 [1]	do	do	34	15	----	----	----	----
Aug. 15	Sand Island	do	41	27	9	30	24	91
Aug. 16	Lower Columbia	Female	24	30	5	24	18	66
Aug. 16	Sand Island	do	38	21	9	31	32	99
Aug. 17	Lower Columbia	do	39	24	12	25	28	62
Aug. 18	Sand Island	Male	37	20	9	23	26	60
Aug. 18	do	do	32	23	9	21	29	118
Aug. 20	Ocean	do	36.5	26	8	19	21	47
Aug. 20	Lower Columbia	Female	34	27.5	7	23	26	70
Aug. 20	do	do	26	10	8	22	23	54
Aug. 22	Astoria	Male	37	25	7	20	23	52
Aug. 23	Sand Island	do	40	26	8	22	28	65
Aug. 23	do	Female	34.75	20	9	28	26	99
Sept. 13	Tongue Point	do	39	23	9	28	29	88
Sept. 17	Lower Columbia	do	36	18	8	30	24	94
Sept. 24	Little White Salmon River hatchery	do	38.5	----	11	33	34	112
Sept. 24		Male	38.75	----	9	18	32	57
Sept. 26		Female	38.5	----	8	28	24	86
Sept. 28		do	38.75	----	----	----	----	----

[1] These dates probably incorrect. Evidence from other sources has shown that observer who reported them made other errors.

TABLE 19.—*Chinook salmon marked at Little White Salmon River hatchery during the summer of 1920, when approximately 10 months old, and recovered during the seasons of 1923 and 1924*—Con.

Date of capture	Place of capture	Sex	Length in inches	Weight in pounds	Scale record, first year: Number of rings: To first incidental check	Number of rings: Total first year	Length of anterior radius, in millimeters×100: To first incidental check	Length of anterior radius, in millimeters×100: Total first year
1924:								
Aug. 2	Sand Island	Female	42	36	12	26	34	78
Aug. 5	do	do			8	29	23	91
Aug. 9	Astoria	Male	39	39	9	25	31	71
Aug. 9	McGowan, Wash	Female	40	32	6	27	24	91
Aug. 10	Sand Island	Male	34	29	7	29	23	92
Aug. 12	do	do	46	40	11	28	32	92
Aug. 14	do	do	45.5	42	9	27	28	99
Aug. 15	do	Female	31	26.5	7	24	24	76
Aug. 16	Clifton	Male	42	52	8	27	23	83
Aug. 16	Astoria	Female	41	40	13	24	37	71
Aug. 18	Lower Columbia	do			10	27	41	92
Aug. 19	McGowan, Wash	do	40	35	8	23	24	68
Aug. 23	Sand Island	do			13	19	41	55
Sept. 11	St. Helens	Male	34	32				
Sept. 20	Little White Salmon River hatchery	Female	43.5		7	28	28	92
Sept. 20		Male	44		6	19	21	52
Sept. 27		Female	42.25					
Sept. 28		do	42		12	32	31	107
Sept. 30		do			6	15	37	63
Oct. 2		do	41.5		7	23	24	73
Oct. 6		do	42		11	38	31	83
No date	Big White Salmon River				7	28	28	92

TABLE 20.—*Chinook salmon marked at Little White Salmon River hatchery during the summer of 1920, when approximately 10 months old, and recovered during the seasons of 1923 and 1924*

Age	Average length: *Inches*	Average length: *Centimeters*	Average weight: *Pounds*	Average weight: *Kilograms*
Fourth year, 1923:				
Males	36.5	92.7	22.2	10.1
Females	35.1	89.2	21.7	9.9
Fifth year, 1924:				
Males	40.6	103.1	39.0	17.7
Females	40.7	103.4	33.9	15.4

One of the objects of this experiment was to determine at what time of year the salmon propagated at the Little White Salmon River hatchery pass through the commercial fishing district on their spawning migration. The date of the earliest reliable record of a recapture is August 2 and the latest recovery from the commercial fishery is September 17. The records of three that were reported as taken during July are believed to be incorrect, as the person who reported them is known to have made other errors in reporting marked fish. The period August 15 to 20, inclusive, during which nearly half of the recaptures reported from the commercial fishery were taken, may be designated as the time of the height of the run. A closed season for commercial fishing is responsible for the lack of recaptures during the period August 25 to September 10.

This was the first experiment in which any number of the adult marked fish returned to the tributary in which they had been liberated as fingerlings. There appears here to be some significance in the fact that the fingerlings were liberated in their native tributary. In most of the other experiments the fingerlings were liberated in a tributary other than that from which the eggs were secured. Even in this experiment the homing was not perfect, as is shown by the recovery of one of the fish in the Big White Salmon River.

The nuclei of the scales of the adult fish from this experiment are of particular interest because of their wide variation and the light these variations throw on the interpretation of the scales of wild fish of unknown history. Scales with typical stream and ocean nuclei, representing, respectively, migration to the ocean before the scales are formed and after the first year's growth is completed, are identified easily and offer no particular problems; but as the senior author has shown (Rich, 1920), the seaward migration of chinooks in the Columbia is not confined to these two periods but is distributed throughout the year. In view of this variation in the time of migration one would expect to find corresponding variations in the scales, ranging from the typical stream type to the typical ocean type, with transitional stages having varying proportions of stream and ocean growth. A third possible variable in the nature of the scale rings is to be expected as a result of the intermediate environment of the estuary, under the influence of which the fish grow more rapidly than in fresh water but not as rapidly as in the ocean. Such variations in the scales have been observed. Gilbert draws attention to them in his first paper on the scales of the Pacific salmon (Gilbert, 1913). The senior author, in extending the work of Gilbert to a more comprehensive study of the chinook salmon of the Columbia River, encountered such a wide range of variation in the nuclear types that he found it necessary to make a careful study of the seaward migrants before continuing with the study of adult scales. The study of the seaward migrants was necessarily confined to the stream and estuary growth, and it was impossible to trace the growth and movement of particular individuals through their life in the ocean. This opportunity to study the scales of mature fish of known age and early history is therefore of great value.

The nuclei of the scales of all of the adult fish in this experiment have a central portion of closely spaced rings, which is set off from the remainder of the scales by an incidental check formed by a slight narrowing of the rings or by contrast with the wider rings immediately following. The cause of this check is not evident. Its formation does not seem to have been coincident with marking or liberation, as the scales of the fingerlings at the time of marking had 3 to 5 rings, whereas there were 5 to 13 rings when the check was formed. It is sufficient in this connection to note that this incidental check is present in all cases and that the portion inclosed by it is typical of stream growth.

The area of the scale between this incidental check and the first winter check shows a wide range of variation. One extreme of variation is shown in Figure 49, which illustrates a scale in which the band following the incidental check consists of

rings similar to those inclosed by it. These two bands, representing the entire first year's growth, form a fairly typical stream nucleus. The opposite extreme is illustrated by Figure 50. Except for the small central portion of stream growth, this scale is typical of the ocean type. The band following the first incidental check in this case is more than twice the width of that in Figure 49, and the rings are spaced more widely. This nucleus is fairly representative of a type very commonly found among the chinook salmon of the Columbia River and for which the term "composite nucleus" is proposed. This term will be used to designate nuclei comprised of both stream and ocean growth.

Many intergrading stages of composite nuclei are found among the scales of this collection. The transition from the typical stream type toward the ocean type is so gradual as to make it impossible to divide the group of nuclei into two classes on the basis of the presence or absence of ocean growth during the first year. Two nuclei that fall about midway between the two extremes of variation are shown in Figures 51 and 52. Some of these intergrading stages probably involve estuary growth. A fish may have spent a part of the first year in each of the three environments, or it may have remained in the estuary during the latter part of the first year. A second incidental check, which is to be found in many of the nuclei, may represent the change from the stream to the estuary or from the estuary to the ocean.

Typical scales of adult fish in their fourth and fifth years are shown in Figures 53 and 54. These also show further variations in the composite type of nucleus.

Returning now to a consideration of the scales of the mature fish in experiment No. 3 we find nuclei similar to some of those in this collection. Eight adult fish were recaptured, the scales of all of which have a central area that unquestionably is stream growth. In all but one this area appears to represent nearly the entire first year's growth but is not terminated by the winter check, which usually is found at the margin of the stream type of nucleus. (See figs. 14 to 18.) This condition, combined with the presence of rings of only moderate width surrounding the stream growth suggests that the fish may have entered the ocean or at least the estuary before the winter check was formed. The check at the twenty-third ring in Figures 17 and 18 may represent the winter check in that scale. In the others the boundary of the first year's growth is not shown definitely.

The stream growth in seven of these is broken by an incidental check at the fifth to seventh rings. (See Table 4 and figs. 14 to 18.) The area inclosed by this check evidently represents the margin of the scale at the time the fish were marked and liberated.

In the eighth scale of this collection (fig. 19) the stream growth extends only to a point corresponding to the first incidental check in the other seven. From this point the rings widen gradually into the second year's growth, leaving no mark to indicate the termination of the first year's growth. This nucleus is more typically a composite type than are the other seven.

EXPERIMENT NO. 9.—BONNEVILLE HATCHERY, SEPTEMBER AND OCTOBER, 1921

Eggs from: McKenzie River, 1920.
Reared and marked at: Bonneville hatchery.
Mark used: Removal of adipose fin and both ventral fins.
Number marked: 50,000.
Liberated: In Tanner Creek during September and October, 1921.
Age: Approximately 13 months.

A sample of 50 fingerlings preserved on August 24, 1921, averages 93.3 millimeters (3.7 inches) in length, The average number of rings on the scales is 13.1, and the average length of the anterior radius of the scales is $\frac{43.9}{120}$ millimeters. (See table 21.) An incidental check at 6 to 10 rings from the center is to be found in about half of the scales (see fig. 55); in others (see fig. 56) there is a slight crowding of the rings, which is not sufficiently pronounced to be termed a check.

TABLE 21.—*Chinook-salmon fingerlings marked at Bonneville hatchery August 24, 1921*

Length in millimeters (mid-value of class)	Scale record																																					Males	Females	Total
	Number of rings										Length of anterior radius, in millimeters × 120 (mid-value of class)																													
	7	9	10	11	12	13	14	15	16	17	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	61												
72.5	--	1	--	--	1	--	--	--	--	--	1	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	2
77.5	--	1	2	1	--	--	--	--	--	--	--	--	--	1	1	--	2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3	1	4
82.5	--	1	2	--	--	--	1	--	1	--	--	1	--	--	--	1	1	1	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	1	4	5
87.5	1	--	1	--	1	5	2	--	1	--	--	--	1	--	--	1	--	--	3	2	1	2	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	5	5	11
92.5	--	--	--	--	--	1	3	--	1	--	--	--	--	--	--	--	--	1	--	--	--	1	2	--	--	--	--	1	--	--	--	--	--	--	--	--	--	1	4	5
97.5	--	--	--	--	1	1	2	1	--	1	--	--	--	--	1	--	--	--	--	1	1	1	--	--	1	1	--	--	--	--	--	--	--	--	--	--	--	3	3	6
102.5	--	--	--	1	--	2	1	2	3	1	--	--	--	--	--	--	1	--	--	--	--	1	1	1	4	1	1	--	--	--	--	--	--	--	--	--	--	9	1	10
107.5	--	--	--	1	1	--	1	--	1	--	--	--	--	--	--	--	1	1	1	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	2	4
112.5	--	--	--	--	--	1	1	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	2	-------	2
122.5	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--	--	-------	1	1
Total	1	3	5	3	4	10	11	3	7	3	1	1	1	1	2	2	6	3	5	3	2	5	4	1	7	2	1	3										26	24	50
Average	13.1										43.9																											95.3	91.0	93.3

The returns from this experiment are represented by three 4-year-olds recovered during 1924, thirty-three 5-year-olds recovered during 1925, and six 6-year-olds recovered during 1926. The detailed data regarding these recoveries are given in Table 22. The 5-year-old males average 31.3 inches (79.6 centimeters) in length and 30 pounds (13.6 kilograms) in weight. The females of that age average 34.3 inches (87.1 centimeters) in length and 19.5 pounds (8.9 kilograms) in weight. The 4-year-olds and 6-year-olds are represented by too few individuals to give reliable averages.

TABLE 22.—*Chinook salmon marked at Bonneville hatchery during the fall of 1921, when approximately 13 months old, and recovered during the seasons of 1924, 1925, and 1926*

Date of capture	Place of capture	Sex	Length, in inches	Weight, in pounds	Scale record first year	
					Number of rings	Length of anterior radius in millimeters × 120
1924:						
May 6	Warrendale	Male	25.75	13	17	54
May 17	Astoria cannery	do	36.5	18	17	53
May 14	Warrendale cannery	do			26	73
1925:						
May 2	do	do	25.4	31	19	51
May 3	Astoria cannery	do	34.5	20	15	56
May 4	do	Female	35	20	19	54
Do	Sand Island	do			13	39
Do	St. Helens	do	35.5	8.5	14	51
Do	do	do	27.25	30.25	14	44
Do	Rainier	do	35	15		
Do	Ellsworth cannery	do	37	28	22	65
Do	do	Male	26	17.5	22	54
Do	Bonneville	Female	37.5	17.5	20	59
May 5	Astoria cannery	do	30	12.5	14	44
Do	Ellsworth cannery	do	32	24.5	13	39
Do	Bonneville	Male	32.75	11.25	21	69
May 6	Ellsworth cannery	do	36.5	27.75	19	42
Do	Warrendale cannery		36.5	17	20	62
Do	do		35	17	17	56
May 8	Dahlia, Wash	Male	41	29	22	59
Do	The Dalles	Female	35	18	14	47
May 11	Warrendale cannery	do	38	18	18	54
May 12	Ellsworth cannery	do	32.5	20	21	60
May 16	do	do	37	26	18	48
May 29	Bonneville cannery	Male	23.5	14.5	17	53
Do	Warrendale cannery		37	16		
June 2	do	Female	36	16	20	60
June 18	Astoria cannery	do	30		17	53
Date of capture not reported	Pillar Rock	Male	28	9	20	51
	Pillar Rock cannery	do	38	22	21	56
	Ellsworth cannery	do	22	17	21	51
	Warrendale cannery	Female	37	19		
	do		37.5	21		
	do				22	56
	do	Male	37	21		
	do		44	34	23	56
1926:						
February	Clatskanie, Oreg		42	37	17	53
May 2	Ellsworth cannery		37	32	19	63
May 4	do		35	17		
May 5	Cascade Locks	Female	41	27	27	71
May 14	Ellsworth cannery	do	36.5	24	18	57
May 27	do	Male	37	23.5	18	50

As in all other experiments with chinook salmon of the spring run, these adults entered fresh water during the early part of the season. They returned to the Columbia River but not to the tributary in which they were liberated. One of the 6-year-olds was taken in February. This is additional evidence that the marked spring chinooks start their spawning migration some time before the commercial fishing season opens on May 1.

The scales of the adult fish have typical stream nuclei surrounded by ocean growth, which is divided by distinct annual checks into the expected number of summer bands. The margins of many of the scales have been absorbed, but enough of the scale remains in every case to show that the fish is of the correct age. The scale of a 5-year-old (shown in fig. 60) illustrates well the extent of absorption. As an illustration of the scale of a fish in its sixth year, one from the fish caught in February

has been selected. (See fig. 61.) It will be noted here that the winter check of the fifth year is represented by only a slight narrowing of the marginal rings and that no new growth of the sixth year is present.

The scales of one of the fish recovered during 1924 are very unusual. One of them is shown in Figure 58. The nucleus of this scale is the largest in the collection, and the radius of the scale to the second winter check is unusually small. This makes the second year's growth appear extremely slight. The cause of such unusual growth proportions is unknown. It is possible that this fish remained in fresh water for a part of the second year, in which case the nucleus would represent more than the first year. A more typical scale of a fish in its fourth year is shown in Figure 57.

This experiment is nearly an exact duplicate of experiment No. 7. Both involved the progeny of the spring run of chinooks that spawn in the headwaters of the Willamette River. The fingerlings in both cases were reared at Bonneville and liberated at approximately the same time of the year. The fingerlings preserved in experiment No. 7 are slightly larger than those in experiment No. 9, but this difference may well be due to the difference of about six weeks in the dates on which the samples were preserved. The size of the fish at the end of the first year, as shown by the size of the nuclei, was nearly identical.

The number of returns from these experiments, however, differs widely. The recoveries from experiment No. 7 represent 0.39 per cent of the fingerlings marked, whereas only 0.08 per cent (less than one-fourth as many) were recovered from experiment No. 9. No satisfactory explanation for this difference has been suggested. It could not have been due to a failure of our data to be representative of the actual returns. This may be seen by comparing the returns from the two experiments during the season of 1925. The 5-year-olds that returned from experiment No. 9 were nearly equaled by the 6-year-olds in experiment No. 7, whereas invariably a much larger proportion of fish from any brood mature during their fifth year than during the sixth. These two groups of fish were running simultaneously, and there is no reason to believe that the cannery employees and others who were searching for marked salmon selected one mark in preference to the other.

EXPERIMENT NO. 10.—BONNEVILLE HATCHERY, AUGUST AND SEPTEMBER, 1922

Eggs: McKenzie and Santiam Rivers, 1921.
Reared and marked at: Bonneville hatchery.
Mark used: Removal of adipose fin and right ventral fin.
Number marked: 100,000.
Liberated: In Tanner Creek during August and September, 1922.
Age: Approximately 12 months.

A sample of 25 of the fingerlings preserved on August 28, 1922, averages 76 millimeters (3 inches) in length. Their scales have an average of 11.6 rings and an average anterior radius of $\frac{33.9}{120}$ millimeters. The scales of all but two of the fingerlings show an incidental check about 7 rings from the center. The incidental check is followed typically by 3 to 5 rings, which stand out as distinctly heavier and more widely spaced than those preceding the check. (See fig. 62.) The length and scale data are given in Table 23.

TABLE 23.—*Chinook-salmon fingerlings marked at Bonneville hatchery August 28, 1922*

Length, in millimeters (mid-value of class)	Scale record														Males	Females	Total
	Number of rings						Length of anterior radius, in millimeters × 120 (mid-value of class)										
	9	10	11	12	14	15	23	29	31	33	35	37	43	45			
62.5		2	1				1		2							3	3
67.5		3	1					2	1	1						4	4
72.5	1	1	2	2				1	2	2	1				3	3	6
77.5		1	1	1		1				1		2		1	2	2	4
82.5				1		1				1			1		1	1	2
87.5			1	1	3					1		1	3		5		5
92.5					1								1			1	1
Total	1	7	6	5	4	2	1	3	5	6	1	3	5	1	11	14	25
Average	11.6						33.9								81.2	71.8	76.0

Returns from this experiment were obtained during the years 1924 to 1927, when the fish were in their third, fourth, fifth, and sixth years. The 3-year class is represented by 1 recovery, the fourth by 4 recoveries, the fifth by 39, and the sixth by 31. The data relating to these recoveries are given in Table 24.

TABLE 24.—*Chinook-salmon fingerlings marked at Bonneville hatchery during the fall of 1922, when approximately 12 months old, and recovered during the seasons of 1924, 1925, and 1926*

Date of capture	Place of capture	Sex	Length, in inches	Weight, in pounds	Scale record, first year			
					Number of rings		Length of anterior radius, in millimeters ×120	
					Stream growth	Intermediates	Stream growth	Total
1924: May 3	The Dalles	Male	18	3	13	4	43	52
1925:								
May 1	Bonneville	do			20	0	42	0
May 11	Cascade Locks	do	25	9	16	0	44	0
May 15	Astoria	Female	28.25	10.5	28	0	74	0
No date	Warrendale cannery	do	40	35	25	0	60	0
1926:								
May 1	Ellsworth cannery		39					
May 3	do		32.5	18.5				
Do	do	Female	35	17.5				
Do	Rainier	Male	38	14				
Do	Ellsworth cannery	Female	37.5	24	18	6	56	71
May 4	do	do	34	21	18	12	54	87
Do	Warrendale cannery	do	37	20	20	5	53	74
May 5	Ellsworth cannery		34	17				
Do	do		40	33				
Do	do		40	39				
Do	do	Female	35.5	24	17	7	45	66
Do	Warrendale cannery	Male	34.5	15.5				
Do	do	Female	34	15	15	7	54	75
Do	do	do	36	19	18	4	59	72
Do	Ellsworth cannery	do	37	25	16	4	39	50
Do	Cascade Locks	do	37	22	17	7	42	63
May 6	Warrendale cannery	Male	34	21	18	5	59	72
Do	Ellsworth cannery	do	33	24	18	6	56	72
Do	Warrendale cannery	do	38	27	16	5	50	63
May 7	Ellsworth cannery	Female	32	14	14	5	42	56
Do	do	Male	29.5	19.5	13	6	36	50
May 8	do	do	28.5	18	12	5	39	56
Do	Warrendale cannery	do	34	17.5	16	11	44	69
May 10	do	do	36	18	17	6	56	72
May 11	Cascade Locks	Female	38.75	25.5	15	5	45	57
Do	Ellsworth cannery	Male	38	29	16	0	48	0

TABLE 24.—*Chinook-salmon fingerlings marked at Bonneville hatchery during the fall of 1922, when approximately 12 months old, and recovered during the seasons of 1924, 1925, and 1926*—Contd.

Date of capture	Place of capture	Sex	Length, in inches	Weight, in pounds	Scale record, first year			
					Number of rings		Length of anterior radius, in millimeters ×120	
					Stream growth	Intermediates	Stream growth	Total
1926—Continued.								
May 15	Ellsworth cannery	Female	32	17	14	0	38	0
May 16-22	Dixon Entrance, southeastern Alaska	do	36	19	17	6	44	62
May 17	The Dalles	Male	38.5					
May 25	Ellsworth cannery	Female	28	18	11	4	29	36
June 4	do	do	34	21	12	8	36	54
June 8	do	Male	40	36	16	8	48	72
Do	do	Female	36	24.5	21	2	50	56
Sept. 23	Warrendale cannery	do	36	23.5	22	10	63	93
No date	Ellsworth cannery	Male	31	17	17	0	44	0
	do	Female	34	18	19	0	54	0
	do		15	13			30	39
	Warrendale cannery Tanner Creek	Female	33	15	18	0	48	0
1927:								
Feb. 22	Astoria cannery	Female	48	32				
Feb. 24	do	Male	48	37				
May 1-3	Warrendale cannery				18	0	46	0
Do	do	Male	45	40	13	5	35	46
Do	do				19	0	49	0
May 4	do							
May 1-6	Ellsworth cannery				16	0	55	0
Do	do				15	4	41	48
May 8	do				17	4	50	63
Do	do				17	6	54	68
Do	do				15	11	42	74
May 9	do				19	6	54	71
Do	do				12	0	41	0
May 4-9	Warrendale cannery				22	0	56	0
Do	do	Female	35	30	15	12	40	80
Do	do	do	41	30	14	8	44	65
Do	do	Male	22	12	21	7	47	62
Do	do	do	44	31				
May 10	do							
May 11	do							
May 10-11	do				21	8	58	86
May 12	Vancouver	Male	38.5	25	14	5	44	55
May 13	Ellsworth cannery				14	8	30	48
May 16	Astoria	Male			14	7	35	50
May 14-19	Ellsworth cannery							
May 20	do				12	0	39	0
May 12-29	Warrendale cannery				21	0	65	0
Do	do				15	9	46	70
June 18	Ellsworth cannery				13	4	41	49
June 21	The Dalles	Female	39.5	24	14	0	45	0
July 5	Warrendale cannery	do	39	24	15	4	44	58

One of the 5-year-olds was caught by troll in the ocean off the coast of southeastern Alaska, approximately 600 miles from the mouth of the Columbia River. This record is of much interest, because it corroborates data obtained from other sources showing that salmon travel great distances in the ocean. The tagging of adult salmon caught by troll in the ocean has shown that chinooks found as far north as Queen Charlotte Islands, British Columbia, may later enter the Columbia River (Williamson, 1927). This record extends the known range of the Columbia River chinooks to include southeastern Alaska.

In this experiment we find, for the sixth time, the progeny of the spring run of salmon entering fresh water on their spawning migration at a definite and regular time of the year. As in the other similar experiments, the majority of the recoveries

were reported during the first week of the commercial fishing season. Only 14 of the 75 recoveries were made after the middle of May.

One of the 6-year-olds, which was caught on September 23, represents an exception to this rule. As only one other exception was found, this record has been checked carefully to determine if it is authentic. The scars were found to be typical of those produced by marking, and no reason for questioning any part of the data presented itself. The nuclei of the scales from this fish do not agree exactly with those of the other fish recovered from this experiment; but the record could not be invalidated on this score, because the nuclei in the collection show a wide range of variation, one extreme of which might be represented by the scale in question. The age indicated by the scales is correct.

Three possible explanations for the irregularity of this record might be suggested: 1. It may be an authentic exception to the rule that the progeny of the spring run return in the spring. 2. The fingerling from which this fish developed may have been one from the fall run of chinooks that by accident became mixed with the spring chinooks at the hatchery. 3. The fish may have lost the fins by some other means. As there is no evidence that the second or third possibility is true, the first must be accepted tentatively.

One of the 5-year-olds returned to Tanner Creek and was recovered in the spillway from the hatchery ponds in which it was reared as a fingerling. This is the fourth of the marked spring chinooks that has returned to the tributary in which it was liberated.

The nuclei of the scales of the adult fish in this collection are more variable than those of any other marked spring chinooks. Most of the variations may be grouped into a single general type, however. In this general type the nucleus consists predominately of stream growth surrounded by a narrow band of intermediates. (See Table 24.) The presence of the band of intermediates at the end of the first year typically results in a gradual transition in the nature of the rings and obscures the points of demarcation, both between the stream and intermediate growth and between the intermediate and ocean growth. The scale shown in Figure 63 is a good example of this condition. A scale with the three types of growth more clearly differentiated is illustrated in Figure 64. In some cases the intermediates are distinctly differentiated from the ocean growth but closely resemble the rings of stream growth. A scale of this nature is illustrated in Figure 65. Without a series of scales with which to compare it, this nucleus might be considered as a pure stream type.

The band of intermediates varies in width from a maximum of 12 rings, as shown in Figure 66, to none, as shown in Figure 67. Figures 63 and 64 show more average widths. The apparent absence of intermediates in some cases may be due to a lack of contrast between them and the rings of stream or ocean growth. It is especially difficult to distinguish the intermediates when they are only 1, 2, or 3 in number. An extremely wide band of intermediates combined with a slight contrast between the stream and intermediate growths gives the nucleus in Figure 66 the appearance of an ocean type, and it is possible that the outer rings of this nucleus actually were formed in the ocean. If this be the case, the nucleus should be classed as a composite type.

The stream growth shown on these scales generally is divided into two parts by an incidental check, the inner of which corresponds to a similar portion observed on the scales of the fingerlings.

The presence of the band of intermediates within the nucleus of these scales indicates that the fish migrated, at least to the estuary, during their first year. Spring chinooks normally remain in the stream for their entire first year, and it is believed that the probable reason for these fish leaving fresh water before that time was the unfavorable nature of conditions in Tanner Creek, where the fingerlings were liberated. It would be impossible for this small creek to support the large numbers of fingerlings that are liberated in it each year from the hatchery. Similar conditions and scale peculiarities were found in experiment No. 5. Intermediate rings have not been found among the other marked spring chinooks, probably because they were liberated at about the end of the growing season.

Typical scales of mature fish in their third, fourth, and fifth years are shown in Figures 68, 69, and 70.

EXPERIMENT NO. 11.—KLASKANINE HATCHERY, AUGUST, 1922

Eggs from: Willamette River system, 1921.
Reared and marked at: Klaskanine hatchery.
Mark used: Removal of adipose fin and dorsal fin.
Number marked: 50,000.
Liberated: In Klaskanine River during August, 1922.
Age: Approximately 10 months.

An unselected sample of 20 fingerlings preserved on August 18, 1922, averages 73.5 millimeters in length. The anterior radius of the scales of these fish averages $\frac{31.0}{120}$ millimeters in length. The average number of rings is 9.8. All but two of the scales have an incidental check, which incloses 5 to 9 rings and is followed by 1 to 5 more widely spaced rings. The size and scale data are given in Table 25. A typical scale is illustrated in Figure 71.

TABLE 25.—*Chinook-salmon fingerlings marked at Klaskanine hatchery August 18, 1922*

Length, in millimeters (mid-value of class)	Scale record														Males	Females	Total
	Number of rings					Length of anterior radius, in millimeters × 120 (mid-value of class)											
	8	9	10	11	12	23	25	29	31	35	37	39	41	45			
57.5	2	1				1	1	1							2	1	3
62.5			1					1								1	1
67.5	2		1	1		1	1			1		1			1	3	4
72.5	1	1	1			1		1	1						1	2	3
77.5			1	1	1			1			2				2	1	3
82.5		2		1				2	1						2	1	3
87.5					2							1		1	1	1	2
92.5				1									1		1		
Total	5	4	4	4	3	3	2	6	2	1	2	2	1	1	10	10	20
Average	9.8					31.0									75.2	71.8	73.5

Only one adult fish that could be identified as belonging to this experiment has been recovered. This one, a 5-year-old, was found during the spring of 1926 in the spillway from the rearing ponds at the Klaskanine hatchery. The scales of this fish are absorbed at the margin, but at least a trace of the fourth winter check is to be found at some points. The nucleus is of the composite type. (See figs. 72 and 73.) The bands of stream and ocean growth in the nucleus are of about equal widths, the combined radius being $\frac{107}{120}$ millimeter. At the margin of the stream growth are five rings, which may be intermediates.

It is interesting to note that here, as in experiment No. 10, a spring chinook, upon being liberated in a tributary that normally supports only a fall run, left fresh water before the end of the first year.

EXPERIMENT NO. 12.—BIG WHITE SALMON RIVER HATCHERY, MAY AND JUNE, 1923

Eggs from: Big White Salmon River and Spring Creek, 1922.
Reared and marked at: Big White Salmon River hatchery.
Mark used: Removal of adipose fin and left ventral fin.
Number marked: 100,000.
Liberated: In Columbia River at Big White Salmon River hatchery during May and June, 1923.
Age: Approximately 8 months.

The Big White Salmon River hatchery is situated at the mouth of a small creek (Spring Creek) that empties into the Columbia River about 1 mile below the mouth of the Big White Salmon River. At this point the Columbia River is paralleled closely by a high cliff, and at the base of this cliff a large spring breaks out and forms a small creek, which flows for only a few hundred yards across a sand bar to the Columbia River. It is from this spring that the creek derives its name. By constructing a dam across the mouth of the creek a rearing pond for salmon fingerlings was formed. The same pond is used for holding adult salmon from the time they reach the creek until they are ready to spawn. In its natural condition the creek was not accessible to salmon and none were known to attempt to enter it, but since the hatchery has been operated there a thousand or more adult chinooks annually attempt to find spawning grounds there, and their eggs are taken for artificial propagation. No attempt is made to keep the eggs taken in Spring Creek separate from those taken in the Big White Salmon River. As a result the fingerlings marked in this experiment developed from eggs taken at both places.

The first few thousand marked fingerlings were liberated in Spring Creek, but at the mouth of the creek they were attacked by predatory fishes (probably the squawfish, *Ptychocheilus oregonensis*), which congregated there in large numbers, presumably attracted by food drifting out from the pond and occasional fingerlings that escaped from the hatchery. The rest of the marked fingerlings were carried to a little cove in the Columbia about 100 yards below the mouth of the creek, where apparently they were not molested by predatory fishes.

A sample of 50 fingerlings preserved on June 12, 1923, averages 52.2 millimeters (2 inches) in length. Their scales have an average of 5.9 rings and an average anterior radius of $\frac{20.6}{120}$ millimeters. A typical scale is illustrated in Figure 74. The detailed data are given in Table 26.

TABLE 26.—*Chinook-salmon fingerlings marked at Big White Salmon River hatchery June 12, 1923*

Length, in millimeters (mid-value of class)	Scale record															Males	Females	Total
	Number of rings						Length of anterior radius, in millimeters×120 (mid-value of class)											
	3	4	5	6	7	8	11	15	17	19	21	23	25	27	29			
42.5	1		1				1		1								2	2
47.5	1	2	5	3	1			1	2	3	4	2				7	5	12
52.5			5	10	5				2	7	5	3	1	1	1	13	7	20
57.5			1	8	4	2			1	2	5	1	2	3	1	8	7	15
62.5						1									1	1		1
Total	2	2	12	21	10	3	1	1	6	12	14	6	3	4	3	29	21	50
Average	5.9						20.6									52.3	51.9	52.2

This experiment has produced a greater number of returns than any other experiment with chinook salmon. A total of 453 fish (0.45 per cent of the number liberated as fingerlings) has been recovered. Four that matured during their second year were taken near Astoria during August, 1924. Sixty-two 3-year-olds were taken in the commercial fishery during the season of 1925; an additional 25 returned to Spring Creek that season, and 1 ran into the Big White Salmon River. Ten of those reported from the commercial fishery were taken by troll in the ocean. During the season of 1926 two hundred and seventy-one 4-year-olds were recovered—230 in the main Columbia River, 5 in the ocean, 33 in Spring Creek, and 1 in each of three tributaries that empty into the Columbia not far from the mouth of Spring Creek. Five-year-olds recovered during the season of 1927 totaled 90; 66 were reported from the commercial fishery and 24 ran into Spring Creek. One also was reported from the Little White Salmon River egg-taking station, but as the scars showing which fins were lacking were not preserved this report is not presented as a valid record of the recovery of a marked fish. A few 6-year-olds from this experiment may be recovered during the season of 1928.

Nearly all of the adult fish recovered from the commercial fishery were found after they had reached the canneries. As a result it was generally impossible to determine just where the fish were caught. As the recoveries for which the exact place of capture was reported are too few to be of any significance, the data from the commercial fishery have been grouped into three general localities—(1) the ocean, (2) the lower Columbia, which includes from the mouth of the river to Vancouver, Wash., and (3) the upper Columbia, including the portion of the main Columbia from Vancouver to the upper limit of the commercial-fishing district. The recoveries are tabulated according to place and date of capture in Table 27.

TABLE 27.—*Chinook salmon marked at Big White Salmon River hatchery during the spring of 1923, when approximately 8 months old, and recovered during the seasons of 1924, 1925, and 1926*

Place and date of capture	1924	1925	1926	1927
Ocean:				
May 22			1	
June 14		1		
July 22				1
July 26		1	1	
Aug. 4		1		
Aug. 6			1	
Aug. 9			1	
Aug. 14		1		
Aug. 22		1	1	
Aug. 25 [1]				1
Sept. 1		1		
Sept. 12				1
No date		4		
Total		10	5	3
Lower Columbia:				
June 16		[2] 1		
Aug. 2	2			
Aug. 4				1
Aug. 6			1	
Aug. 7			2	
Aug. 8			2	
Aug. 9			1	
Aug. 10		1	2	
Aug. 11		1	1	
Aug. 12			5	1
Aug. 13			5	
Aug. 14			1	
Aug. 15				1
Aug. 16			5	2
Aug. 17		1	5	1
Aug. 18			5	2
Aug. 19		2	4	4
Aug. 20			2	4
Aug. 21			5	1
Aug. 22	1	3	1	2
Aug. 23			7	1
Aug. 24		2	7	3
Aug. 25 [1]	1	3	15	6
Aug. 29		[2] 1		
Sept. 2			[2] 1	
Sept. 10			3	3
Sept. 11		2	21	3
Sept. 12		4	17	6
Sept. 13			16	1
Sept. 14			8	
Sept. 15		4	10	1
Sept. 16		1	6	1
Sept. 17		1	3	
Sept. 18			1	
Sept. 20			5	
Sept. 21		1	2	
Sept. 23				1
Sept. 25			1	
Lower Columbia—Continued.				
Sept. 26			2	
Oct. 2				1
No date		9	11	10
Total	4	37	183	56
Upper Columbia:				
Sept. 12		3		1
Sept. 13		1	7	2
Sept. 14		3	1	1
Sept. 15		5	6	
Sept. 16		2	9	1
Sept. 17			8	
Sept. 18			1	2
Sept. 20			1	
Sept. 21		1		
Sept. 22			2	
Sept. 23			10	
No date			2	
Total		15	47	7
Spring Creek:				
Sept. 8		1		
Sept. 10			1	
Sept. 11		3		
Sept. 14		4		
Sept. 15		3	1	
Sept. 16				1
Sept. 19		4		
Sept. 20				3
Sept. 25			1	
Sept. 26				1
Sept. 27			1	
Sept. 29			1	1
Oct. 1			17	
Oct. 2		5		13
Oct. 4			2	
Oct. 5		2		
Oct. 6		2		
Oct. 7		1	5	
Oct. 8				2
Oct. 11			1	
No date			3	3
Total		25	33	24
Big White Salmon River:				
Sept. 30		1		
Oct. 5			1	
Total		1	1	
Little White Salmon River: Sept. 29			1	
Tanner Creek: No date			1	

[1] A closed season for commercial fishing accounts for the absence of records from the Columbia River during the period Aug. 25 to Sept. 10.

[2] The place of capture for this recovery was not reported. As it is from a cannery that handles a large quantity of troll-caught salmon, this fish probably was caught in the ocean.

The length and weight data for the adult fish appear in Tables 28 and 29. Because of the unreliability of measurements made by so large a number of persons as have reported marked salmon, lengths and weights were not required during the season of 1927. This accounts for the relatively few size data for that season.

TABLE 28.—*Chinook salmon marked at Big White Salmon River hatchery during the spring of 1923, when approximately 8 months old, and recovered during the seasons of 1924, 1925, and 1926*

Length, in inches (mid-value of class)	Fish in their second year, 1924, males	Fish in their third year, 1925		Fish in their fourth year, 1926		Fish in their fifth year, 1927	
		Males	Females	Males	Females	Males	Females
21.5	1						
22.5	2	1		1			
23.5		2	2				
24.5		4	2		1		
25.5			1	1	3		
26.5		4	1	1			
27.5		1	1		2		
28.5		6	2	4	2		
29.5		7	2	3	1		
30.5		6		4	3		
31.5		2		8	6		
32.5		8	1	8	4		
33.5		2		12	2		
34.5		5	1	12	17		1
35.5				7	23		2
36.5			1	8	12	1	5
37.5				11	16		3
38.5				7	13	1	5
39.5				10	10		1
40.5				10	2		2
41.5				4	3	1	2
42.5				5		3	2
43.5							1
Total	3	48	14	116	120	6	24
Average length	22.2	30.0	28.2	35.6	35.5	40.7	38.5

TABLE 29.—*Chinook salmon marked at Big White Salmon River hatchery during the spring of 1923, when approximately 8 months old, and recovered during the seasons of 1924, 1925, and 1926*

Weight, in pounds (mid-value of class)	Fish in their second year, 1924, males	Fish in their third year, 1925		Fish in their fourth year, 1926	
		Males	Females	Males	Females
5.5	1				
6.5	2		2		
7.5		3			
8.5			1		
10.5				1	
11.5		2	2	2	1
12.5		4		2	
13.5		1	4		1
14.5		4		1	
15.5		4	1	2	3
16.5		3	1	6	3
17.5		4		5	2
18.5				7	4
19.5		1		1	5
20.5		3		4	6
21.5		1	1	5	6
22.5				8	7
23.5				8	8
24.5		1		9	11
25.5				2	15
26.5				6	5
27.5				1	4
28.5				6	8
29.5				1	2
30.5				9	3
31.5				4	2
32.5				3	3
33.5				3	
34.5				2	
35.5				3	
38.5				1	
40.5				1	
42.5				1	
Total	3	31	12	104	99
Average weight	6.2	15.3	12.7	24.5	23.8

The recoveries reported by the fishermen who troll for salmon in the ocean add to our meager knowledge of the movements of salmon in the ocean. Sixteen of the 18 fish taken by this means were caught by trollers who operate out of the

Columbia River ports. These records indicate that some of these fish were to be found within a short distance of the mouth of the Columbia during the entire fishing season of each year. Recoveries from this district range in date from May to September. The two remaining records of recoveries in the ocean are from more remote localities. Both are from the west coast of Vancouver Island—one from near Barkley Sound, taken on August 6, 1926, the other from near Ucluelet, British Columbia, taken on August 9, 1926. These two recoveries agree with data obtained from tagging experiments in showing that fish that will enter the Columbia River during the fall may be found only a short time before at a considerable distance up the coast.

The data for the recoveries of 4-year-olds give the best indication of the time of the spawning migration. Appearing first at the mouth of the Columbia River during the first week of August, these fish increased in abundance up to August 25, when a closed season for commercial fishing cut off our records. When fishing was resumed on Septemer 10 they were caught at the mouth of the river in even greater numbers than during August, and they appeared for the first tme in the vicinity of Cascade Locks. About the middle of September the run began to drop off, and by the 1st of October the fish disappeared completely from the commercial fishery.

The dates of recovery at Spring Creek give little indication of the time at which the fish reach the creek, because most of them were not discovered until spawning time. The hatchery records of the general run into Spring Creek are more reliable for this purpose. These records show that the majority of the fish enter the creek during September. Starting early in the month, about half of the run has passed by the 20th and only a few come in after the 1st of October. The fish are nearly ready to spawn at the time they enter the creek, but, in the absence of a gravel bottom on which to spawn, they retain their eggs and sperm. This makes it possible to delay the stripping process until most of the fish have matured. The bulk of the eggs then are taken in one or two days. This restricted egg-taking period accounts for the bunching of recoveries at Spring Creek.

The data at hand indicate that most of the adult fish that escaped the commercial fishery returned to Spring Creek to spawn. Eighty-two were recovered in that creek, and only four are known to have chosen other tributaries. The records from the commercial fishery of the upper Columbia are such that it is impossible to determine whether the fish were caught above or below the mouth of Spring Creek, but none was reported definitely from above that point, and one of the best fishermen from that region has reported that he searched for marked salmon but found none. Although a few of the fish have gone astray, there can be no question that most of them sought and, if not previously captured, found the very small tributary from whence they came.

The scales of these adult marked fish present an interesting series of composite nuclei, which, when studied as a group, offer no problems to one who is familiar with scales of this type. To the inexperienced observer, however, the many incidental checks that characterize this type would constitute a perplexing problem. A scale that is representative of this collection is illustrated in Figures 75 and 76. The innermost 5 or 6 rings of this scale are slightly lighter and more closely spaced than those immediately surrounding them. This portion of the scale corresponds exactly with the entire scale of the fingerlings at the time of liberation. (See table 26 and fig. 74.) At about 15 rings from the center a second break in the continuity of the rings (an

incidental check) may be seen. Still a third break is to be found at 35 rings. From this point there is a gradual widening of the rings into the rings of rapid growth of the second year. Following this second summer's growth is a band of closely spaced rings representing the second winter. This is followed in turn by the rapid growth of the third summer, the third winter check, and finally by a narrow marginal band of more widely spaced rings of the fourth summer. The last band and in some places even the third winter check have been removed by absorption.

An inexperienced observer might find difficulty in determining which check on this scale represents the first winter. If he decided upon the second check (at 15 rings), he would be forced to consider the third check (at 35 rings) as representing the second winter. His interpretation then would be that the fish was in its fifth rather than its fourth year. An experienced observer would not have this difficulty. His interpretation would be based upon a knowledge of the general nature of the different types of nuclei and the impression he gained from the appearance of the whole scale, neither of which is described easily. In this particular case the portion of the scale inclosed by the second check does not resemble a stream nucleus and it is too small to represent an ocean nucleus. Futhermore, the band between the second and third checks (in comparison to the other summer bands) is too narrow to represent a second year's growth in the ocean. Even a relatively inexperienced person probably would interpret correctly the age of this scale if he compared it with a series of scales of the same general type.

TABLE 30.—*Chinook salmon marked at Big White Salmon River hatchery during the spring of 1923, when approximately 8 months old, and recovered during the seasons of 1924, 1925, and 1926*

Length of anterior radius, in mm.×120 (mid-value of class)	Scale record of first year's growth											
	To first incidental check				To second incidental check				Total			
	Fish in their second year, 1924	Fish in their third year, 1925	Fish in their fourth year, 1926	Fish in their fifth year, 1927	Fish in their second year, 1924	Fish in their third year, 1925	Fish in their fourth year, 1926	Fish in their fifth year, 1927	Fish in their second year, 1924	Fish in their third year, 1925	Fish in their fourth year, 1926	Fish in their fifth year, 1927
7.5			2									
12.5	1	4	5	4								
17.5	2	16	14	23								
22.5	1	27	38	26								
27.5		12	11	13			2	1				
32.5		3	1	1		2	3	9				
37.5				1	2	6	19	8				
42.5					1	12	12	11				
47.5					1	10	11	16				
52.5						9	18	19			2	
57.5						11	13	5			1	1
62.5						6	5	6				3
67.5						5	2	2		5	7	5
72.5						5	1	1			4	3
77.5						6	1	2		3	4	4
82.5										9	5	8
87.5							1		1	1	11	6
92.5							1			3	8	11
97.5									3	11	10	8
102.5										6	8	6
107.5										7	5	4
112.5										5	12	10
117.5										1	8	4
122.5										3	2	4
127.5										4	4	2
132.5										3	3	0
137.5										2	1	1
142.5										6	1	
147.5										2		
152.5										1		
Total	4	62	71	68	4	72	89	80	4	72	96	80
Average	17.2	21.6	20.8	20.6	42.5	54.0	48.9	49.5	93.8	105.5	97.6	95.2

TABLE 31.—*Chinook salmon marked at Big White Salmon River hatchery during the spring of 1923, when approximately 8 months old, and recovered during the seasons of 1924, 1925, and 1926*

Number of rings	Scale record of first year's growth											
	To first incidental check				To second incidental check				Total			
	Fish in their second year, 1924	Fish in their third year, 1925	Fish in their fourth year, 1926	Fish in their fifth year, 1927	Fish in their second year, 1924	Fish in their third year, 1925	Fish in their fourth year, 1926	Fish in their fifth year, 1927	Fish in their second year, 1924	Fish in their third year, 1925	Fish in their fourth year, 1926	Fish in their fifth year, 1927
3		2	1									
4	1	1	4	3								
5		12	14	11								
6	3	16	20	19								
7		19	20	21								
8		9	9	10								
9		3	1	4								
10			1									
11			1			1	3	3				
12						6	4	2				
13					2	1	9	10				
14					1	7	10	8				
15						11	11	11				
16					1	7	16	17				
17						10	11	7				
18						6	11	8				
19						8	6	8				
20						4	3	3			2	
21						5	2				1	
22						3	1	1		2	1	2
23						1		1		3	4	4
24										1	6	5
25						1	1			7	3	3
26								1	1	3	7	9
27						1	1		1	2	6	3
28									1	4	5	10
29										8	12	7
30										7	15	8
31										5	7	5
32									1	5	12	4
33										5	4	3
34										5	2	11
35										6	2	2
36										3	2	3
37										2	3	
38										1	2	
39										2		1
40										1		
Total	4	62	71	68	4	72	89	80	4	72	96	80
Average	5.5	6.4	6.4	6.5	12.5	17.0	16.1	16.0	28.2	30.5	29.2	29.3

These nuclei are complicated further by the presence of an incidental check in the second year. This check may be seen in Figure 78. In this case the check is not sufficiently pronounced to cause any trouble. Ordinarily it causes no trouble in so far as age determination is concerned, but it may lead to some question as to what point on the scale represents the end of the first year's growth. This is especially true where the nucleus is poorly differentiated. The scale shown in Figures 79 and 80 gives difficulty on this score. If the check at 39 rings is the winter check, this nucleus is among the largest in the collection, the second summer band is extremely narrow, and the usual incidental check in the second year is absent. If, however, the check at 23 rings is the first winter check, the nucleus falls at the lower end of the range of size and the usual check formed at the time of liberation is lacking; but the second summer band, with its incidental check, is typical of this collection. The latter explanation appears to be the more logical.

Figures 81, 78, and 75 illustrate scales of fish that matured in their second, third, and fourth years, respectively.

EXPERIMENT NO. 13.—SALMON (IDAHO) HATCHERY, AUGUST, 1924

Eggs from: Little White Salmon River, 1923.
Reared and marked at: Salmon (Idaho) hatchery.
Mark used: Removal of both ventral fins and the adipose fin.
Number marked: 50,000.
Liberated: In the Lemhi River on August 22, 1924.
Age: Approximately 11 months.

A sample of fingerlings preserved at the time the remainder were liberated averages 58.1 millimeters in length. The scales average $\frac{22.2}{120}$ millimeters in radius and have an average of 7.8 rings. The innermost three or four rings frequently are conspicuously finer and more closely spaced than those nearer the periphery. A typical scale from a fingerling of average size is shown in Figure 82. The size and scale data are tabulated in Table 32.

TABLE 32.—*Chinook-salmon fingerlings marked at Salmon (Idaho) hatchery August 22, 1924*

Length in mm. (mid-value of class)	Scale record														Males	Females	Total
	Number of rings					Length of anterior radius, in mm. ×120 (mid-value of class)											
	6	7	8	9	10	15	17	19	21	23	25	27	29	31			
47.5		1				1										1	1
52.5	2		1			1			2						2	1	3
57.5	2	4	6	1	2		2		6	1	3	1	2		7	8	15
62.5		2	1	3	1			1	2		2		1	1	3	4	7
67.5		1		1					1					1	2		2
Total	4	8	8	5	3	2	2	1	11	1	5	1	3	2	14	14	28
Average	7.8					22.2									58.9	57.3	58.1

Two 3-year-olds and sixteen 4-year-olds were recovered from this marking. Others, which will mature in their fifth year, will return to spawn during the season of 1928. The detailed data concerning the recoveries appear in Table 33.

TABLE 33.—*Chinook salmon marked at Salmon (Idaho) hatchery during the fall of 1924, when approximately 11 months old, and recovered during the seasons of 1926 and 1927*

Date of capture	Place of capture	Scale record, first year					
		Number of rings			Length of anterior radius, in millimeters×120		
		To first incidental check	Total stream growth	Intermediates	To first incidental check	Total stream growth	Intermediates
1926:							
Aug. 10	Astoria cannery	7	15	9	22	41	74
During August	Cathlamet	7	16	0	27	46	0
1927:							
July 11	Ocean	7	19	0	21	51	0
July 25	do	7	15	7	21	36	56
July 28	do	5	14	5	15	39	55
Aug. 12	Ilwaco cannery	7	17	6	20	43	63
Aug. 13	Astoria cannery						
Aug. 16	Altoona cannery	9	18	0	17	51	0
Aug. 17	do						
Aug. 17	Chinook cannery	7	16	0	16	57	0
Aug. 17	Astoria cannery						
Aug. 20	do	7	18	0	27	63	0
Aug. 23	do	4	14	8	16	44	76
Aug. 24	Ilwaco cannery	9	16	6	23	45	64
Aug. 25	Astoria cannery	4	12	10	15	36	64
Aug. 25	do	6	16	6	17	45	67
Aug. 25	do	5	14	7	19	39	60
During September	do						

The chief purpose of this experiment was to furnish further information regarding the conditions that determine whether a given chinook will return at maturity as a part of the so-called spring or fall runs. Several experiments with the progeny of the spring run have shown that a change in the early environment does not alter the time of year at which the mature fish will start their spawning migration. This experiment furnishes similar evidence regarding chinooks of the fall run. In this case eggs from a run that enters the Columbia River during August and September and spawns at a distance of approximately 150 miles from the ocean were transferred to a station at approximately five times that distance from the ocean, where only a spring run of chinooks naturally spawns.

If these fish were to become adapted to the conditions under which they spent their early life, they would be expected to return to spawn in the headwaters where they were liberated. They would be expected to store in their bodies a quantity of fat sufficient to furnish energy for the long migration in fresh water. They would also be expected to leave the ocean early enough to allow time for the long migration before spawning time. None of these conditions seems to have prevailed. The time at which they passed through the lower Columbia on their spawning migration was no earlier than that of the Little White Salmon River chinooks that remained under natural conditions. As in the case of the latter, they appeared in the commercial catches of the lower Columbia during the last two-thirds of August. None of these fish returned to the Lemhi River, where they were liberated, nor did any enter the Little White Salmon River, where the eggs were taken. In fact, none were recovered as spawners. If any of them succeeded in passing the commercial-fishing district, we have no knowledge of where they went or whether they succeeded in reaching suitable spawning grounds. Records of the quantity of fat stored in the body of the fish were obtained for only four individuals. Although these records were merely approximations based upon the appearance of the flesh, they indicate that the quantity of fat was about average for fish of the fall run, which is much less than that of chinooks of the spring run.

The nuclei of the scales of the fish that were recovered in this experiment show very little variation. All have a central area of 12 to 19 rings (anterior radius $\frac{36}{120}$ to $\frac{63}{120}$ millimeters) of stream growth, which in most cases is surrounded by a band of from 5 to 10 rings of intermediates. (See Table 33.) The stream growth is broken by an incidental check, which incloses from 4 to 9 rings. A typical nucleus is shown in Figure 85. Scales from fish recovered during their third and fourth years are shown in Figures 83 and 84.

CONCLUSIONS

PERCENTAGE OF RETURN

The reported returns from these experiments range from 1 out of 50,000 liberated to 1 out of each 300 liberated. These figures have very little significance, however, because they represent not the total returns but an unknown and varying proportion of the total. As has been pointed out in the introduction, the authors and other employees of the Bureau of Fisheries who have assisted them with the collection of data have been unable to observe personally more than a small fraction of the fish

taken from the Columbia during the time when these experiments were in progress. It has been necessary, therefore, to depend upon fishermen and cannery employees for most of the records of returning marked fish. The number of persons who have searched for marked fish and the conditions that affect the efficiency of their efforts have varied so greatly as to make it impossible even to estimate with any degree of accuracy what proportion of the total recaptures have been reported. The apparent failure of some of the early experiments probably was due in part to the fact that no inducement was offered to those finding marked salmon to report their captures. The first real interest on the part of fishermen and cannery employees came in 1920 as a result of the Oregon fish commission's offer of a reward of 50 cents for each record of the capture of a marked fish. An increase in the reward to $1 in 1922 caused a greater response from those connected with the industry, but even with this inducement a great deal of encouragement and publicity was required to get people started reporting their captures. The system of collecting data has been improved constantly, until during the last few years it is believed that most of the recoveries have been reported.

Another source of error is in connection with the escapement; that is, those fish that succeeded in evading the commercial gear and continued on to the spawning grounds. In the experiments involving fish from Little White Salmon River and Big White Salmon River, nearly all of the escaped fish probably returned to their parent tributary and were caught in the course of the egg-taking operations. This is not true, however, of experiments involving chinooks of the spring run, the greater part of which did not enter the tributary in which they were liberated but continued on up the Columbia. No record is available of those that succeeded in passing the upper limit of the commercial fishery.

In view of the many sources of error it is useless to assign the experiments to rank in the order of success; but so little is known of the results of either natural or artificial propagation that even an approximation of the general success of these experiments will be of interest. Experiment No. 12 was the most successful, the reported recoveries representing 0.45 per cent of the fingerlings liberated. Experiment No. 7, with the reported recoveries representing 0.39 per cent of the liberation, stands second. The records of this experiment are not accurate, in that they do not include the escapement, which continued on up the main Columbia beyond the commercial-fishing district. Third in success is experiment No. 6, with 0.24 per cent recovered. Here again the escapement is not represented. Experiment No. 8, with 0.18 per cent recovered, is fourth. In these four experiments the records from the commercial fishery are believed to represent the majority of the marked fish that were caught. The returns that have not come to our attention certainly would not add enough to make the totals more than 1 or 2 per cent of the liberation.

SUCCESS OF LONG AND SHORT PERIODS OF REARING

One of the most important problems confronting those interested in the artificial propagation of salmon is the determination of the length of time the fingerlings should be held at the hatchery in order to get the greatest return. Some hatchery men prefer to liberate their fingerlings very soon after the yolk sack is absorbed, whereas others are of the opinion that best results are obtained from much longer rearing.

Two of the more recent marking experiments were designed to provide an answer to this question. Each of these involved five lots of marked fingerlings, which were liberated at varying ages. None of the fish in these experiments have reached maturity to date and have not been discussed in this report; but even the comparatively unreliable records of return from the various experiments herein described give some indication of the relative success of the long and short periods of rearing.

For consideration thereof the experiments may be arranged in groups. Those involving the progeny of the spring run into the Willamette River may be taken as one group. This will include experiments Nos. 1, 2, 5, 6, 7, 9, 10, and 11. In this category the longer periods of rearing have given the best results, virtually no returns having been obtained from fingerlings liberated during midsummer. Experiments Nos. 3, 8, and 12, which involved fingerlings derived from the fall runs into the Little White Salmon and Big White Salmon Rivers, form another group. In this case better results have come from a very short period of rearing than from liberating during midsummer. The success of the longer periods of rearing has not been determined for this group. On the basis of what is known of the habits of these two classes of chinooks we might have expected such results as have been obtained. As fingerlings of the spring run normally spend the entire first year in fresh water, best returns would be expected from the longer period of rearing. This is especially true if the fingerlings are forced by unfavorable conditions to leave the river as soon as liberated. In the case of the fall chinooks, which normally leave the stream soon after the yolk sac is absorbed, the shorter period of rearing might be expected to be the most successful.

INTERPRETATION OF SCALES

It is hardly necessary now to argue for the validity of the methods developed for determining the age and other features of the life history of salmon by means of a microscopic examination of their scales. These methods already have given abundant proof of their value, especially through the careful and extensive researches of Gilbert on the sockeye salmon. It is important to note, however, that the scales of these fish of known history corroborate fully the theory that the arrangement of the concentric rings (circuli) provides an accurate record of the previous history.

Moreover, a study of the scales of these marked fish has aided materially to solve the many perplexing problems that have arisen in the interpretation of the scales of the chinook salmon, particularly in connection with the early history as recorded in the nuclear area of the scales. Frequent mention of these matters has been made in the discussion of the returns obtained from the various experiments. It has been shown, particularly, that the growth of the first year (the "nuclear" growth) is subject to numerous variations, which intergrade so completely that it is impossible to draw any sharp line of distinction. At one end of the series we have the typical stream nucleus, denoting that the first year was spent entirely in fresh water, and at the other end the typical ocean nucleus, denoting that the fish ran out to the ocean immediately after emerging from the gravel of the spawning beds and spent the entire first year there. The majority of the Columbia River chinooks, however, have neither typical stream nor typical ocean nuclei but apparently have spent part of the first year in fresh water and part in the ocean. The result has been

a nuclear area composed in part of stream growth, with fine, narrow rings, and in part of ocean growth, with wide, strongly marked rings. This is amply explained by the habit of the young fish in the Columbia of migrating throughout the year and not, as in many other cases, during a definite and restricted season (Rich, 1920). According as the length of time in fresh water is short or long, the amount of stream growth is less or greater; in the first instance the nuclei approach the ocean type and in the second they approach the stream type, and the intergradations apparently are complete. For these nuclei, composed in part of stream and in part of ocean growth, we propose the term "composite nuclei."

A further complication arises as a result of the presence on many scales of "intermediate" growth—that formed during the life in the estuary while on the seaward migration. The rings formed at this time are "intermediate" in position and in appearance between the stream and ocean rings and vary so materially that it is difficult to distinguish them with certainty, sometimes from the stream rings and at other times from the ocean rings. Nuclei composed only of stream rings and intermediates blend indistinguishably with certain types of composite nuclei.

As a result of these variations the first year's growth on the scales of Columbia River chinooks frequently is very confusing and presents, in extreme cases, as many as four or five checks, each of which might easily be mistaken for an annulus by an inexperienced observer. As a matter of fact, however, with experience this confusion is eliminated almost completely, at least in so far as the determination of age is concerned. It may never be possible to interpret correctly the details of history recorded in a complicated composite type of nucleus, but that is relatively immaterial for practical purposes as long as there is no error in age determination, and our experience with the scales of fish of known history has provided sufficient information so that such errors may be eliminated almost entirely.

TIME OF ENTERING FRESH WATER

Perhaps the most important contribution which these experiments have made to our knowledge of the biology of the salmon is that relating to the hereditary character of the factors that determine the time of year when the adults enter fresh water and begin their migration to the spawning grounds. The great practical value of determining beyond question whether this is strictly an hereditary character or not is associated with the fact that the early run of chinooks (spring chinooks) is of much better quality and is, consequently, of much greater value to the fishery than the later run (fall chinooks). The spring fish are sought most earnestly, and the maintenance of the spring run has been the chief concern of those interested in practical conservation. This question has been asked frequently: Is it necessary to breed from fish of the spring run in order to produce spring fish, or is it possible, by proper handling of the progeny of the fall run, to produce fish that will return as adults to fresh water early in the spring?

The evidence of these marking experiments shows beyond question the heritable quality of this character. In 8 of the 13 experiments the young fish were derived from eggs taken either on the Willamette River or its tributaries, the McKenzie and the

Santiam, where the spawning runs are composed exclusively of salmon that enter the Columbia early in the spring. The fish were reared and liberated on tributaries of the Columbia that normally are inhabited by fall-running salmon only, but the marked fish returned to the river as adults during the spring. Of the 390 adults that have been recovered from these experiments, 365 were taken before June 1, and there is some evidence that all but two of those taken after that date had entered the river some time before they were caught. These fish not only were subjected to an unnatural environment during their early lives but also were liberated at various ages, ranging from 7 to 18 months. Neither of these conditions seems to have changed the time of their return to fresh water.

A converse experiment (experiment No. 13), in which the progeny of fall chinooks were reared and liberated under conditions normal to spring chinooks, has given similar results. All of 16 mature fish recovered from this experiment started their spawning migration in the fall.

Another interesting feature of the spawning migration demonstrated by these experiments is the comparatively short time during which the fish from each tributary leave the ocean. As has been pointed out, chinooks that spawn in the Willamette, McKenzie, and Santiam Rivers with but few exceptions enter the Columbia River before the 1st of June. The fish that developed from eggs taken on the Little White Salmon and Big White Salmon Rivers were found to be passing though the commercial fishing district in August and September. All the fish in experiment No. 4, which were introduced from the Umpqua River, were caught during a period of less than a month, beginning May 13. It seems fairly clear that the fish belonging to any given tributary enter the main river from the ocean at a definite and characteristic time. This is an important point, as it gives additional evidence of the existence of local races in the tributary streams and shows that each race is present in the main river only a comparatively short time. Knowing, further, that each race is self-propagating, it becomes perfectly apparent that all parts of the salmon run in the Columbia River must be given adequate protection if the run as a whole is to be maintained. The protection of only one or two portions of the run will not be sufficient, inasmuch as certain races will be left entirely unprotected.

AGE AT MATURITY

The relation between the reported returns and the actual returns has varied so greatly as to make only a general consideration of the age at maturity justifiable. For this purpose the experiments again may be divided into two classes—those involving spring chinooks from eggs taken on the Willamette River and its tributaries and those involving salmon from the Big White Salmon and Little White Salmon Rivers, which enter fresh water during the latter part of the season.

Mature spring chinooks that were in their third to sixth years have been recovered. In every case the greatest number matured in their fifth year. The 6-year-olds have always exceeded the 4-year-olds, and the 3-year-olds are represented by only two recoveries.

The data relating to the fall chinooks are very inadequate, but they indicate that the fourth and fifth years are the prevailing ages at maturity. On the whole, the fish of this class mature one year younger than the spring chinooks. A few males mature

in their second year, and a significant number of both males and females return in their third. No 6-year-olds have been recovered as yet. From the standpoint of growth, however, there is very little difference in the time of maturing; that is, the two classes mature after approximately equal intervals of rapid growth. The rate of growth in fresh water is so low, in comparison to that in the ocean, that a year of fresh-water growth is insignificant in comparison to two or more years of ocean growth. The size attained, therefore, is proportional to the length of time spent in the ocean. The fall chinooks normally enter the ocean early in their first year, whereas the spring chinooks remain in the streams for an entire year before going to the ocean. In addition, the former remain in the ocean for three or four months of the rapid-growing season of the year in which they mature, whereas the spring chinooks start their spawning migration so early in the year that they make little or no growth during the last season. As a result of the earlier seaward migration and later spawning migration the fall fish spend approximately one full growing season more in the ocean than do the spring chinooks of the same age and have spent about the same time in the ocean as spring chinooks one year older. The relation between ocean residence and time of maturing is therefore about the same for the two classes.

HOMING INSTINCT

The so-called "parent-stream" theory or "home-stream" theory is now substantiated by such a wealth of evidence that it seems nearly superfluous to state that none of the salmon marked on the Columbia have been recovered in any other river system.

The records of marked Columbia River chinooks taken off the coast of British Columbia and southeastern Alaska show something of the wide oceanic migrations of these fish and are in agreement with the results of the tagging experiments. The tagging experiments in British Columbia in 1925 (Williamson, 1927) showed conclusively that a large percentage of the spring (chinook) salmon caught by troll in these northern waters originated in the Columbia River. In view of this wide range in the ocean, the fact that no marked fish were reported in any other stream than the Columbia indicates clearly the force and discrimination of the homing instinct as it affects the return to the home stream.

It is evident, furthermore, that under normal circumstances salmon predominantly return to spawn in the tributary in which they spent the early part of their lives, although they have been shown not to do so in some instances. It is important to note, in this connection, that the transplanted fish have shown no tendency to return to the stream from which the eggs were taken. The homing instinct is not a purely hereditary matter, therefore, but is determined largely by the early environment. These experiments have shown that under certain circumstances the return to the home tributary is by no means invariable and that the major part of a run may fail to return to the tributary in which it was reared and liberated. Experiment No. 7 gave the most conclusive evidence on this point. Nearly half of the 252 adults recovered from this experiment were taken in the Columbia River several miles above the mouth of Tanner Creek, where the fingerlings were liberated. As only three were taken in Tanner Creek, it is apparent that the majority chose not to enter that

tributary and continued up the main river. Six other experiments, which, like experiment No. 7, involved spring chinooks that were liberated in tributaries other than the one in which the eggs from which they developed were taken, have given similar results. From these experiments only four returns to the place of liberation have been reported. It may be concluded tentatively that, in part at least, some element in the complex known as the homing instinct is hereditary, so that the instinct does not function perfectly in the case of transplanted fish. It seems possible that this might be a determining factor in the establishment or rehabilitation of salmon runs by means of artificial propagation.

The experiments with chinooks of the fall run have resulted in much greater returns to the place of liberation. Ninety-nine of the 504 recoveries recorded for the experiments with salmon of this group were caught at the hatcheries at which the fingerlings were reared and liberated. Five of these fish entered near-by tributaries, but no others are definitely known to have strayed, the remainder having been taken either in the ocean or in the Columbia River below the mouth of the home tributary. The most striking instance of this return to the home stream is that to Spring Creek. This stream is so extremely small that it is difficult to see how the salmon could find it at all, and yet 82 of the fish marked here were recaptured here as adults, while only 4 were taken in other spawning tributaries. This is the most definite evidence known to us of the validity of the home-stream theory as applied to tributaries.

The reason for this difference in the homing of the spring and fall chinooks is not shown conclusively by the data at hand. It seems, however, that the homing instinct is disturbed to some extent by transplanting the eggs from one tributary to another, the disturbance being greatest when the eggs are transferred to tributaries that offer least favorable conditions for the returning mature fish. The marked spring chinooks in every experiment were transplanted in tributaries that could not support a spring run. The fall chinooks, on the other hand, were liberated in either their native stream or another that offered favorable conditions for a fall run. While by no means conclusive, the evidence indicates that the transplanting of eggs from one tributary to another has an unfavorable influence on the homing instinct of the resulting fish. This is a matter of considerable importance in fish-cultural operations, particularly in cases where attempts are made to rehabilitate runs by transplantation from other streams. So far as these experiments go, they indicate that a better practice would be to stock each stream with eggs native to that stream.

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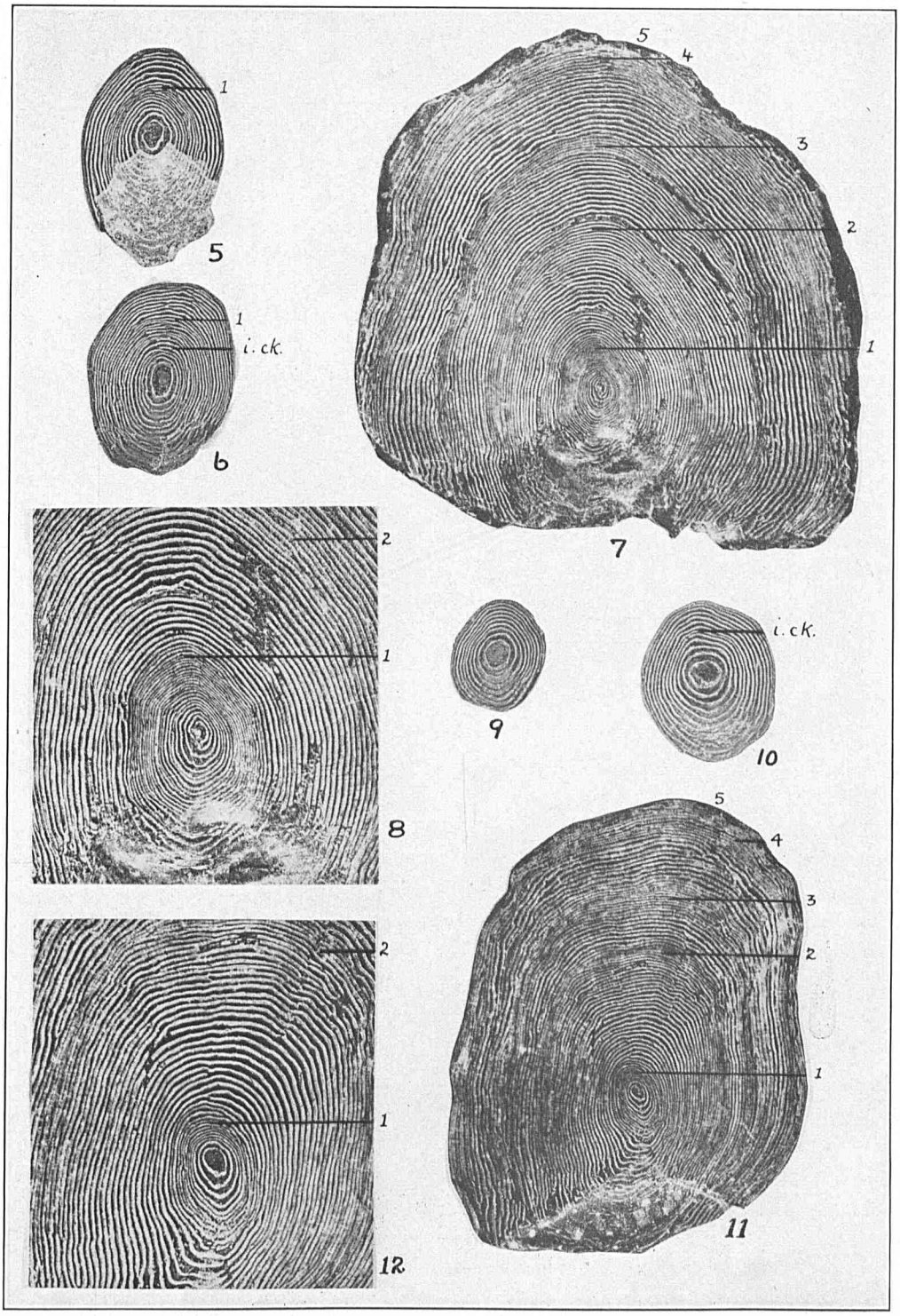
EXPLANATION OF FIGURES

The magnifications indicated in all of the legends are only approximate. Abbreviations used in the figures: *i. ck.* indicates incidental check; *st. gr.*, stream growth; *int.*, intermediate growth; *1, 2, 3*, etc., the age of the fish in years when the corresponding points on the scales were marginal.



EXPERIMENT 1

FIG. 5.—Yearling, 132 millimeters, Bonneville hatchery, March 2, 1926, showing well defined winter check. × 25

FIG. 6.—Yearling, 122 millimeters long, marked at Bonneville hatchery, March 11, 1916. Typical scale showing poorly defined incidental and winter checks. × 25

FIG. 7.—Marked at Bonneville hatchery during the spring of 1916 as a yearling. Recovered near The Dalles, Oreg., May 4, 1920, in its sixth year. Male, 48 pounds in weight. The scale is absorbed to such an extent that the winter band of the fifth year and whatever may have been formed of the sixth year's growth do not show. × 13

FIG. 8.—Nuclear region of the scale shown in Figure 7. × 25

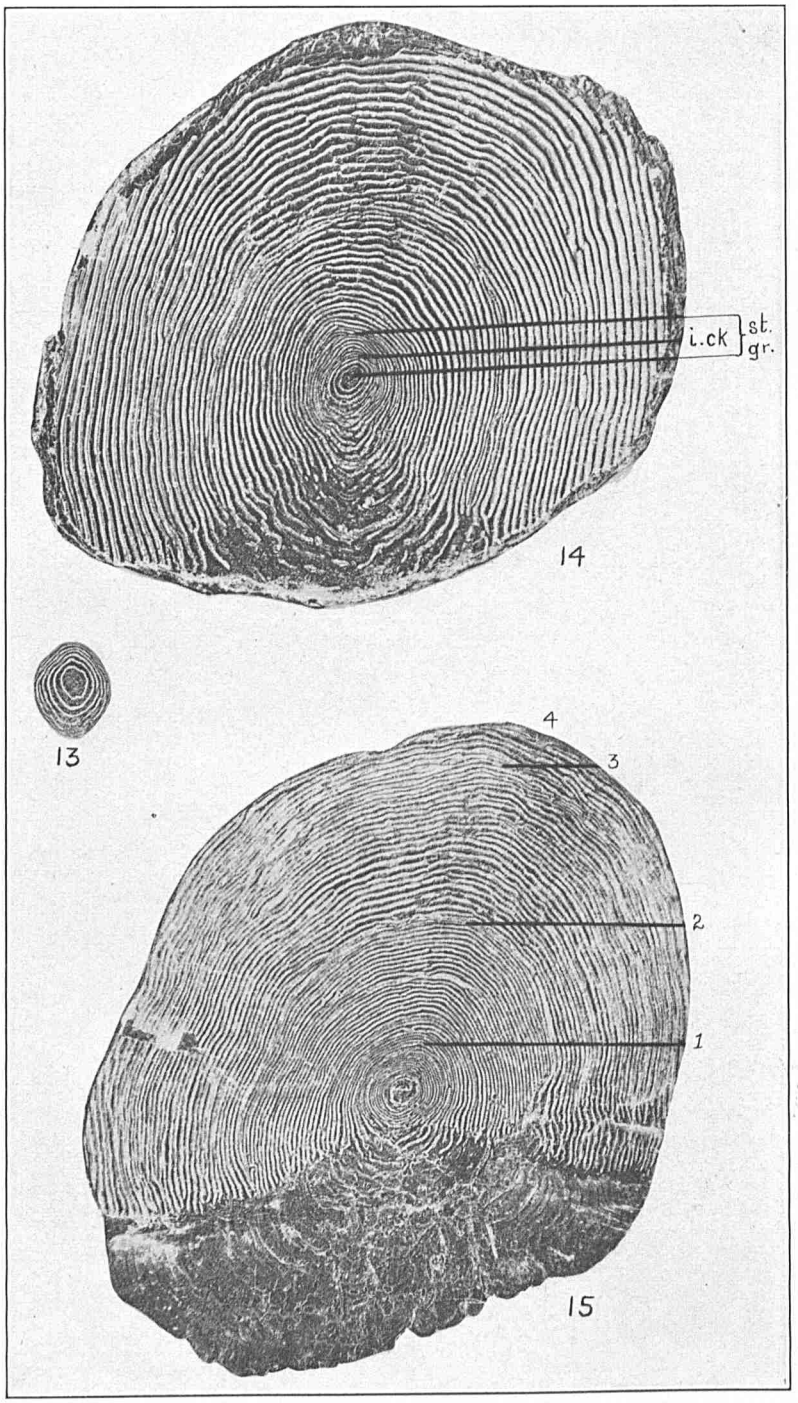
EXPERIMENT 2

FIG. 9.—Fingerling, 81 milimeters, Klaskanine hatchery, July 16, 1916. A typical scale with no incidental check. × 25

FIG. 10.—Fingerling, 94 millimeters long, marked at Klaskanine hatchery, July 16, 1916, showing incidental check. × 25

FIG. 11.—Marked at Klaskanine hatchery during the summer of 1916, when approximately 11 months old. Recovered at Astoria, Oreg., between May 25 and June 21, 1920, in its fifth year. This scale was taken from the skin attached to the scar of the dorsal fin, which accounts for its small size. × 13

FIG. 12.—Nuclear region of scale shown in Figure 11. × 25

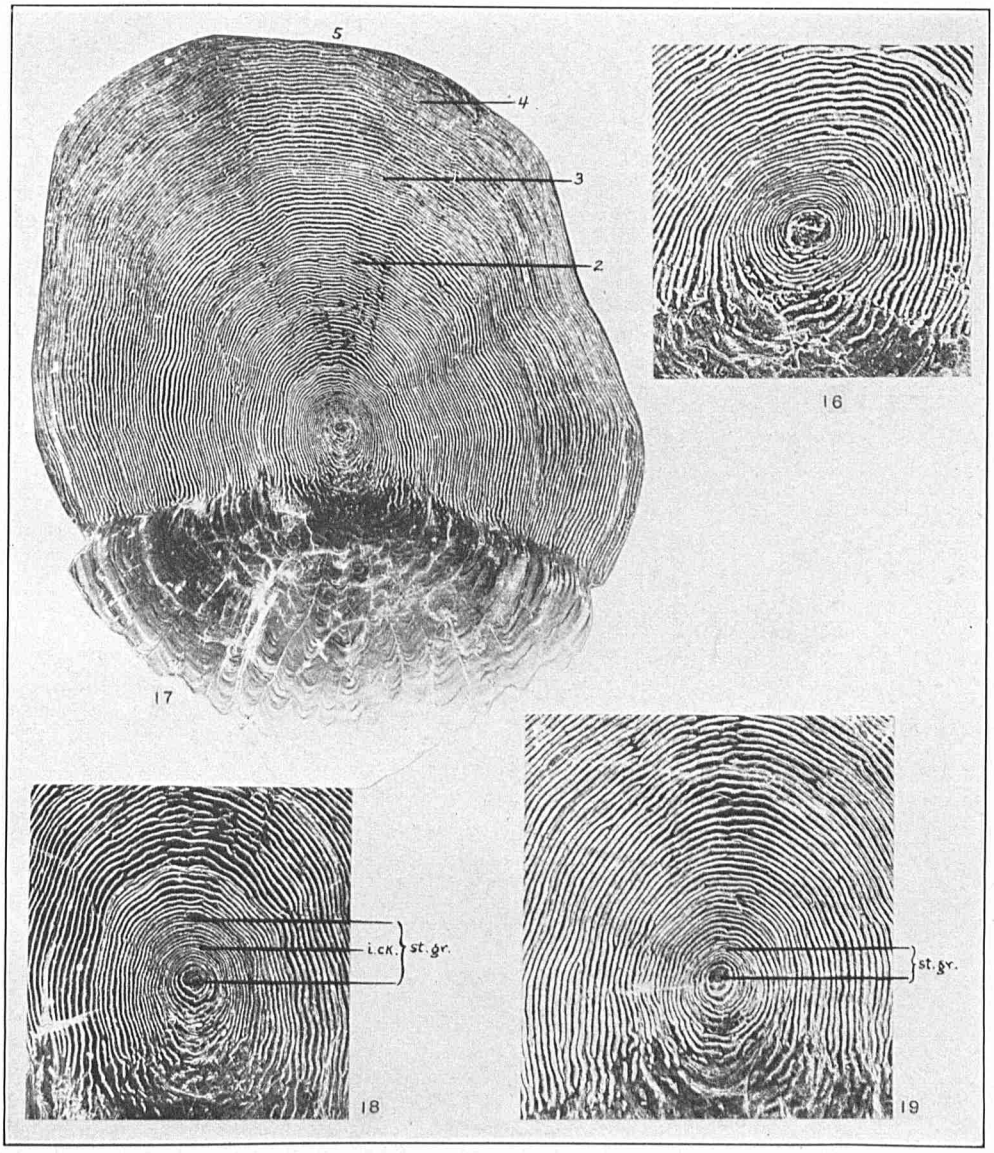


EXPERIMENT 3

FIG. 13.—Fingerling, 60 millimeters long, marked at Little White Salmon River hatchery July 28, 1916. × 25

FIG. 14.—Marked at Little White Salmon River hatchery during the summer of 1916 when about 10 months old. Recovered as a spawning fish in the Little White Salmon River during the fall of 1918, in its third year. Male, 19.5 inches long. A considerable portion of the third year's growth has been lost by absorption. × 25

FIG. 15.—Marked at Little White Salmon River hatchery during the summer of 1916, when about 10 months old. Recovered at Astoria, Oreg., August 25, 1919, in its fourth year. Female. No data as to size. × 13



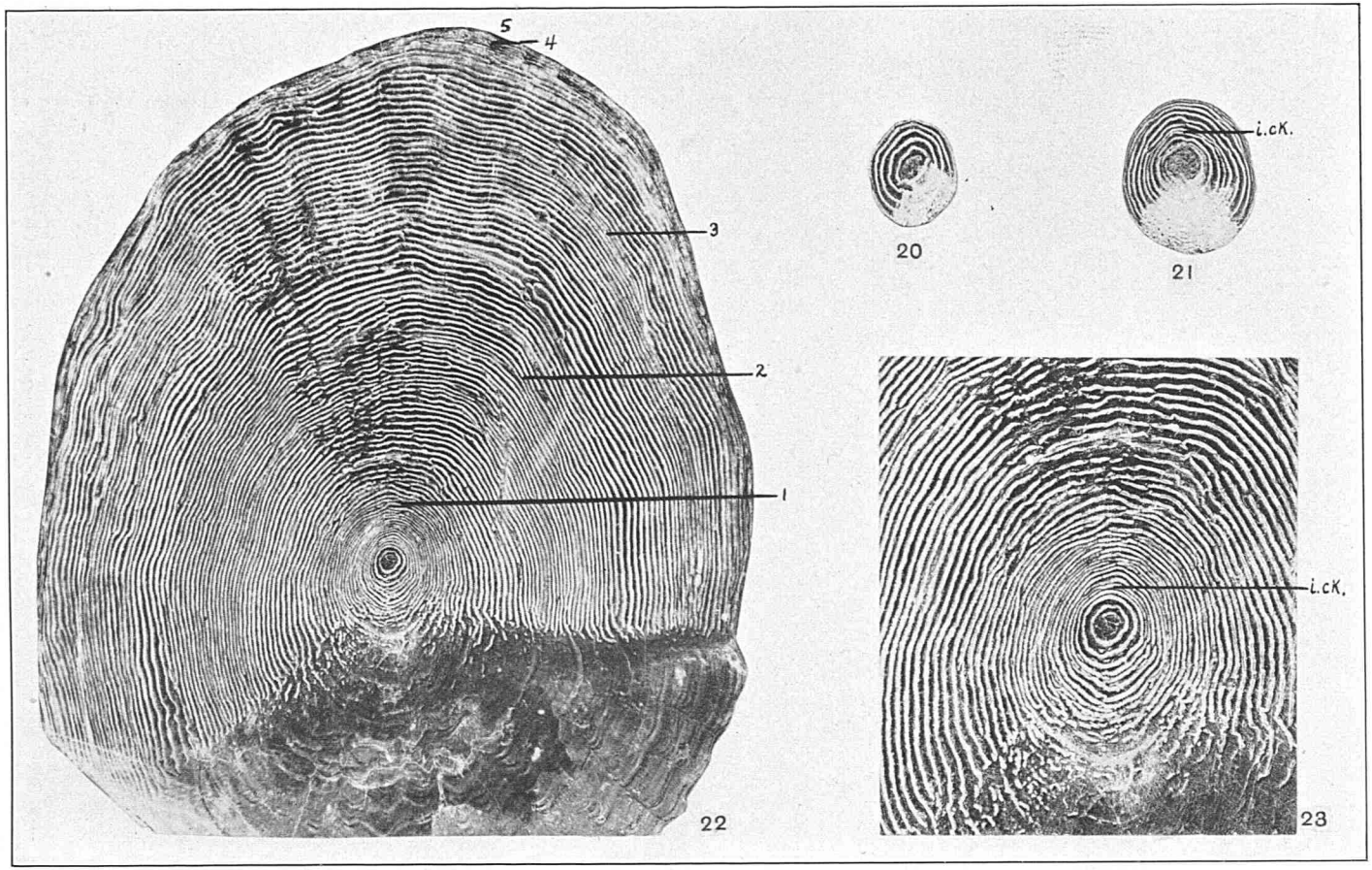
EXPERIMENT 3

FIG. 16.—Nuclear region of scale shown in Figure 15. × 25

FIG. 17.—Marked at Little White Salmon River hatchery during the summer of 1916, when about 10 months old. Recovered by purse seine off the mouth of the Columbia River, August 21, 1920, in its fifth year. Female, 39 inches long and weighing 27 pounds. × 13

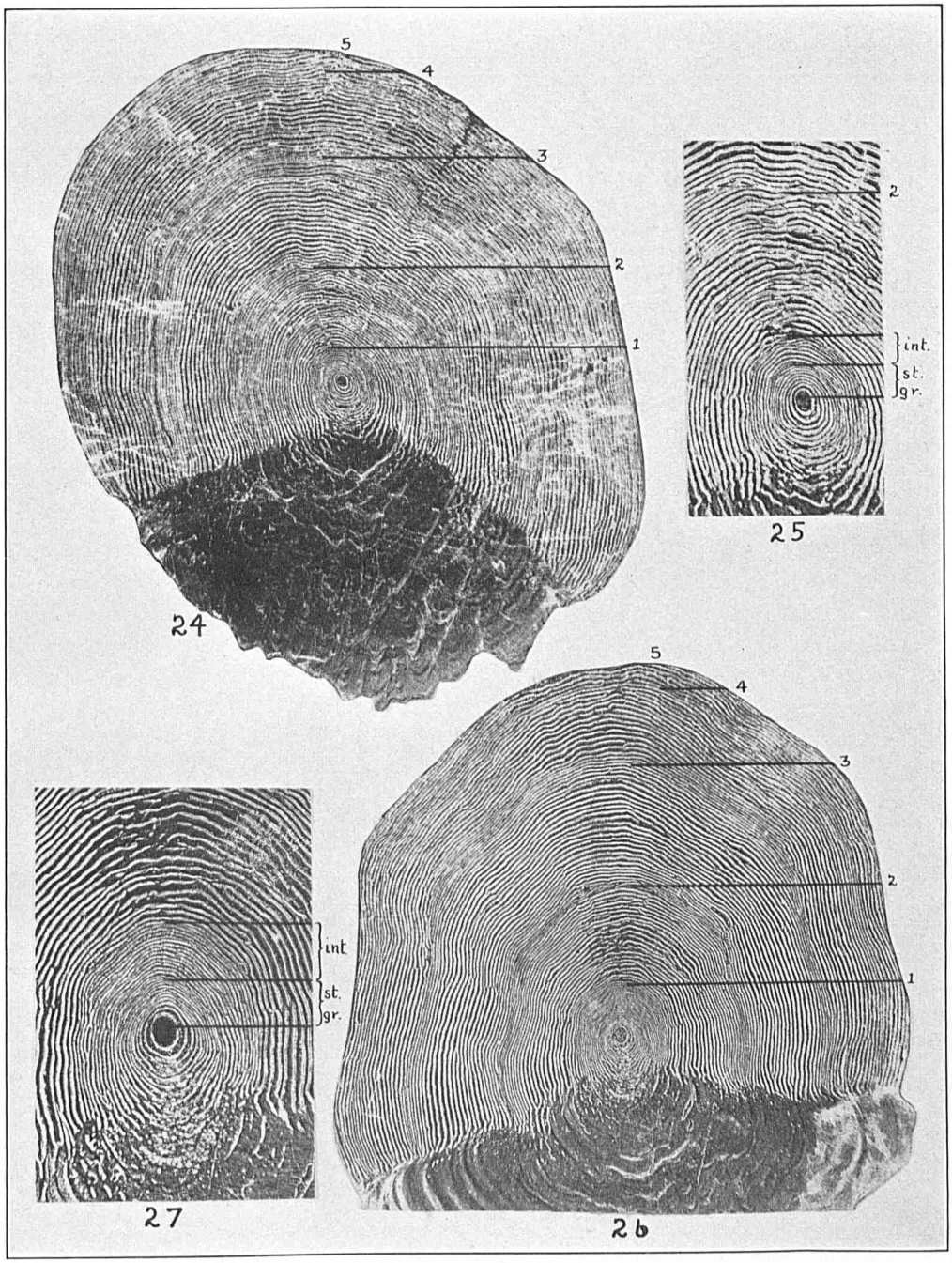
FIG. 18.—Nuclear region of scale shown in Figure 17. × 25

FIG. 19.—Marked at Little White Salmon River hatchery during the summer of 1916, when about 10 months old. Recovered in the Little White Salmon River, September 27, 1920, in its fifth year. Female, 36.75 inches in length. × 25



EXPERIMENT 4

FIG. 20.—Fingerling, 47 millimeters long, marked at Bonneville hatchery, September 13, 1916. Smallest fish in the collection. × 25
FIG. 21.—Fingerling, 69 millimeters long, marked at Bonneville hatchery, September 13, 1916. Typical scale showing incidental check. × 25
FIG. 22.—Marked at Bonneville hatchery during September, 1916, when approximately 12 months old. Recovered at Astoria, Oreg., May 21, 1920, in its fifth year. Female, 31 inches long and weighing 18 pounds. × 13
FIG. 23.—Nuclear region of scale shown in Figure 22. A poorly differentiated nucleus. × 25



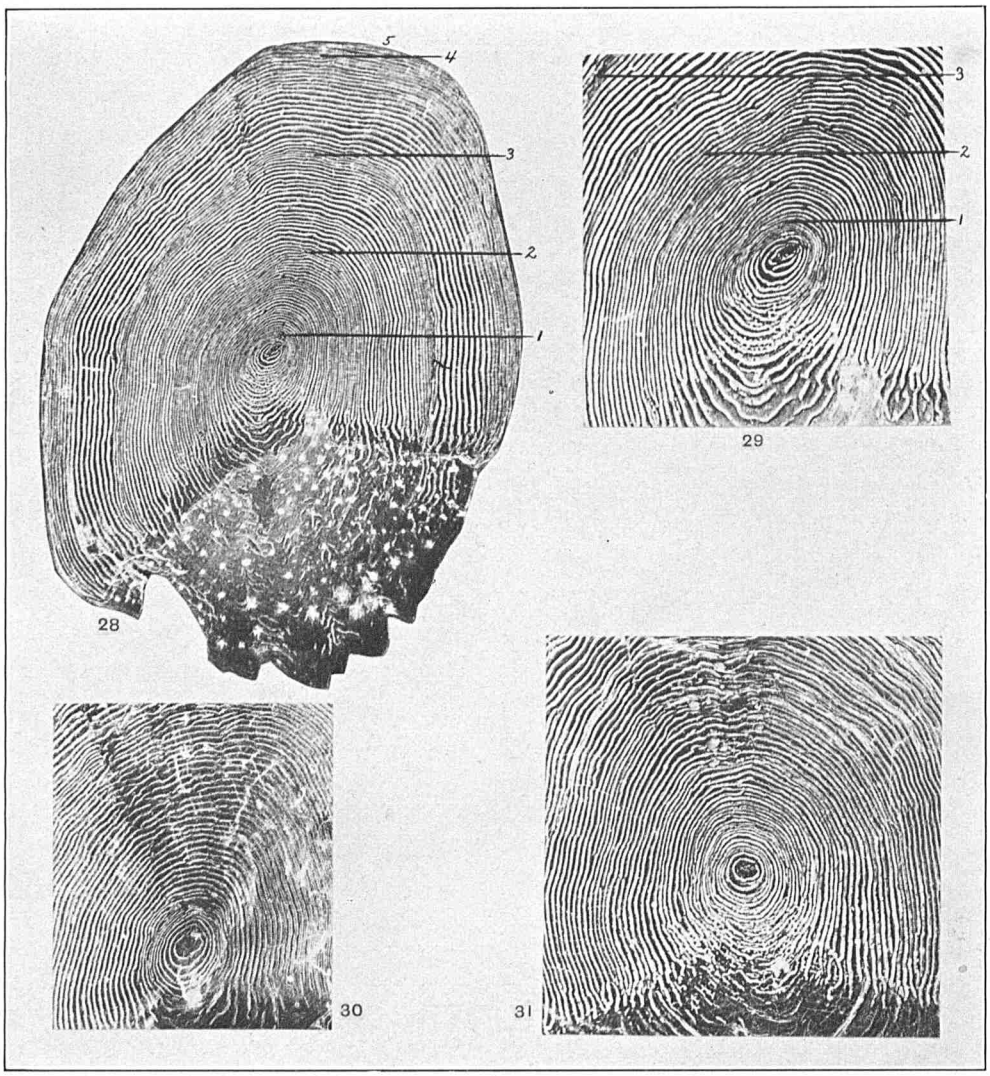
EXPERIMENT 4

FIG. 24.—Marked at Bonneville hatchery during September, 1916, when approximately 12 months old. Recovered at Wallace Island, June 5, 1920, in its fifth year. Male, 26.25 inches long and weighing 28.25 pounds. × 13

FIG. 25.—Nuclear region of scale shown in Figure 24. A more clearly differentiated nucleus. × 25

FIG. 26.—Marked at Bonneville hatchery during September, 1916, when approximately 12 months old. Recovered at Astoria, Oreg., May 25, 1920, in its fifth year. Female, 35.5 inches long and weighing 20 pounds. × 13

FIG. 27.—Nuclear region of scale shown in Figure 26, showing wide band of intermediate growth. × 25



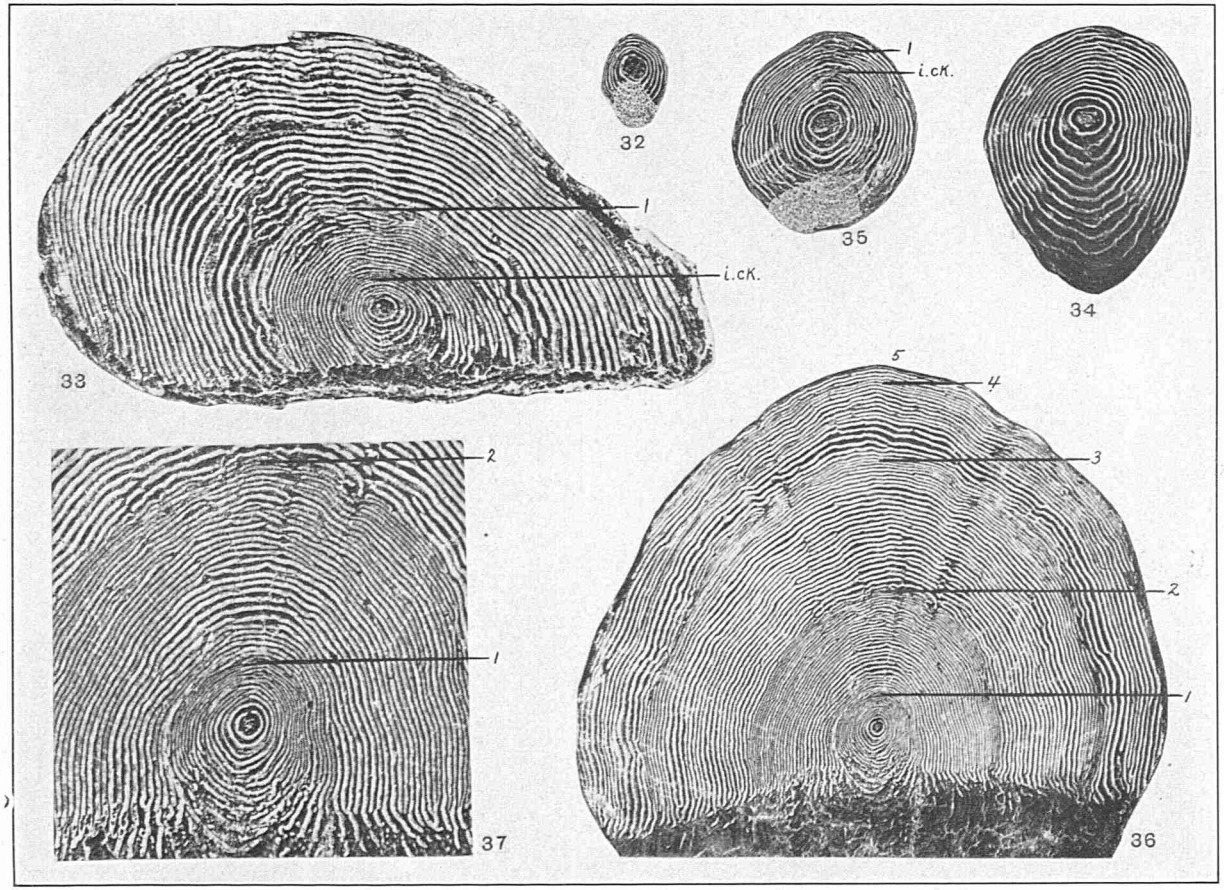
EXPERIMENT 4

FIG. 28.—Marked at Bonneville hatchery during September, 1916, when approximately 12 months old. Recovered at Astoria, Oreg., May 18, 1920, in its fifth year. Female, either 16 or 21 pounds in weight. This scale was taken from the skin attached to the scar of the dorsal fin, which accounts for its small size. This is the most confusing scale in the entire collection from marked chinook salmon. In the absence of knowledge of the early history of the fish, the check marked 2 might have been mistaken for the first winter check. × 13

FIG. 29.—Nuclear region of scale shown in Figure 26. × 25

FIG. 30.—Marked at Bonneville hatchery during September, 1916, when approximately 12 months old. Recovered near Altoona, Wash., June 5, 1920, in its fifth year. Female, 32 inches long and weighing 21 pounds, showing nucleus lacking incidental check and having only two or three rings of intermediate growth. × 25

FIG. 31.—Marked at Bonneville hatchery during September, 1916, when approximately 12 months old. Recovered at Ilwaco, Wash., May 17, 1920, in its fifth year. Female, 35.4 inches long and weighing 21.5 pounds, showing a very poorly differentiated nucleus. × 25



EXPERIMENT 5

FIG. 32.—Fingerling, 55 millimeters in length, marked at Little White Salmon hatchery, July 18, 1917. × 25

FIG. 33.—Marked at Little White Salmon River hatchery during the summer of 1917, when approximately 10 months old. Recovered as a spawning fish in the Little White Salmon River, October 12, 1920, in its fourth year. Female, 27 inches long and weighing 10.5 pounds. Record of all but the first 2 years' growth has been eaten away by absorption of the scale. × 25

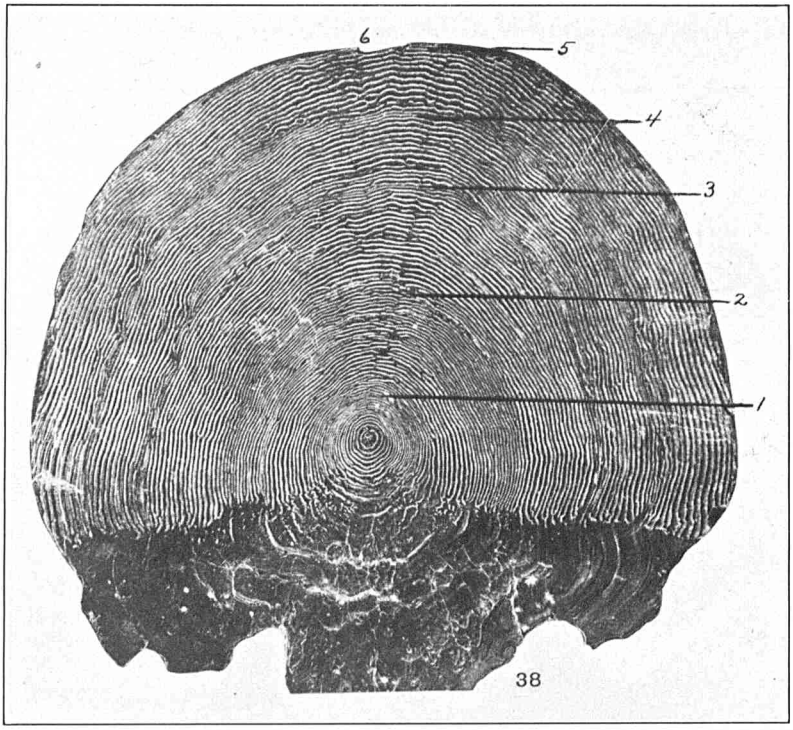
EXPERIMENT 6

FIG. 34.—Fingerling, 145 millimeters, marked at Herman Creek hatchery March, 1920, showing absence of incidental and winter checks. × 25

FIG. 35.—Fingerling, 126 millimeters in length, marked at Herman Creek hatchery during March, 1920, showing incidental check, winter check, and three rings of rapid growth of the second year. × 25

FIG. 36.—Marked at Herman Creek hatchery during the spring of 1920, when approximately 18 months old. Recovered at Ellsworth, Wash., May 20, 1923, in its fifth year. Male, 36 inches long and weighing 15 pounds. × 13

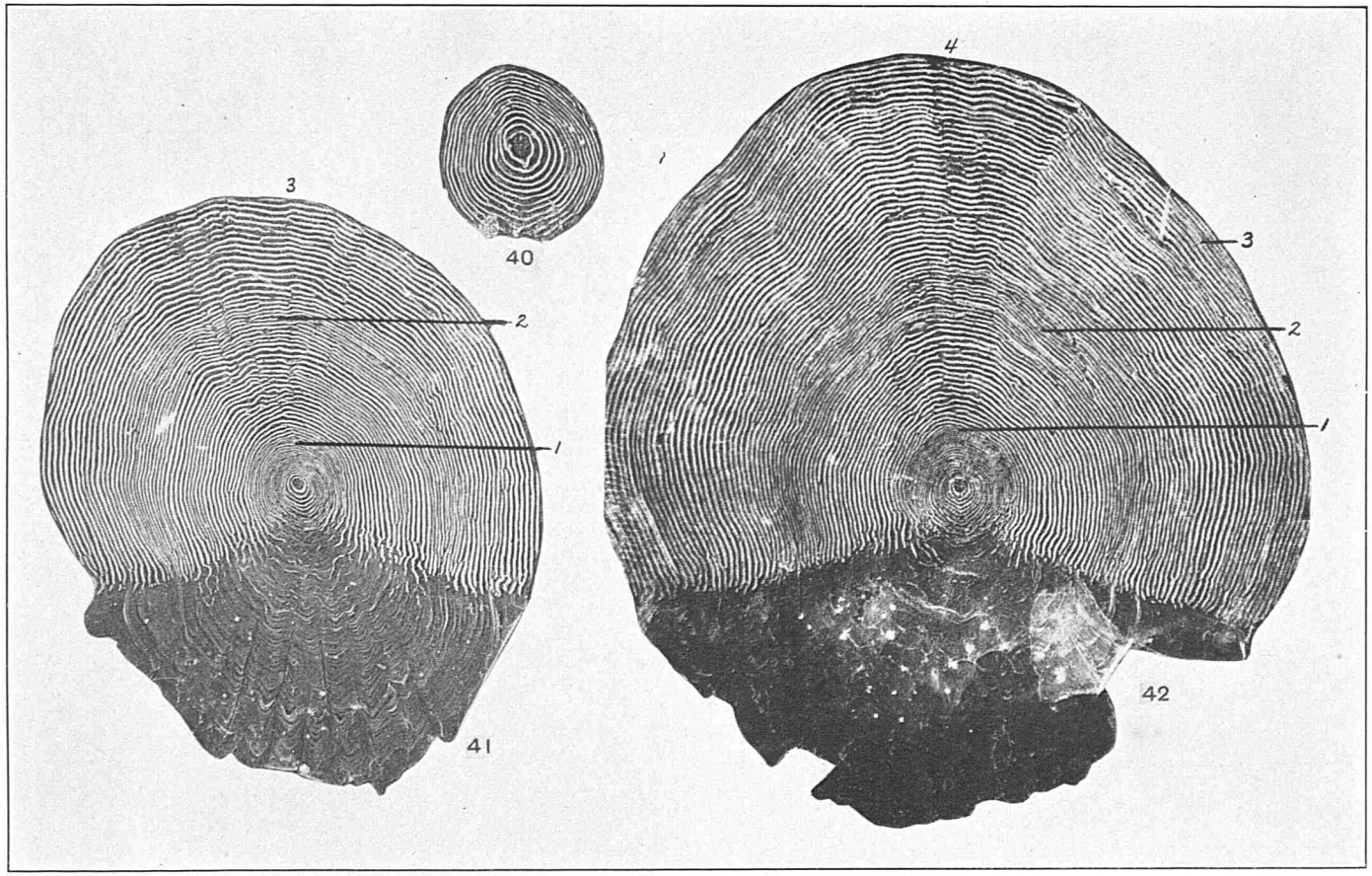
FIG. 37.—Nuclear region of scale shown in Figure 36. × 25



EXPERIMENT 6

FIG. 38.—Marked at Herman Creek hatchery during the spring of 1920 when approximately 18 months old. Recovered at Clatskanie, Oreg., May 7, 1924, in its sixth year. Length, 38 inches; weight, 22 pounds. × 13

FIG. 39.—Nuclear region of scale shown in Figure 38. ×25

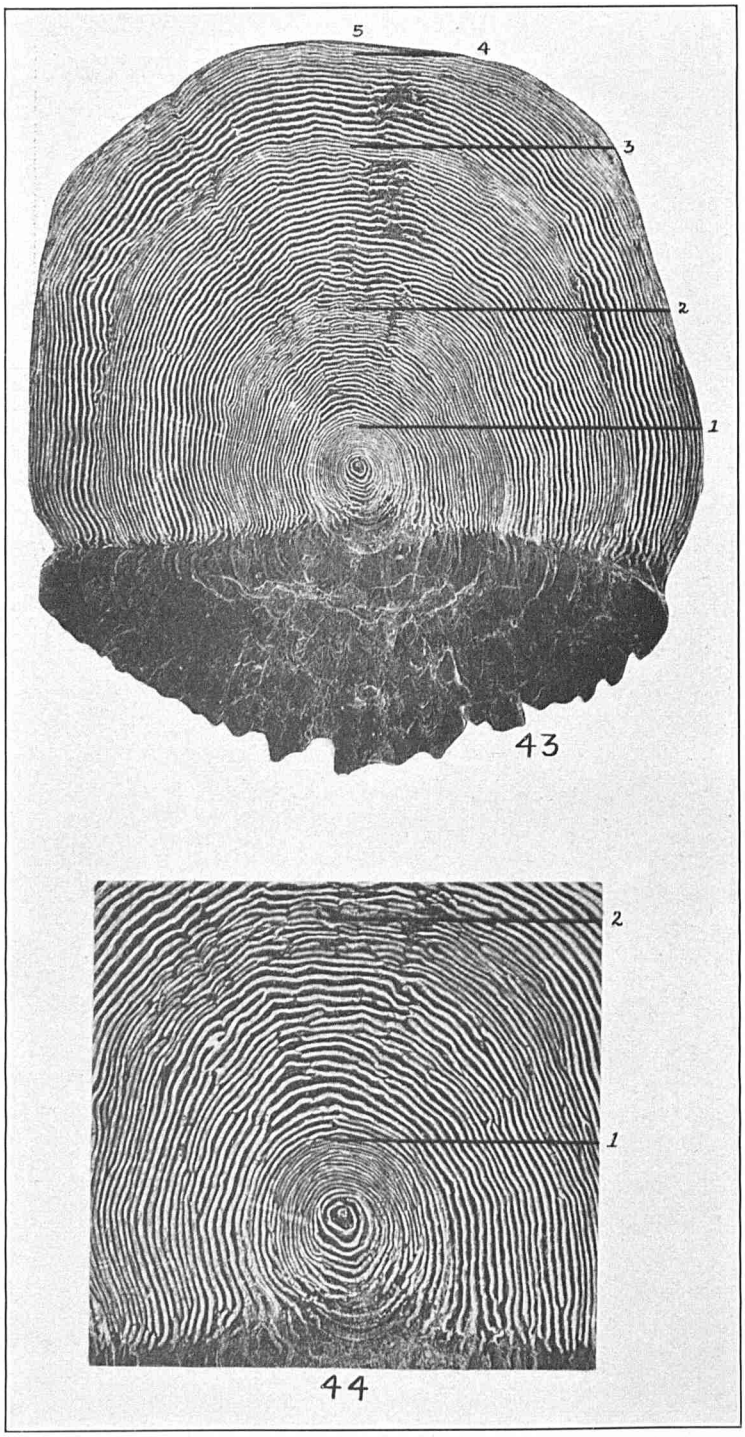


EXPERIMENT 7

FIG. 40.—Fingerling 102 millimeters long marked at Bonneville hatchery October 14, 1920. × 25

FIG. 41.—Marked at Bonneville hatchery during October, 1920, when approximately 13 months old. Recovered by troll in the ocean on August 9, 1922, in its third year. Male, 23.25 inches long and weighing 5.5 pounds. × 13

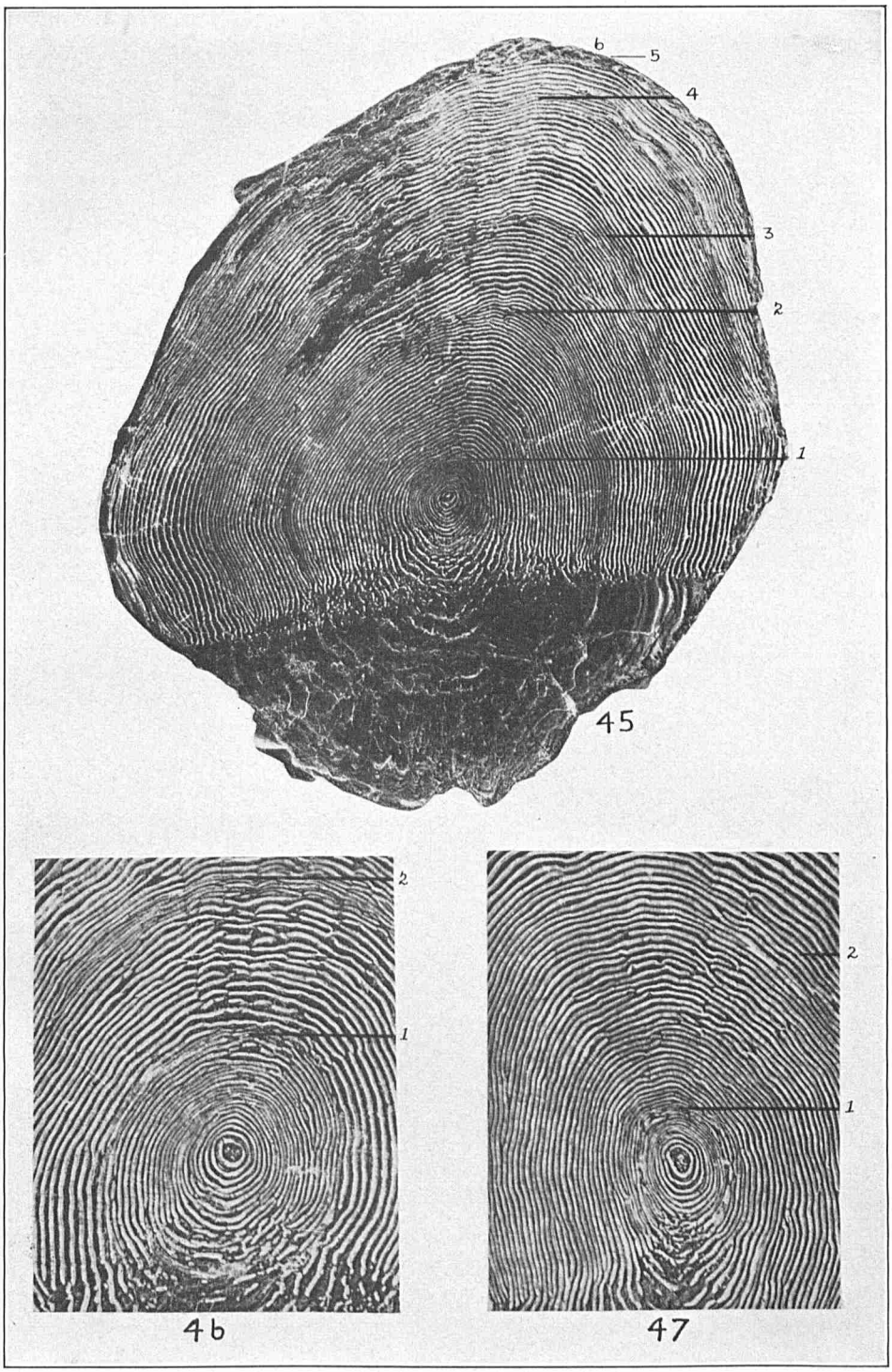
FIG. 42.—Marked at Bonneville hatchery during October, 1920, when approximately 13 months old. Recovered in the lower Columbia, May 9, 1923, in its fourth year. Female, 32 inches long and weighing 18 pounds. × 13



EXPERIMENT 7

FIG. 43.—Marked at Bonneville hatchery during October, 1920, when approximately 13 months old. Recovered at Westport, Oreg., May 1, 1924, in its fifth year. Female, 38 inches long and weighing 22 pounds. ×13

FIG. 44.—Nuclear region of scale shown in Figure 43, showing nucleus of average size. ×25

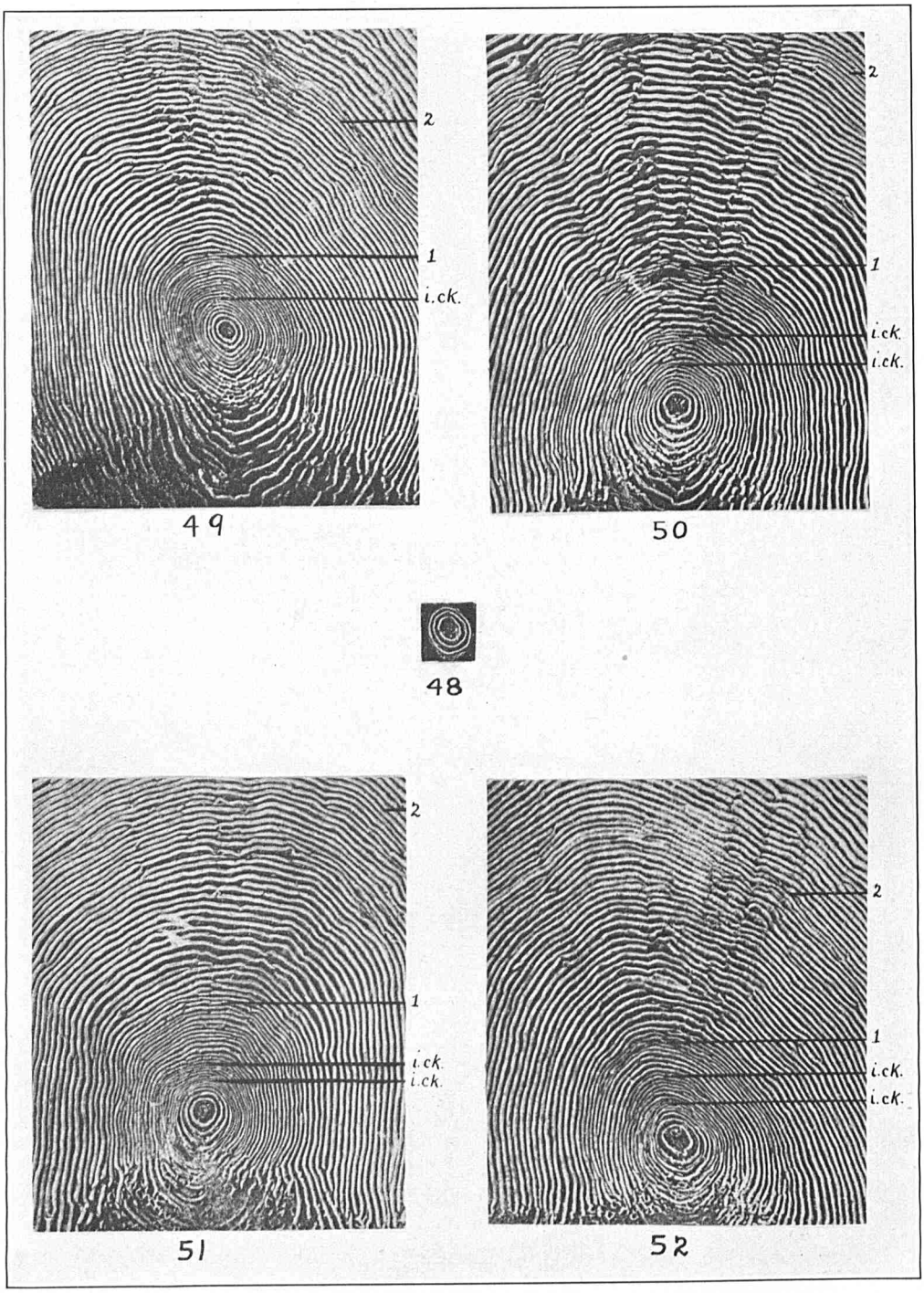


EXPERIMENT 7

FIG. 45.—Marked at Bonneville hatchery during October, 1920, when approximately 13 months old. Recovered near Bonneville, Oreg., May 7, 1925, in its sixth year. Male, 40.5 inches long and weighing 27 pounds. The last half year's growth has been removed by absorption of the scale. × 13

FIG. 46.—Marked at Bonneville hatchery during October, 1920, when approximately 13 months old. Recovered at Cascade Locks, Oreg., May 8, 1924, in its fifth year. Female, 32.5 inches long and weighing 13 pounds, showing an extremely large nucleus. × 25

FIG. 47.—Marked at Bonneville hatchery during October, 1920, when approximately 13 months old. Recovered at Corbett, Oreg., May 6, 1924, in its fifth year. Female, 34.5 inches long and weighing 18 pounds, showing an extremely small nucleus. × 25



EXPERIMENT 8

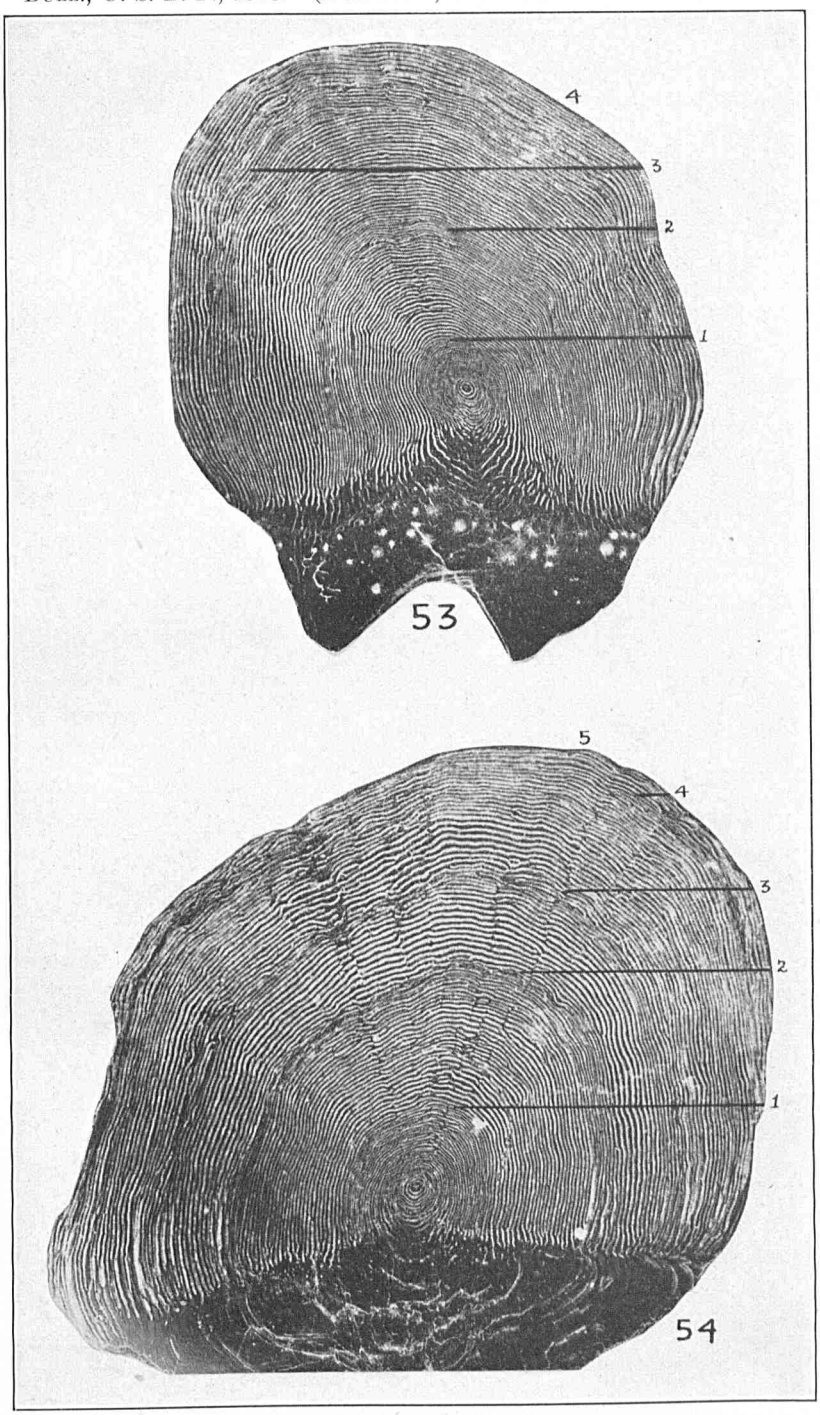
FIG. 48.—Fingerling, 50 millimeters, marked at Little White Salmon River hatchery summer of 1920. × 25

FIG. 49.—Marked at Little White Salmon River hatchery summer of 1920, when approximately 10 months old. Recovered at Astoria, Oreg., August 22, 1923, in its fourth year. Male, 37 inches long and weighing 25 pounds. × 25

FIG. 50.—Marked at Little White Salmon River hatchery summer of 1920, when approximately 10 months old. Recovered at Sand Island, August 14, 1923, in its fourth year. Male, 45.5 inches long and weighing 42 pounds. × 25

FIG. 51.—Marked at Little White Salmon River hatchery summer of 1920, when approximately 10 months old. Recovered at Sand Island, August 23, 1923, in its fourth year. Female, 39 inches long and weighing 23 pounds. × 25

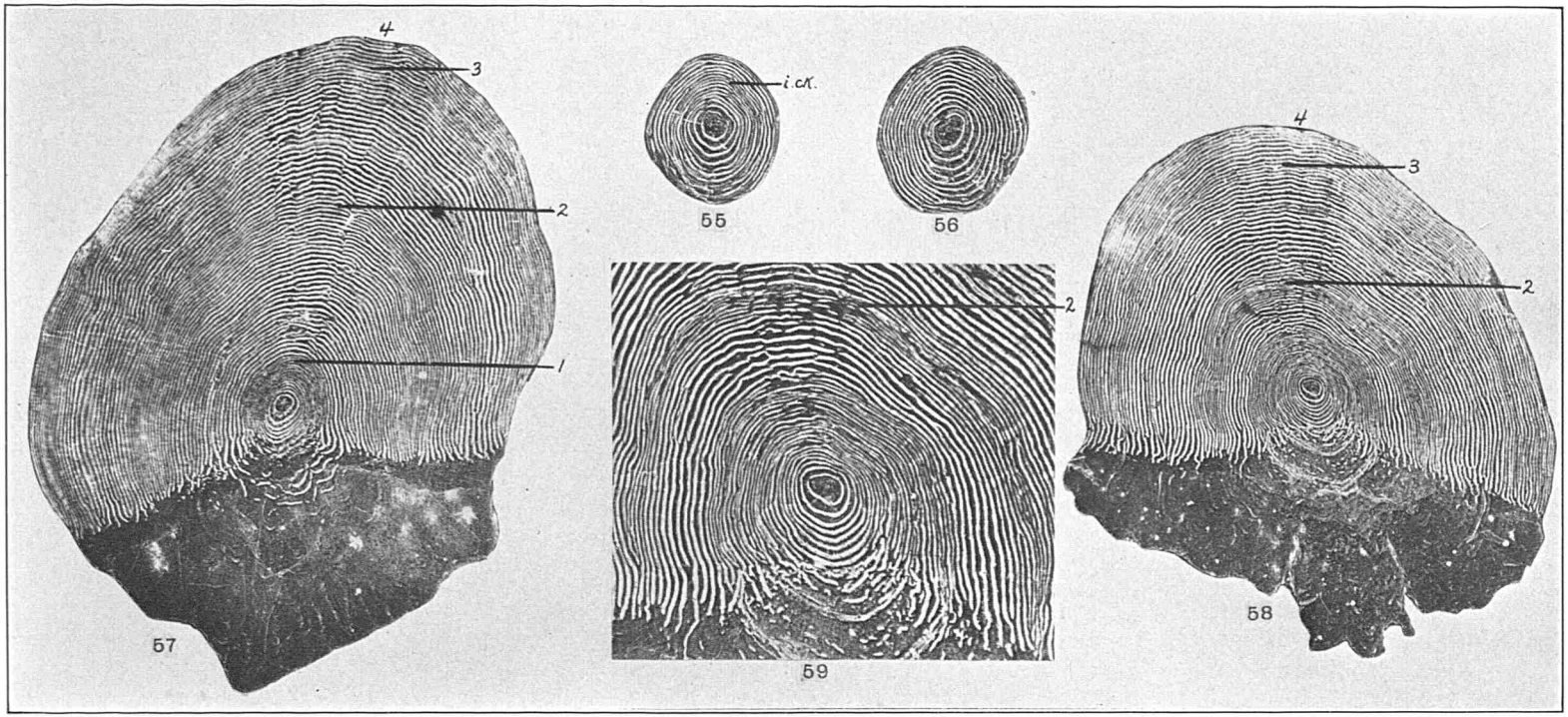
FIG. 52.—Marked at Little White Salmon River hatchery summer of 1920, when approximately 10 months old. Recovered in the lower Columbia, August 20, 1923, in its fourth year. Female, 26 inches long and weighing 10 pounds. × 25



EXPERIMENT 8

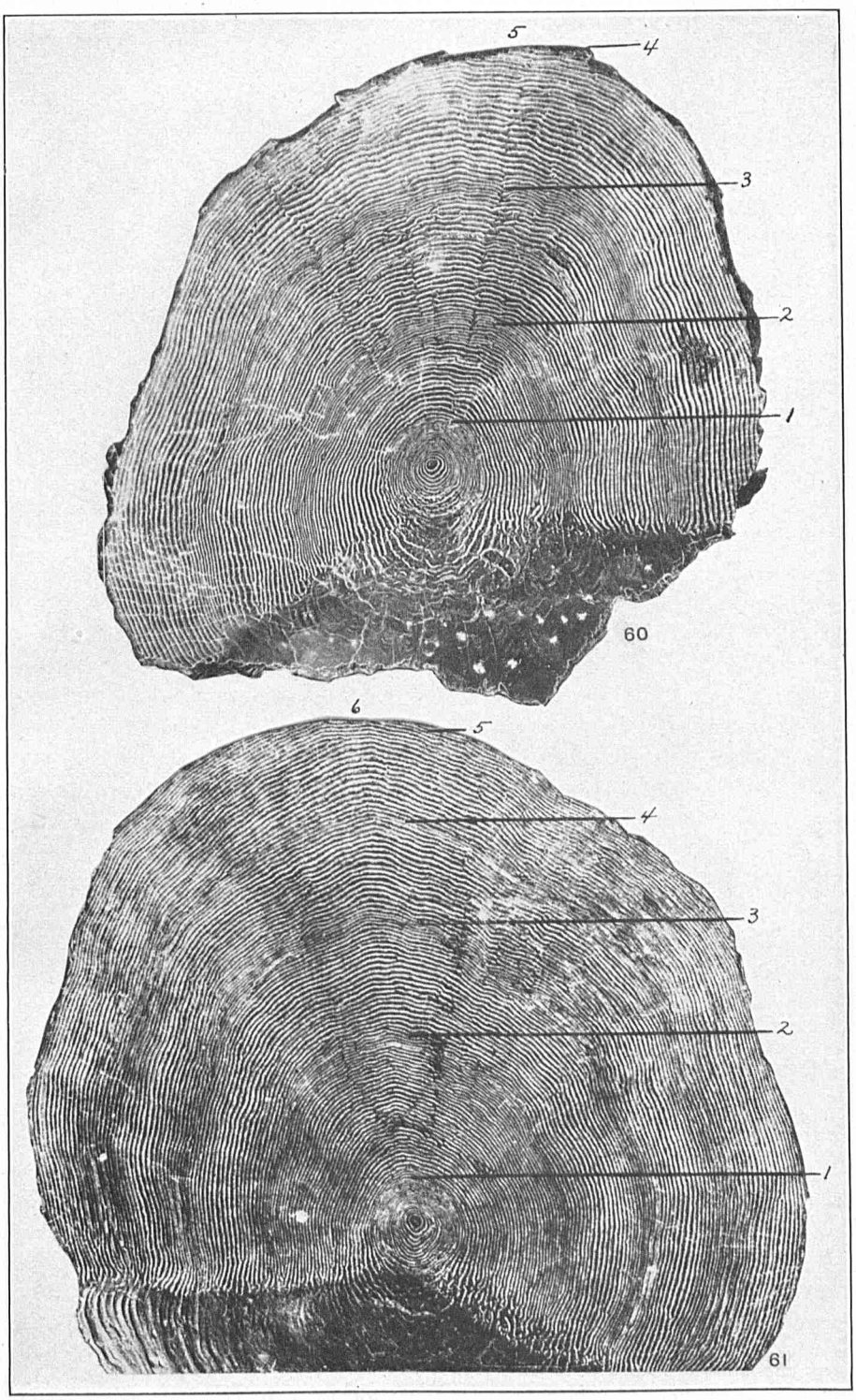
FIG. 53.—Marked at Little White Salmon River hatchery during the summer of 1920, when approximately 10 months old. Recovered in the lower Columbia, August 17, 1923, in its fourth year. Female, 39 inches long and weighing 24 pounds. × 13

FIG. 54.—Marked at Little White Salmon River hatchery during the summer of 1920, when approximately 10 months old. Recovered at Sand Island, August 10, 1924, in its fifth year. Male, 33.9 inches long and weighing 29 pounds. × 13



EXPERIMENT 9

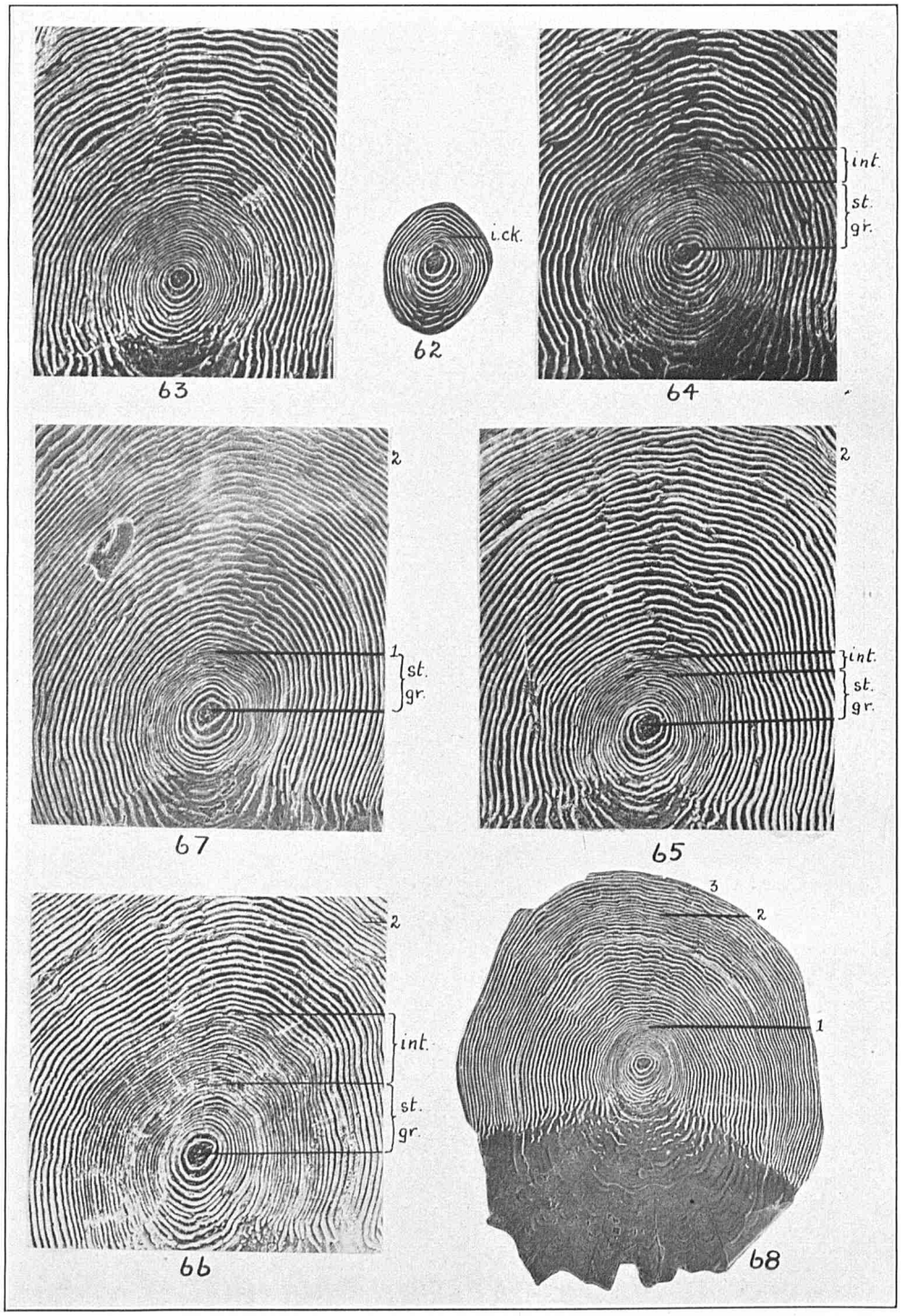
FIG. 55.—Fingerling, 82 millimeters long, marked at Bonneville hatchery, August 24, 1921, showing a distinct incidental check. × 25
FIG. 56.—Fingerling, 106 millimeters long, marked at Bonneville hatchery, August 24, 1921, showing absence of incidental check. × 25
FIG. 57.—Marked at Bonneville hatchery during the fall of 1921, when approximately 13 months old. Recovered at Warrendale, Oreg., May 6, 1924, in its fourth year. Male, 25.75 inches long and weighing 13 pounds. × 13
Fig. 58.—Marked at Bonneville hatchery during the fall of 1921, when approximately 13 months old. Recovered at Astoria, Oreg., May 17, 1924, in its fourth year. The growth proportions in this scale are very unusual. (See p. 244.) × 13
FIG. 59.—Nuclear region of scale shown in Figure 58. × 25



EXPERIMENT 9

FIG. 60.—Marked at Bonneville hatchery during the fall of 1921, when approximately 13 months old. Recovered at Dahlia, Wash., May 8, 1925, in its fifth year. Male, 41 inches long and weighing 29 pounds. The fourth winter band and whatever was formed during the spring of the fifth year have been removed by absorption of the scale. × 13

FIG. 61.—Marked at Bonneville hatchery during the fall of 1921, when approximately 13 months old. Recovered at Clatskanie, Oreg., during February, 1926, in its sixth year. No data as to sex; length 42 inches, weight 37 pounds. The rapid growth of the sixth year had not started at the time the fish was caught. × 13



EXPERIMENT 10

FIG. 62.—Fingerling, 78 millimeters, marked at Bonneville hatchery August 28, 1922. A typical scale. × 25

FIG. 63.—Marked at Bonneville hatchery fall of 1922, when approximately 12 months old. Recovered at CascadeLocks, Oreg., May 5, 1926, in its fifth year. Female, 37 inches and 22 pounds. A poorly differentiated nucleus. × 25

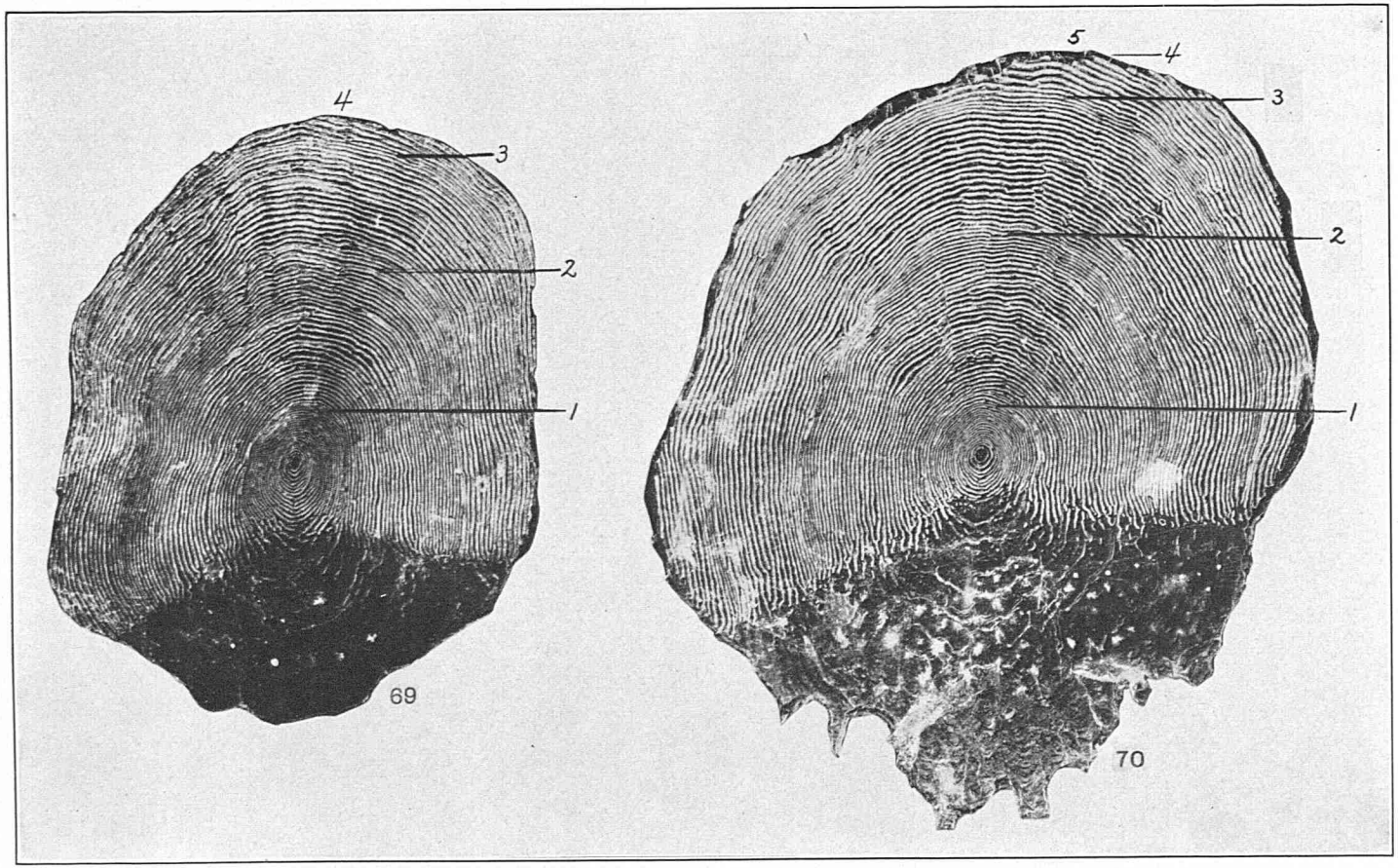
FIG. 64.—Marked at Bonneville hatchery during the fall of 1922, when approximately 12 months old. Recovered in a cannery at Warrendale, Oreg., May 10, 1926, in its fifth year. Male, 36 inches long and weighing 18 pounds, showing a clearly differentiated nucleus. × 25

FIG. 65.—Marked at Bonneville hatchery during the fall of 1922, when approximately 12 months old. Recovered in a cannery at Ellsworth, Wash., May 7, 1926, in its fifth year. Male, 29.5 inches long and weighing 19.5 pounds, showing intermediate growth that closely resembles stream growth. × 25

FIG. 66.—Marked at Bonneville hatchery during the fall of 1922, when approximately 12 months old. Recovered in a cannery at Ellsworth, Wash., May 4, 1926, in its fifth year. Female, 34 inches long and weighing 21 pounds, showing a nucleus with an extremely wide band of intermediate growth. × 25

FIG. 67.—Marked at Bonneville hatchery during the fall of 1922, when approximately 12 months old. Recovered in a cannery at Ellsworth, Wash., May 15, 1926, in its fifth year. Female, 32 inches long and weighing 17 pounds, showing a nucleus with no intermediate growth. × 25

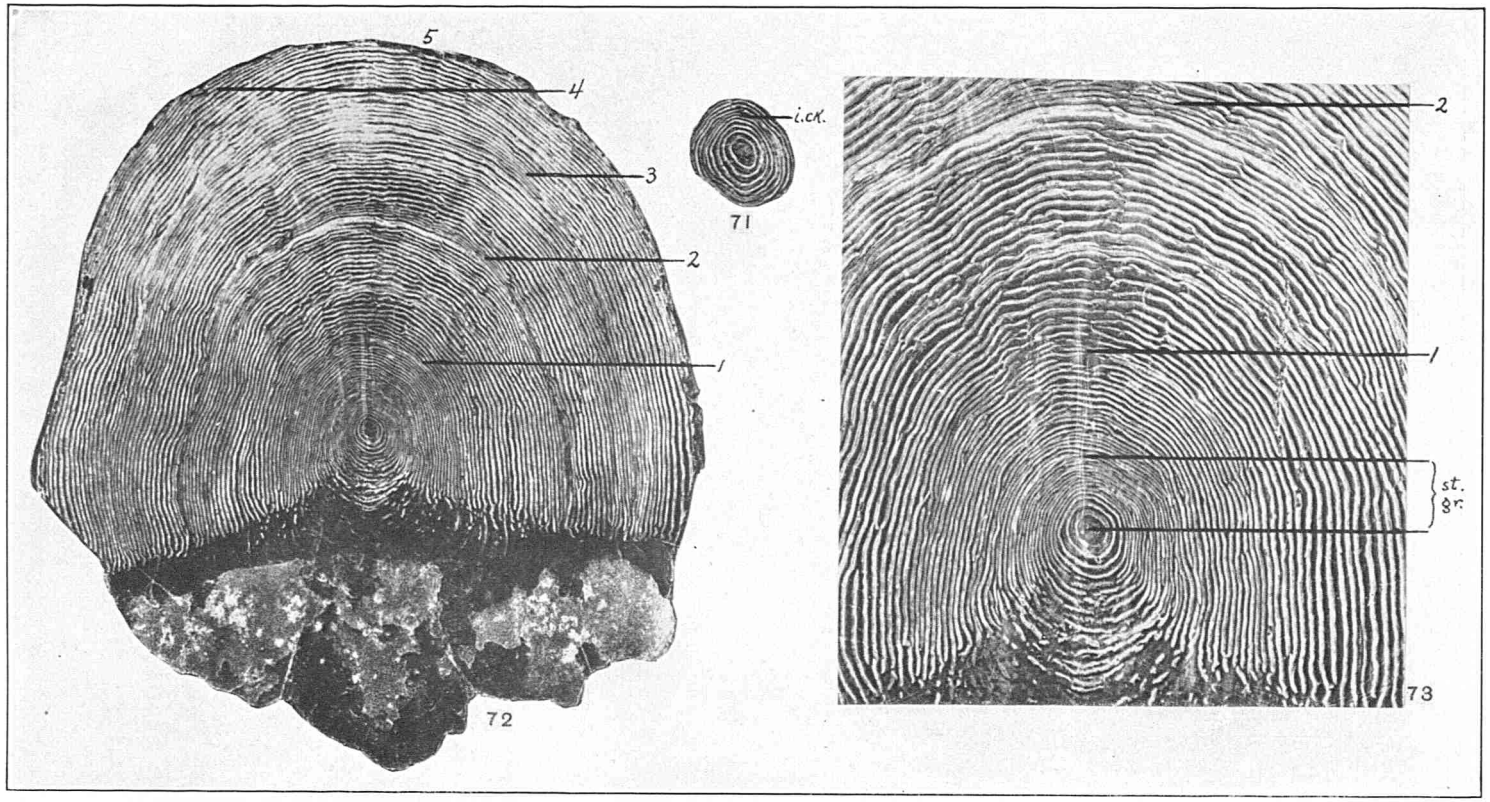
FIG. 68.—Marked at Bonneville hatchery during the fall of 1922, when approximately 12 months old. Recovered at The Dalles, Oreg., May 3, 1924, in its third year. Male, 18 inches long and weighing 3 pounds. × 13



EXPERIMENT 10

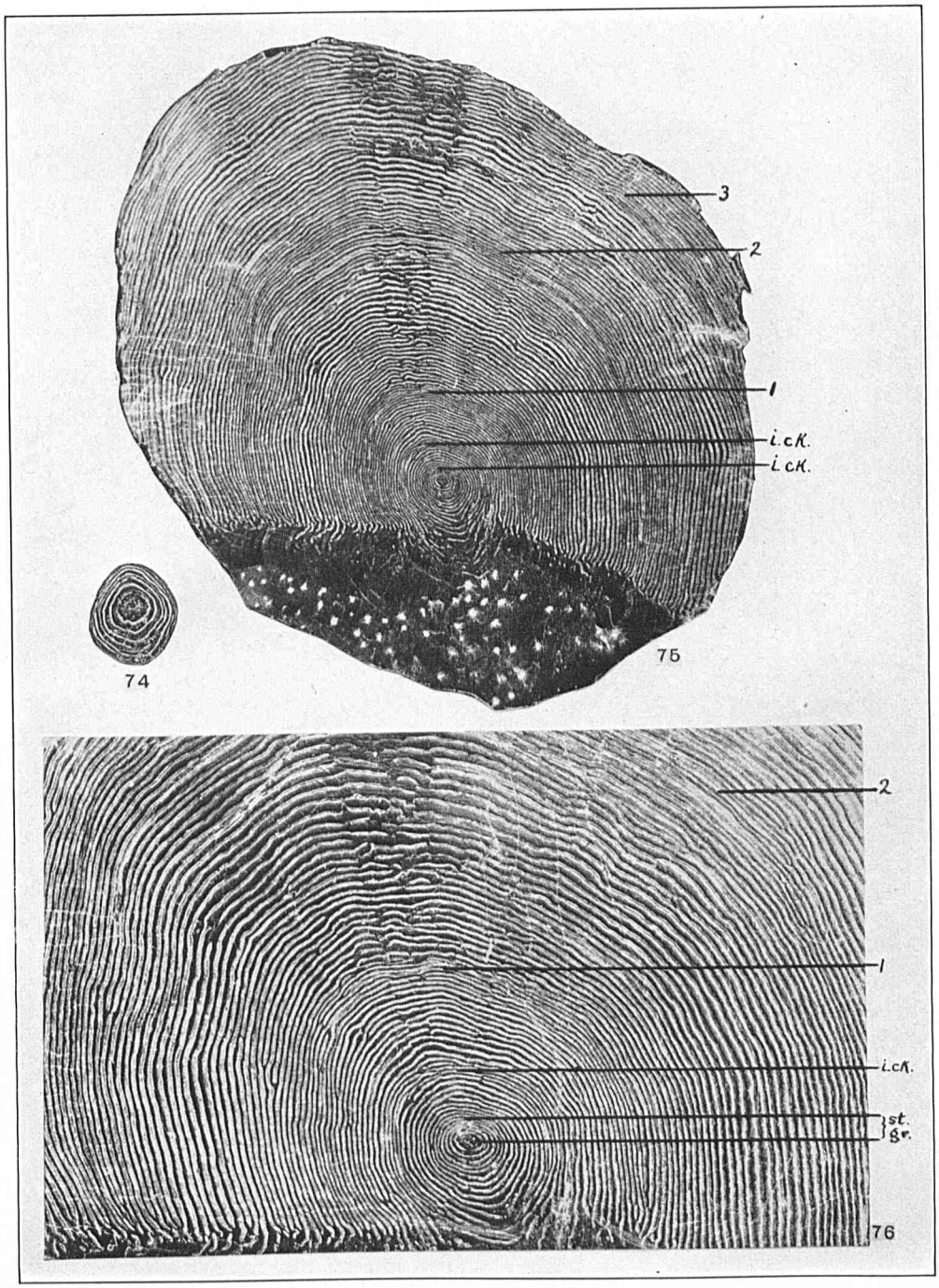
FIG. 69.—Marked at Bonneville hatchery during the fall of 1922, when approximately 12 months old. Recovered in a cannery at Warrendale, Oreg., during the spring of 1925 in its fourth year. Female, 40 inches long and weighing 35 pounds. × 13

FIG. 70.—Marked at Bonneville hatchery during the fall of 1922, when approximately 12 months old. Recovered at Cascade Locks, Oreg., May 5, 1926, in its fifth year. Female, 37 inches long and weighing 22 pounds. The fourth winter band and whatever was formed during the fifth spring have been removed by absorption of the scale × 13



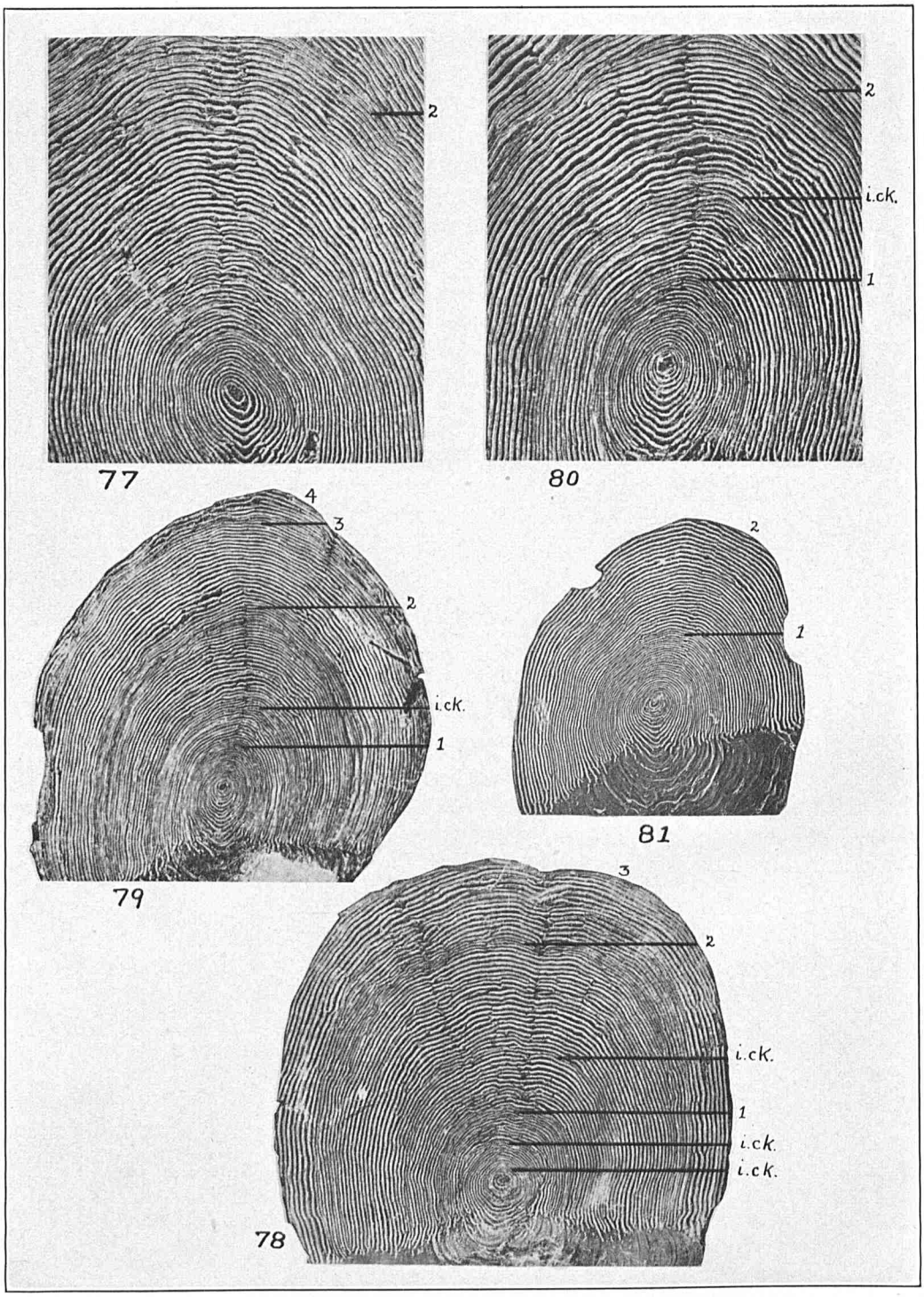
EXPERIMENT 11

FIG. 71.—Fingerling, 75 millimeters long, marked at Klaskanine hatchery, August 18, 1922. A typical scale. × 25
FIG. 72.—Marked at Klaskanine hatchery during the summer of 1922, when approximately 10 months old. Recovered at the Klaskanine hatchery during the spring of 1926, in its fifth year. The margin of the scale has been slightly removed by absorption. × 13
FIG. 73.—Nuclear region of scale shown in Figure 72. × 25



EXPERIMENT 12

FIG. 74.—Fingerling, 56 millimeters in length, marked at Big White Salmon River hatchery, June 12, 1923. × 25
FIG. 75.—Marked at Big White Salmon River hatchery during the spring of 1923, when approximately 8 months old. Recovered at Ilwaco, Wash., August 19, 1926, in its fourth year. Male, 39.3 inches long and weighing 30 pounds. × 13
FIG. 76.—Nuclear region of scale shown in Figure 75. × 25



EXPERIMENT 12

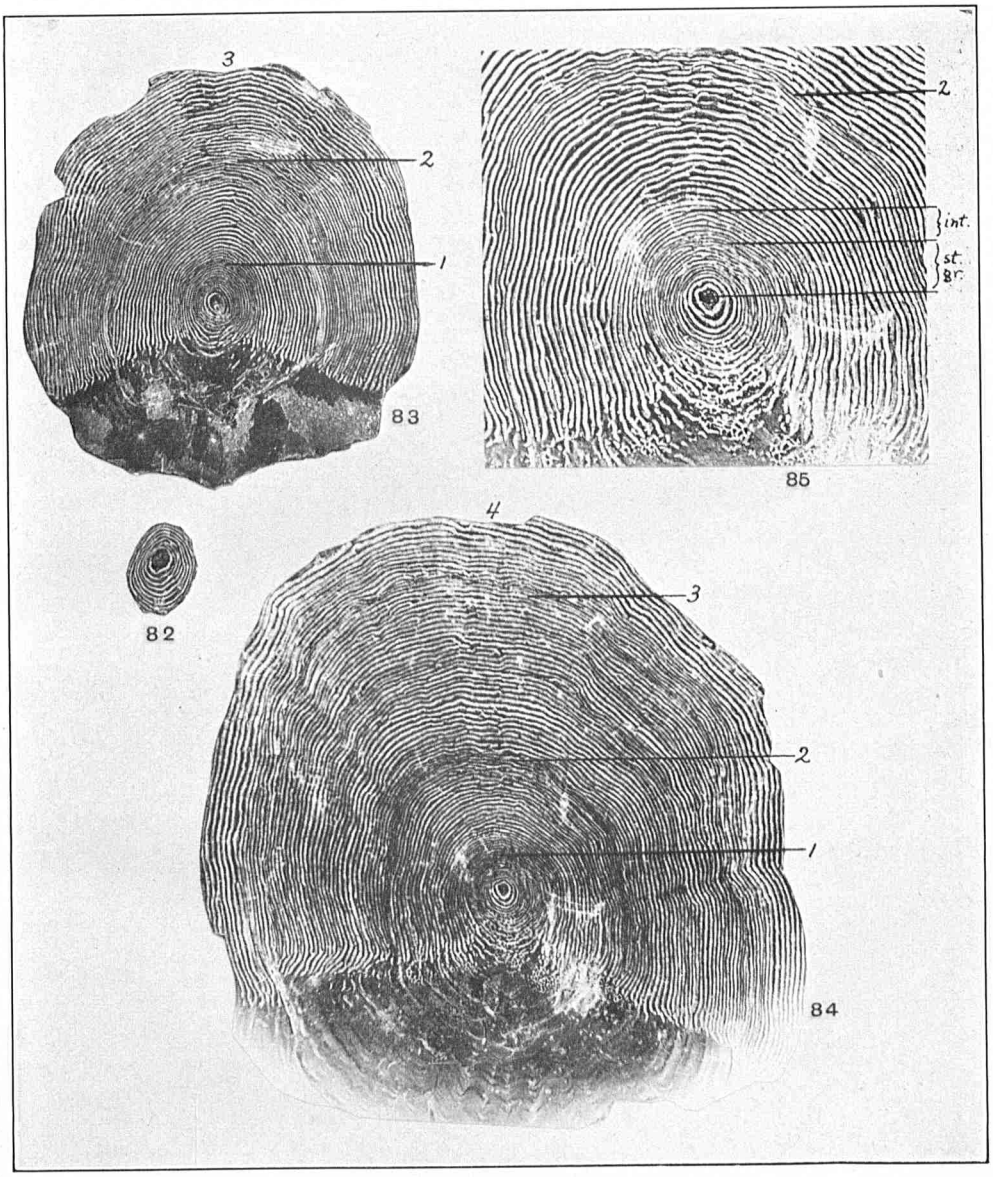
FIG. 77.—Marked at Big White Salmon River hatchery during the spring of 1923, when approximately 8 months old. Recovered at Astoria, Oreg., August 23, 1926, in its fourth year. Male, 39 inches long and weighing 28.5 pounds, showing a poorly differentiated composite nucleus. The first year's growth blends so gradually into that of the second year that it is impossible to determine where the first year ends and the second begins. × 25

FIG. 78.—Marked at Big White Salmon River hatchery during the spring of 1923, when approximately 8 months old. Recovered at Pillar Rock, Wash., August 25, 1925, in its third year. Male, 26 inches long and weighing 12 pounds, showing an incidental check in the second year, which is not sufficiently pronounced to be confused as an annulus. × 13

FIG. 79.—Marked at Big White Salmon River hatchery during the spring of 1923, when approximately 8 months old. Recovered at Astoria, Oreg., August 24, 1926, in its fourth year. Female, 37 inches long and weighing 22.25 pounds, showing an incidental check in the second year, which might be mistaken for an annulus. A part of the fourth summer's growth has been removed by absorption of the scale. × 13

FIG. 80.—Nuclear region of the scale shown in Figure 78. × 25

FIG. 81.—Marked at Big White Salmon River hatchery during the spring of 1923, when approximately 8 months old. Recovered at Astoria, Oreg., August 2, 1924, in its second year. Male, 22 inches long and weighing 5 pounds. × 13



EXPERIMENT 13

FIG. 82.—Fingerling, 58 millimeters long, marked at Salmon (Idaho) hatchery, August 22, 1924. × 25

FIG. 83.—Marked at Salmon (Idaho) hatchery during the fall of 1924, when approximately 11 months old. Recovered in an Astoria cannery, August 10, 1926, in its third year. Male, 25 inches long and weighing 9 pounds. × 13

FIG. 84.—Marked at Salmon (Idaho) hatchery during the fall of 1924, when approximately 11 months old Recovered in the ocean on July 25, 1927, in its fourth year. × 13

FIG. 85.—Nuclear region of scale shown in Figure 84. × 25

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

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INTRODUCTION

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

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

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

THE PROBLEM

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

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

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

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

MATERIAL

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

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

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

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

ACKNOWLEDGMENTS

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

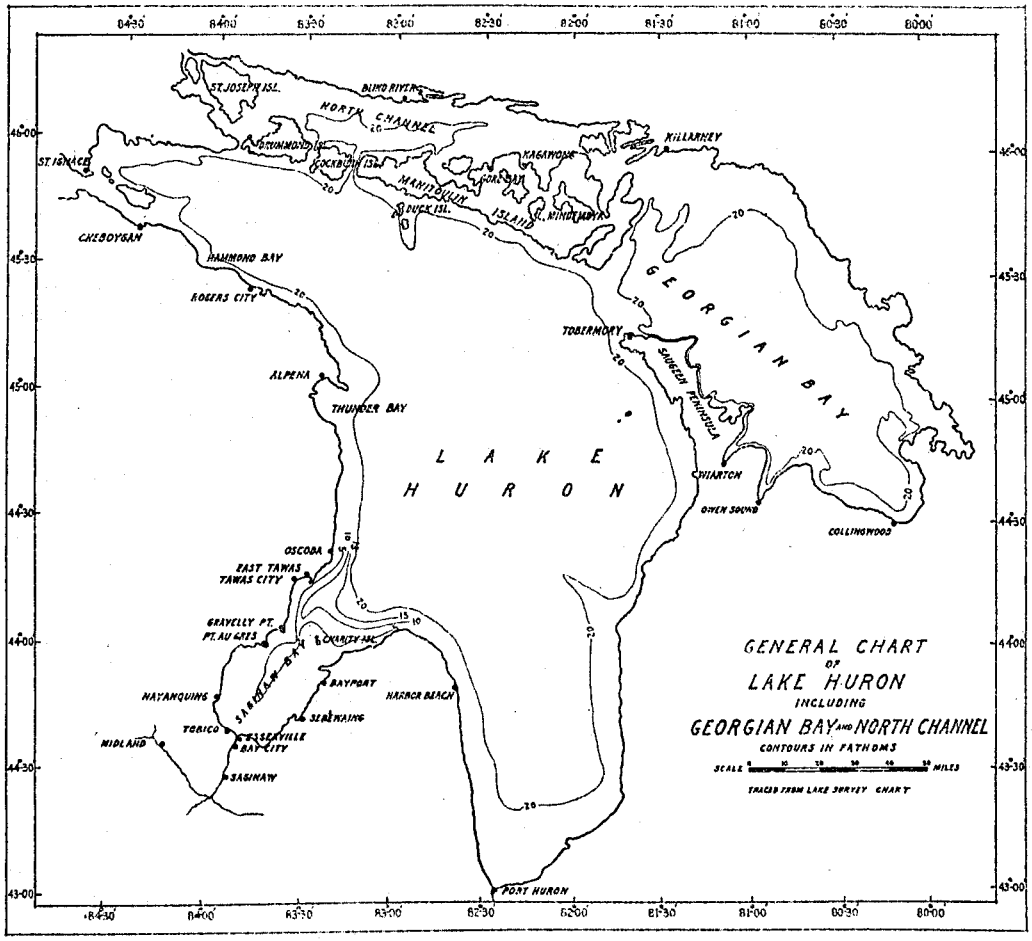

FIG. 1.—Lake Huron

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

GENERAL CONSIDERATIONS

DESCRIPTION OF COREGONID SCALES

TYPICAL SCALES

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

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

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

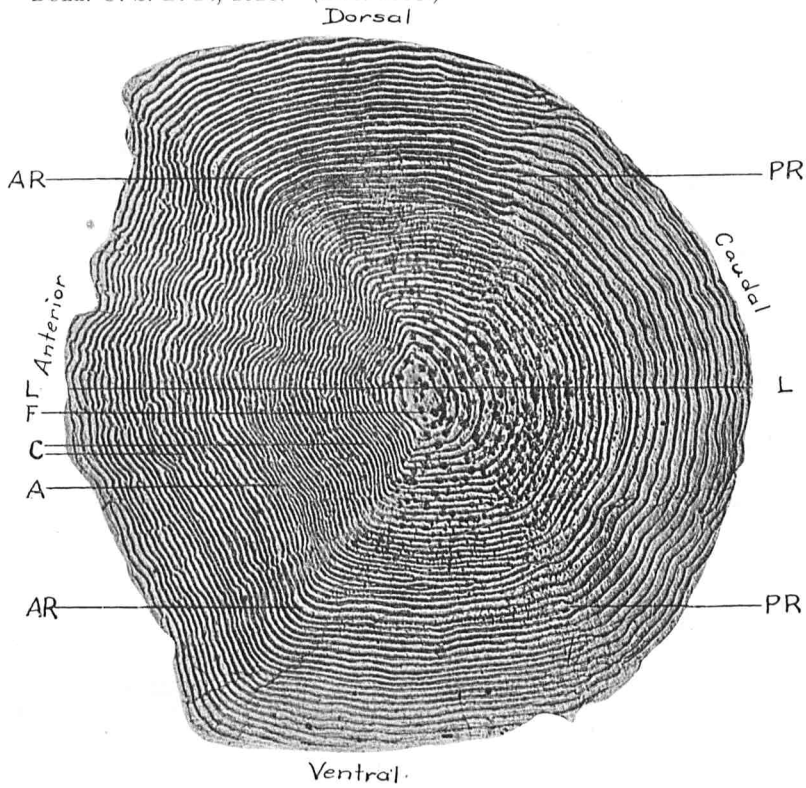

FIG. 2.—Typical scale of Lake Huron whitefish (*Coregonus clupeaformis*, Mitchill) from East Tawas, Mich. Length of fish, 197 millimeters; captured October 22, 1917. *L–L*, length of scale; *F*, focus; *C*, circuli; *A*, annulus of first winter; *AR*, anterolateral ridges; *PR*, posterolateral ridges;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

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

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

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

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

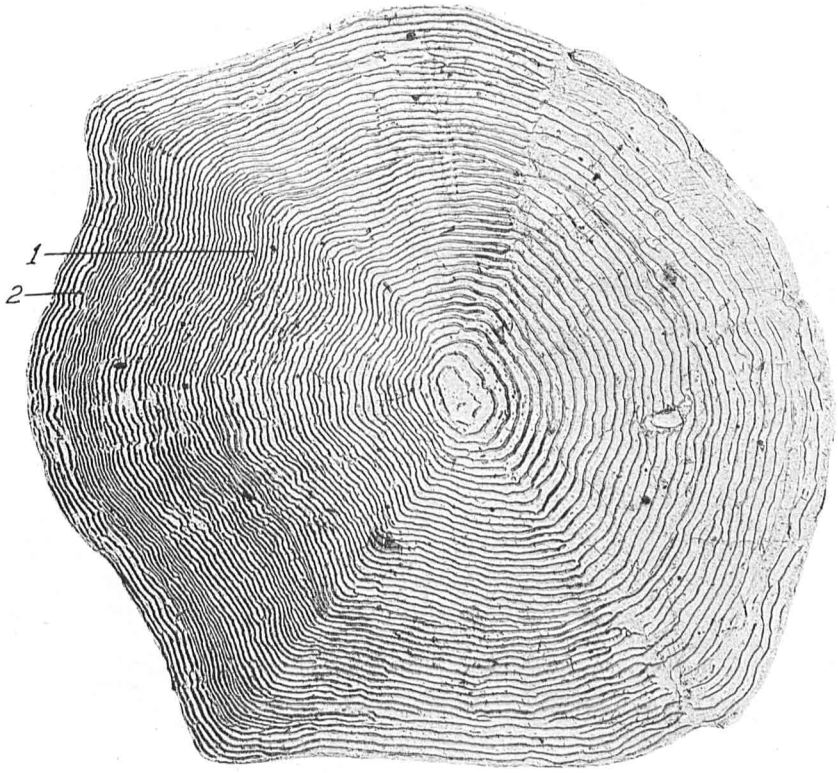

FIG. 7.—Scale of Lake Huron herring (*L. artedi*) taken October 27, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54329. Length, 219 millimeters. Male. Age III. Scale shows a wide double annulus in the second year

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

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

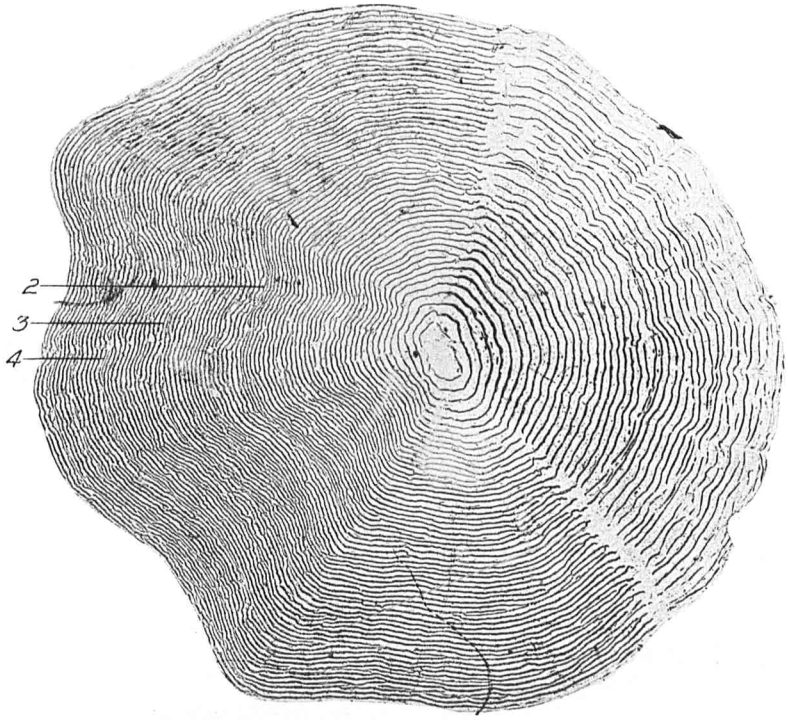

FIG. 10.—Scale from the same individual of which scales are shown in Figures 8 and 9. All trace of the first annulus has disappeared. Compare with Figures 8 and 9

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

IRREGULARITIES IN SCALE STRUCTURE

Various irregularities may occur in the structure of coregonid scales.

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

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

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

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

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

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

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

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

SCALE METHOD AND ITS APPLICATION

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

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

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

METHODS OF MEASUREMENTS AND COUNTS

BODY MEASUREMENTS

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

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

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

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

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

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

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

In the lake herring several other measurements besides total length were employed. H represents the length of the head as measured from the tip of the snout to the most distant point on the margin of the bony suboperculum, excluding the soft opercular membrane. H_1 represents the length of the head as measured from the tip of the snout to the most anterior point of the body proper on the projected

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

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

SCALE MEASUREMENTS AND COUNTS

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

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

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

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

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

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

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

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

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

GENERAL HISTORICAL REVIEW

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

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

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

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

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

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

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

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

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

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

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

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

Fritsch (1893, p. 89) enumerated the circuli (Anwachsringe) in the scales of salmon of known ages and of various lengths (34 millimeters to 90 centimeters) and concluded: "Genaue Verfolgung dieser Zunahme der Anwachsringe der Schuppe mit zunehmendem Alter dürfte einen Anhaltspunkt geben nach der Zahl der Anwachsringe bei grossen Lachsen das Alter zu bestimmen. Bei Salmlingen, von denen ich voraussetzte, dass sie schnell wachsen, fand ich die Anwachsringe weiter von ein-

ander entfernt und in geringerer Zahl im Verhältniss zur Gesammtlänge des Körpers." According to Arwidsson (1910), Hofer (1895), however, refutes Fritsch's conclusion that the age of a salmon can be ascertained from the number of concentric ridges on its scales.

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

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

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

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

Part I—CRITIQUE OF SCALE THEORY AND METHOD

ASSUMPTIONS OF THE METHOD

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

1. That the scales remain constant in number and [retain their] identity throughout the life of the fish.
2. That the annual increment in the length (or some other dimension which must then be used) of the scale maintains, throughout the life of the fish, a constant ratio with the annual increment in body length.
3. That the annuli are formed yearly and at the same time each year [or that some other discoverable relation exists between their formation and increment of time].

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

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

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

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

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

IDENTITY OF SCALES THROUGHOUT LIFE

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

CONSTANCY IN NUMBER OF SCALES THROUGHOUT LIFE

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

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

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

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

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

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

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

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

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

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

Size groups, millimeters	Nov. 12, 1923, age group IV				
	Average scale number			Average size	
	Male	Female	Male and female	Male	Female
211-220					
221-230					
231-240	80.41 (27)	79.74 (19)	80.13 (46)	238 (27)	236 (19)
241-250	81.43 (49)	81.96 (23)	81.60 (72)	246 (49)	245 (23)
251+	81.75 (16)	83.00 (11)	82.26 (27)	254 (16)	253 (11)
Grand average	81.18 (92)	81.38 (53)		245 (92)	244 (53)

Size groups, millimeters	Average scale number of all 1921 herring, age group III			Average scale number of all 1923 herring, age group V		
	Male	Female	Male and female	Male	Female	Male and female
Under 226	77.83 (18)	79.53 (17)	78.66 (35)			
Over 226	82.08 (12)	79.73 (15)	80.78 (27)			
Grand average	79.53 (30)	79.63 (32)				
Under 251				81.36 (25)	80.30 (10)	81.06 (35)
Over 251				82.80 (25)	81.27 (11)	82.33 (36)
Grand average				82.08 (50)	80.81 (21)	

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

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

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

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

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

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

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

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

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

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

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

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

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

Table 5 has been constructed to test the postulate that the fish with the larger number of scales were always large. Each age group of the two collections employed

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

ANNULI AND NUMBER OF YEARS OF LIFE

That the annuli of scales are truly "year marks" has been conceded in the past by most of the investigators who employed the scale method. In many instances the basis for the acceptance of this assumption has been the fact that the scale method actually worked in practice. Masterman (1913) states it as follows: "In studying the average sizes, average weights, and seasonal occurrence of the different age groups

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

CRITICISMS

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

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

[9] The criticisms are numbered consecutively.

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

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

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

migratory check formed in the estuary may occur anytime after the 1st of June in the fry, while the first annulus may form as early as August. The new growth (not the "intermediate" growth of the estuary), outside the first winter rings, may begin any time between August and the May following.

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

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

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

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

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

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

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

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

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

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

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

From a consideration of hypothetical and actual samples Lea concludes:

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

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

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

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

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

INDIRECT EVIDENCES

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

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

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

DIRECT OR EXPERIMENTAL EVIDENCES

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

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

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

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

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

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

number of the circuli in each growth zone, and (4) the distances separating the annuli fell below the normal.

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

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

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

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

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

The observations of Hoffbauer were repeated, and his conclusions were examined critically by Walter (1901), who studied the scales of the carp in commercial ponds. He granted the general truth of Hoffbauer's hypothesis but maintained that unless the finer structures of a scale were known age determinations would be erroneous in a large percentage of cases. Thus, for example, of 24 determinations that he made 13 were found to be incorrect. He found that Hoffbauer's criteria for a true annulus

could not be relied upon with certainty and therefore proceeded to search for other criteria. In doing so he discovered the fundamental principle underlying the method, later devised by Dahl and Lea, of calculating the length of a fish for each year of its life by the proportionate width of the bands on its scales. Walter found that the relative width of a year zone on a scale expressed to a certain degree the relative intensity of body growth, designated in terms of length and height.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Peart (1922) observed that annual growth is not nearly as well differentiated on the scales of artificially fed trout as on those of the wild fishes. The former scales are read with some uncertainty, the doubtful area being confined to the first two or

three years of life, the years of sexual immaturity. Peart ascribes this "vagueness of artificial scales" to the attempts of the breeders to make their fish grow continuously.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

CORRELATION BETWEEN GROWTH OF BODY AND SCALE

HISTORICAL

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Thompson, 1924) that the scales situated below the third dorsal fin are "practically representative throughout of the growth of the fish."

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

calculated from 22 scales varied from 6 to 11 millimeters and averaged 9.3 millimeters or 0.7 millimeter less than the actual.

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

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

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

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

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

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

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

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

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

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

AGE VARIATIONS IN THE GROWTH OF THE HEAD

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

abnormally high and the percentages of increase in length with age in body and scale coincide more closely than is indicated in this table.

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

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

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

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

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

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

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

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

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

[1] Plate.

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

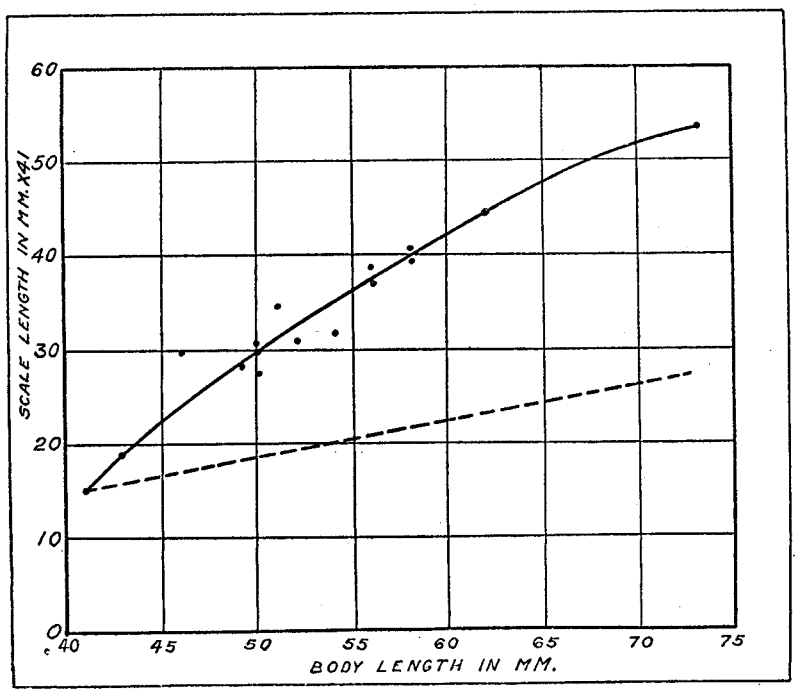

FIG. 12.—Relation between body and scale length in juvenile whitefish (*Coregonus clupeaformis*). The continuous curve is plotted from the body length and scale length data of Table 13. The broken line shows the form the curve would take if scale and body maintained the relation existing at the body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

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

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

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

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

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

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

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

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

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

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

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

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

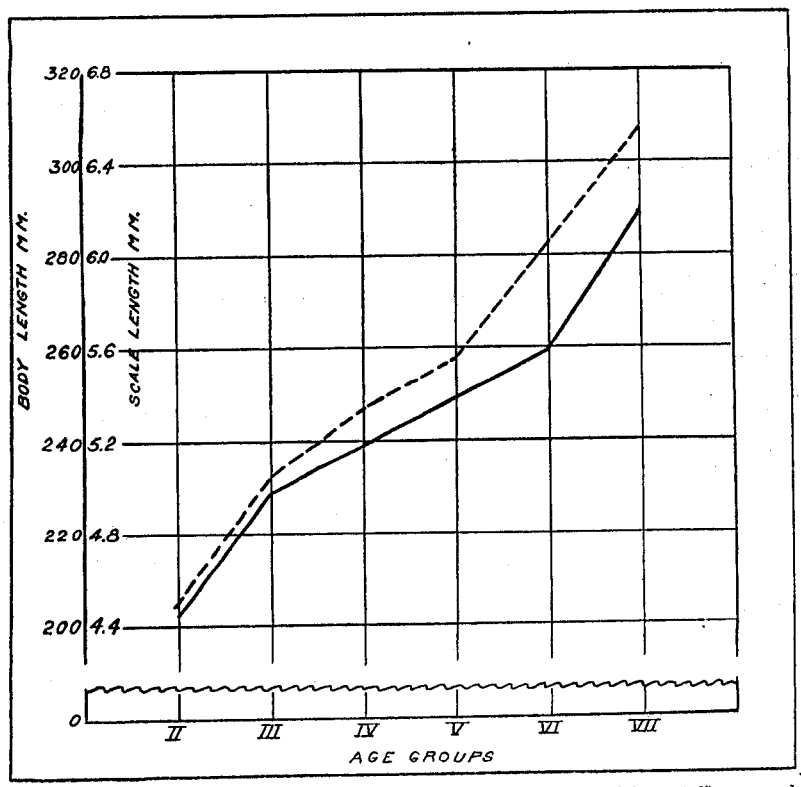

FIG. 13.—Body-scale length relationship of adult lake herring (*Leucichthys artedi*) arranged according to their age. The continuous curve is plotted from the average total lengths of the body, the broken curve from the average total lengths of the scale shown in Table 14

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

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

AVERAGE LENGTH OF BODY AND SCALE COMPARED FOR CORRESPONDING YEARS

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

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

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

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

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

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

the sixth year, when the herring attained an average length of 259 millimeters, the scale increased in length relatively more slowly than the body.

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

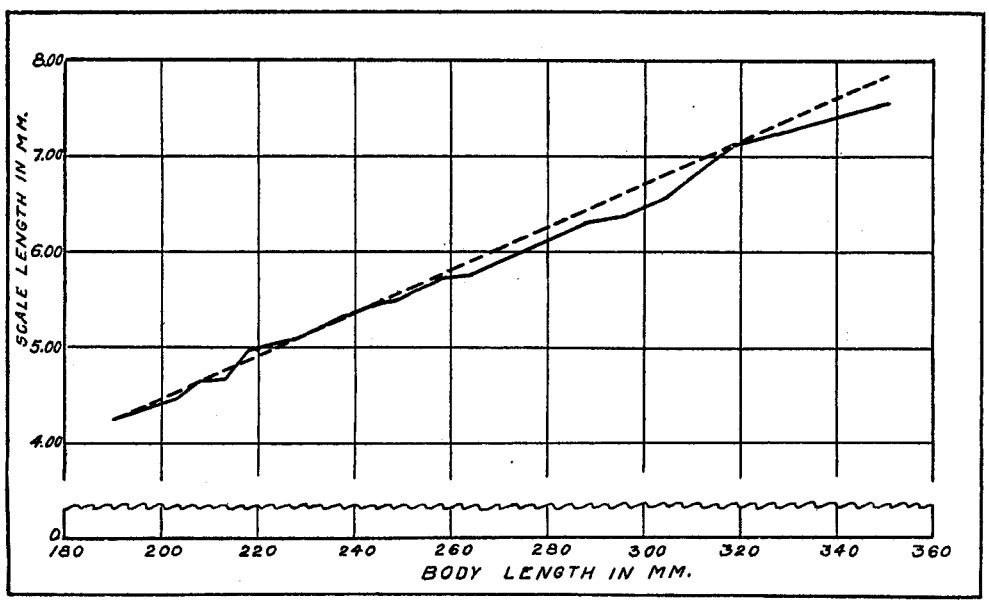

FIG. 14.—Body-scale length relationship of adult lake herring (*Leucichthys artedi*) arranged according to their size. The continuous curve based on the average lengths of body and scale shown in Table 15 represents the actual body-scale length relation; the broken line shows what the relation of the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

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

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

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

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

BAY CITY HERRING COLLECTED OCTOBER 29, 1921

Year	Number of specimens	Average length (K), in millimeters, when captured	Calculated length (K), in millimeters, at end of year[1]											
			I		II		III		IV		V		VI	
			On V	On ac	On V	On ac	On V	On ac	On V	On ac	On V	On ac	On V	On ac
III	50	226	124	111	190	184	------	------	------	------	------	------	------	------
IV	127	233	115	102	179	171	216	213	------	------	------	------	------	------
V	61	240	118	104	166	156	200	194	225	223	------	------	------	------
VI	22	264	117	103	162	151	195	187	224	219	250	247	------	------
VII	6	282	118	104	161	149	194	185	222	214	244	240	265	264

BAY CITY HERRING COLLECTED NOVEMBER 1, 1922

II	4	217	141	128	------	------	------	------	------	------	------	------	------	------
III	148	229	139	128	200	196	------	------	------	------	------	------	------	------
IV	245	236	122	109	183	176	217	216	------	------	------	------	------	------
V	95	241	114	99	171	160	205	199	229	227	------	------	------	------
VI	9	252	117	104	161	150	198	193	224	222	242	241	------	------

BAY CITY HERRING COLLECTED NOVEMBER 12, 1923

II	2	221	137	126	------	------	------	------	------	------	------	------	------	------
III	170	233	142	------	201	------	------	------	------	------	------	------	------	------
IV	240	243	133	120	192	186	224	223	------	------	------	------	------	------
V	90	251	119	105	179	170	213	209	237	236	------	------	------	------
VI	15	263	113	99	166	155	203	198	228	225	247	247	------	------
VII	2	263	119	106	157	150	184	174	210	204	234	230	248	248

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

for corresponding years of life is less in the young than in the old fish, however. This is indicated more clearly in Table 20, in which is shown the amount of correction required to bring the computations of the two series into agreement.

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

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

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

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

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

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

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

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

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

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

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

99760—29——5

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

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

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

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

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

1. The samples of fish are not representative of a year group; that is, the youngest year groups are represented only by their biggest individuals, and as we proceed toward the older groups there appear more and more of those that had been the smaller individuals in their earliest years, so that the average sizes of these older groups tend to show a less increment of growth and a leveling in values is attained (some such thing occurs, according to Lea). This Lee termed "the selective effect of size."

2. The nets are selective, retaining only the largest fish of the youngest year group and excluding the largest fish of the oldest year groups.

3. Conditions of growth are improving and the fish actually are growing more rapidly at present.

4. Females and males that have different growth rates are present in varying proportion.

5. The scale, especially the flexible newest part, contracts when new increments are added. Miss Lee noted that the newest increment in the scale is usually wider

than the scale increment of the preceding year (the reverse of the natural law of decrease of scale increment with age and slower growth rate of body), which seems to prove that the scale increment of the year contracts after being deposited.

6. A part of the scale is absorbed in the maturation of sex organs during the spawning period, as, for example, in the salmon.

7. Occasionally more than one ring forms per year.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Do the scales of herring, therefore, contract with age? Our data suggest that apparently a concentration with age takes place in the first two innermost zones of scales. The data likewise indicate that the third zone changes little with age while the outer zones expand. Do contraction and expansion then occur synchronously in the scales of lake herring? This does not seem possible in view of what is known concerning the structure of teleost scales in general. "In minute structure each scale consists of an outer layer of bone, which, like the bone of the endoskeleton, may either be homogeneous, except for a feeble lamination, or it may contain bone cells arranged in successive layers parallel to the surface of the scale. In addition, there is an inner fibrous stratum in which the fibrous bundles in any one plane cross those in planes above or below them." (Bridge, T. W., in Cambridge Natural History, 1910, Vol. VII, p. 189.) The fibrous bundles of any one plane form a thin lamella. During the growth of the scale these lamellæ are deposited on the lower surface of the scale, each new lamella growing larger than and extending beyond the one most recently formed. Lea (1919) found that in the marine herring (Clupea) the breadth of the zones of these lamellæ "exhibits an irregular progression, broader belts suddenly appearing after a series of narrow zones, * * * that the transition from narrow to broader zones takes place just where the surface of the scale shows a winter ring. Thus, the elementary plates are seen to form their own system of annual rings, corresponding to that of the surface layer, but otherwise differing greatly from this, and more resembling that found in the scales of many salmonoids and gadoids, etc.,

where the winter rings are not so sharply marked, but a gradual transition from summer to winter is seen [p. 90]." As is the case with the circuli, the number of lamellæ deposited each year varies as the growth rate of the scale. Lea found further that the outer or "upper covering layer is of almost equal thickness at the edge and near the center of the scale and evidently does not grow thicker; it is thus easy to understand that the winter rings, for instance, upon the surface of this layer, continue equally distinct many years after formation * * * [p. 89]." "The scale may thus be considered as a greatly flattened cone composed of fibrillary plates * * *. This cone is evidently covered entirely by a nonfibrillary layer, on the upper side of which, however, is found finely marked relief which gives the scale its characteristic appearance [p. 87]."

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

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

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

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

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

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

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

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

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

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

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

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

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

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

for any further increase in the width of this zone in older age groups. In fact, the average of the third year scale increments should probably decrease in the 5-year fish. (See below.) The data of Table 22 show that this average usually increases in the 4-year fish and varies little with the older age groups.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

It is to be noted that Lee's formula proposes to eliminate the "phenomenon" from calculated length values that involve computations based on mathematical proportions. The larger the number of proportional computations involved (as in old fish) the greater will be the correction for the first computation (that is, for year 1; see p. 339). Lee's formula assumes that the "phenomenon" is purely the result of the method of calculation from scales. Obviously, then, late scale formation can not be a factor in the "phenomenon" found in direct measurements of scale diameters, as in them no computations are involved. Even so, there is no relation apparent between the late formation of scales and the progressive decrease in the length of scale diameters with age (Table 22) in fish of the same year class. Tardy scale formation was not considered, therefore, in the discussion of scale-diameter measurements (p. 331).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

TIME OF FORMATION OF AN ANNULUS AND FACTORS INVOLVED IN IT

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

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

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

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

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

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

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

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

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

DESCRIPTION OF ADULTS

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

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

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

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

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

NATURAL HISTORY OF ADULTS

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

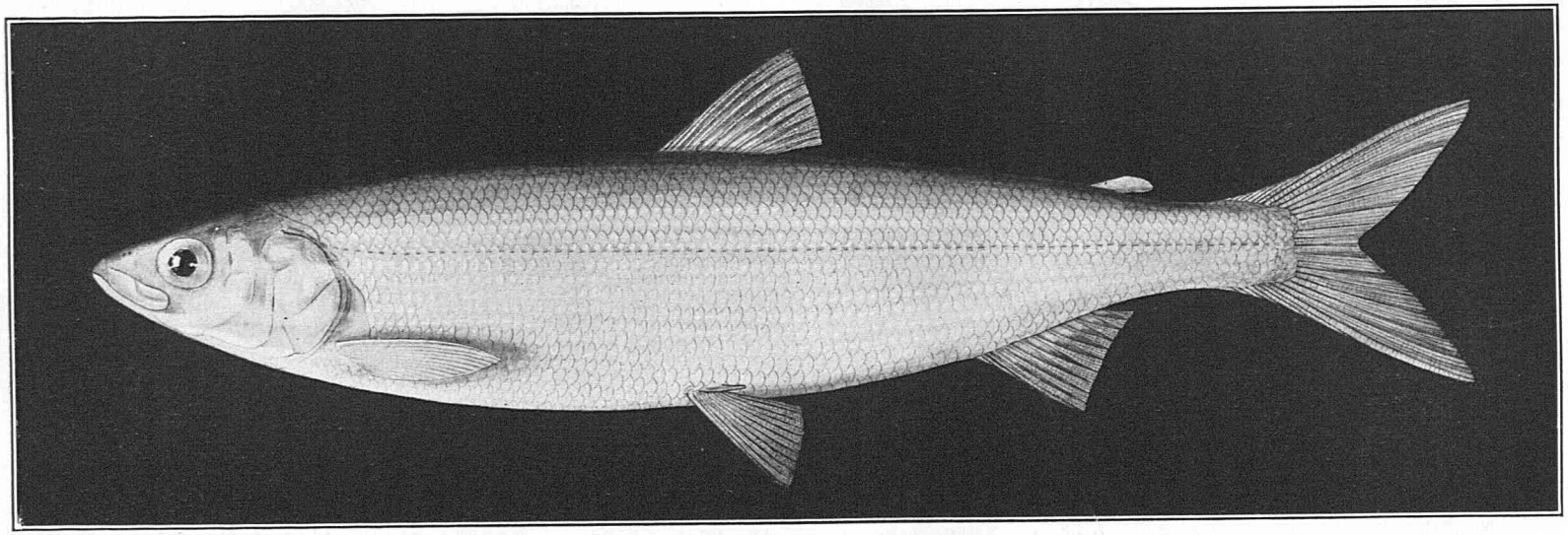

FIG. 15.—*Leucichthys artedi* LeSueur. Lake herring

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

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

Year	Pounds	Value	Average price per pound	Year	Pounds	Value	Average price per pound
1891	3,459,500	$36,203	$0.010	1920	3,387,057	115,199	.034
1892	2,575,200	(?)	----------	1921	2,164,233	66,760	.031
1893	4,050,000	(?)	----------	1922	4,395,902	103,804	.024
1896	6,464,836	28,556	.004	1923	3,038,570	73,389	.024
1897	4,890,650	29,452	.006	1924	2,878,636	62,616	.022
				1925	5,148,121	112,452	.022
Average, 5 years	4,288,037	31,404	.007	Average, 6 years	3,502,087	89,037	.026

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

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

LIFE HISTORY OF ADULTS (AGE AND GROWTH)

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

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

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

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

JUVENILE LAKE HERRING

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

ABUNDANCE OF LAKE HERRING

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

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

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

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

MATERIAL

The following life history of the lake herring, based upon a study of the scales, involves only the Saginaw Bay fish taken by me or sent to me by Mr. Kavanaugh, of Bay City, Mich., in the fall of 1921, 1922, 1923, and 1924. These Saginaw Bay herring are compared later with the herring collected by Doctor Koelz in 1917 and 1919

from various localities on Lake Huron and by me in 1922 at Oscoda, Mich. Doctor Koelz's collections are usually small, taken for taxonomic purposes, and my conclusions based on them must be accepted with such reserve as the relatively small numbers impose.

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

AGE GROUPS

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

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

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

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

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

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

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

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

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

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

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

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

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

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

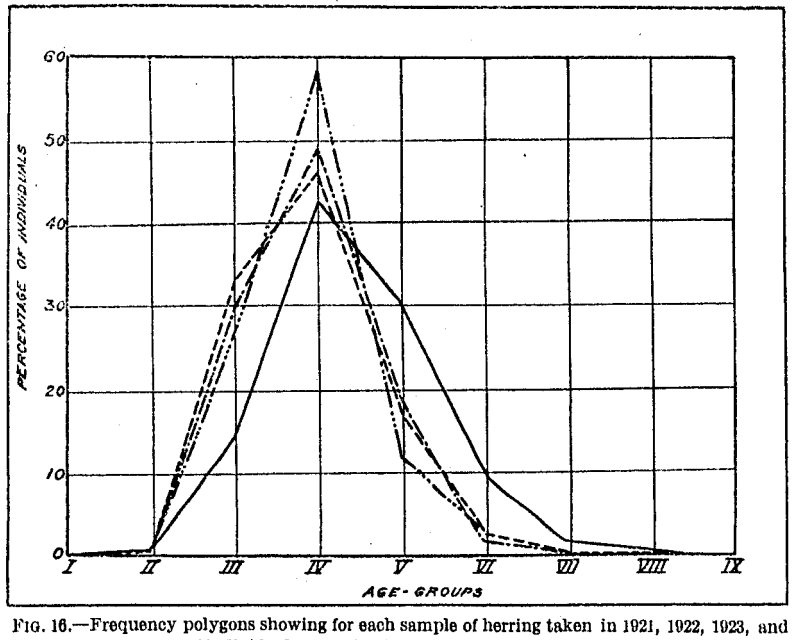

FIG. 16.—Frequency polygons showing for each sample of herring taken in 1921, 1922, 1923, and 1924 the percentage of individuals occurring in each age group. The curves are based on the percentages shown in the lower right half of Table 30. — — —, 1921; — · —, 1922; — — —, 1923; — · · · —, 1924 (Tobico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

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

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

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

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

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

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

YEAR CLASSES

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

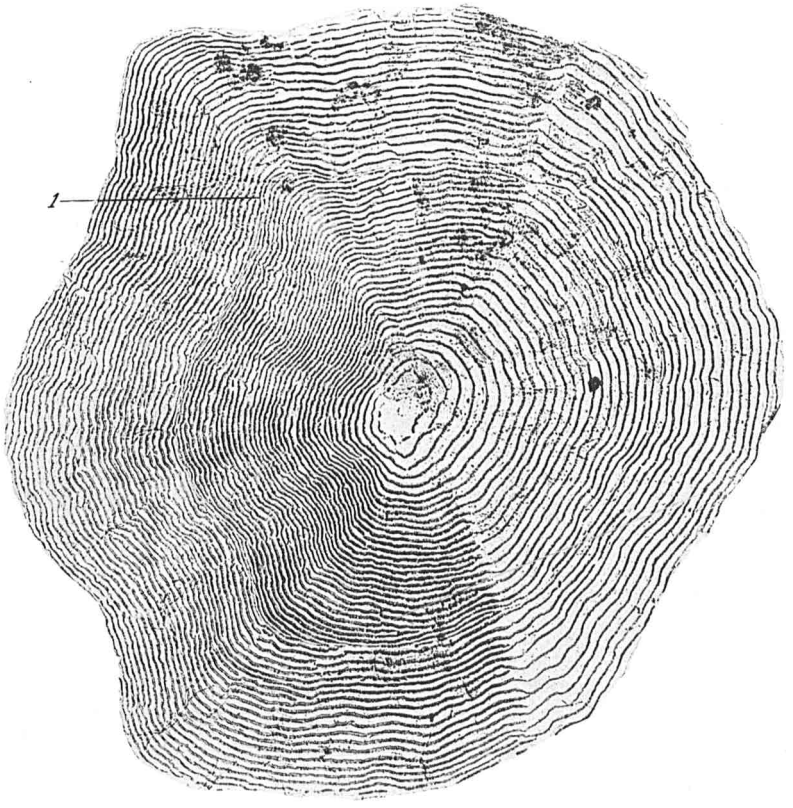

FIG. 17.—Scale of Lake Huron herring (*L. artedi*) taken November 1, 1922, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 58597. Length, 213 millimeters. Weight, 4 ounces. Immature male. Age II. Scale shows one completed annulus and a large marginal growth

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

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

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

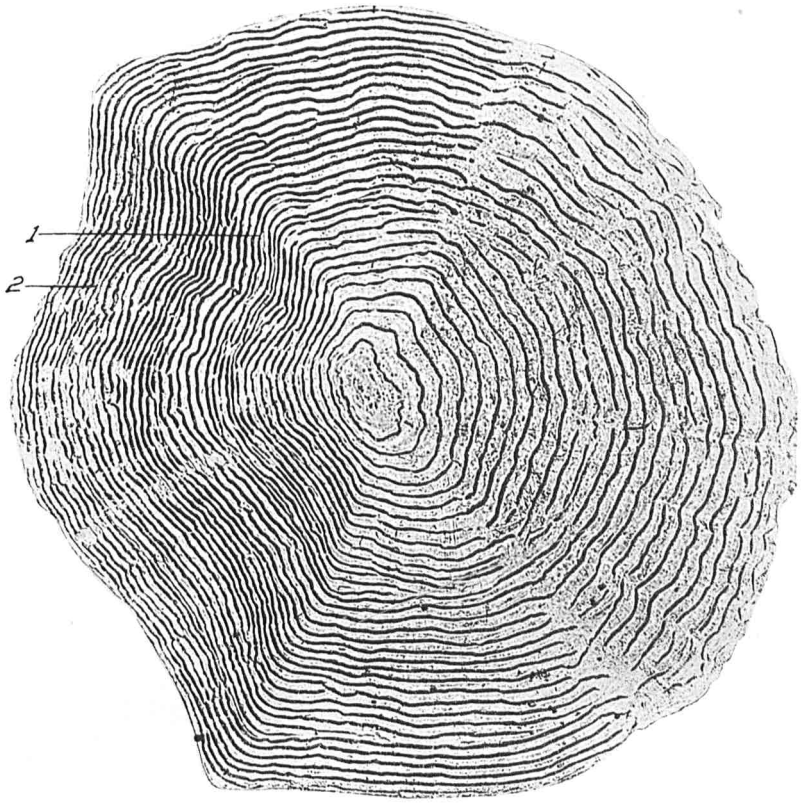

FIG. 21.—Scale of Lake Huron herring (*L. artedi*) taken September 10, 1917, at Alpena, Mich. University of Michigan Museum No. 52195. Length, 175 millimeters. Age III. Scale shows two completed annuli and a marginal growth

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

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

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

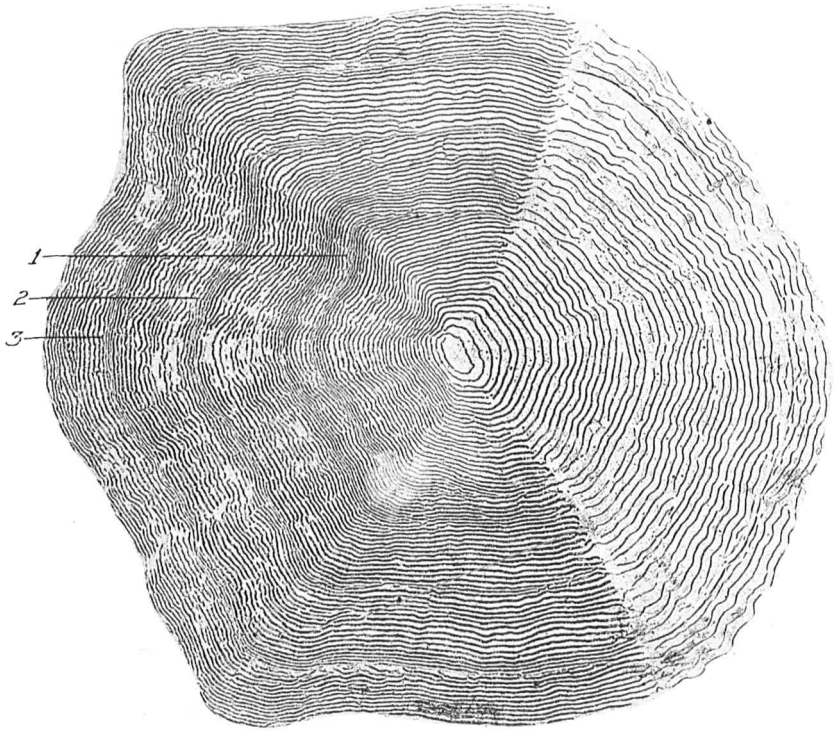

FIG. 25.—Scale of Lake Huron herring (*L. artedi*) taken October 29, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54661. Length, 308 millimeters. Mature female. Age IV. Scale shows three completed annuli and a marginal growth

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

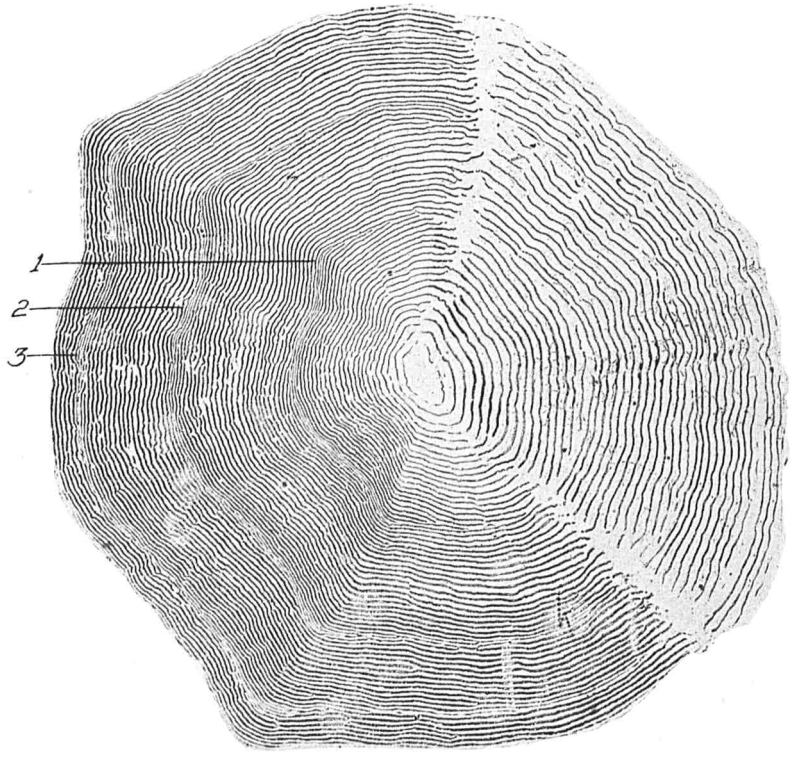

FIG. 27.—Scale of Lake Huron herring (*L. artedi*) taken July 17, 1917, at St. Ignace, Mich. Length, 220 millimeters. Male. Age IV. Scale shows three completed annuli and a marginal growth

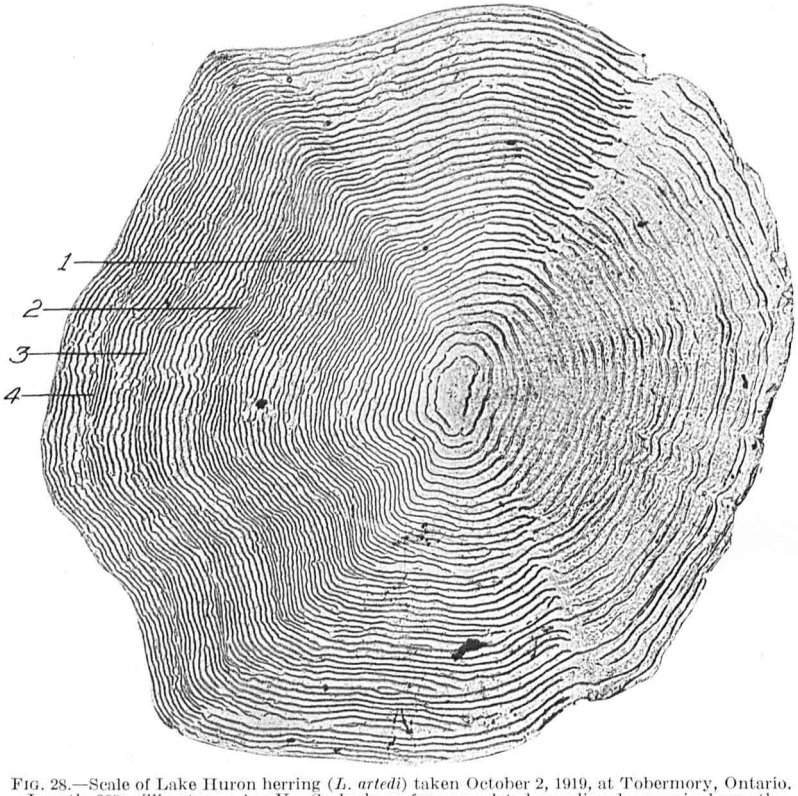

FIG. 28.—Scale of Lake Huron herring (*L. artedi*) taken October 2, 1919, at Tobermory, Ontario. Length, 209 millimeters. Age V. Scale shows four completed annuli and a marginal growth

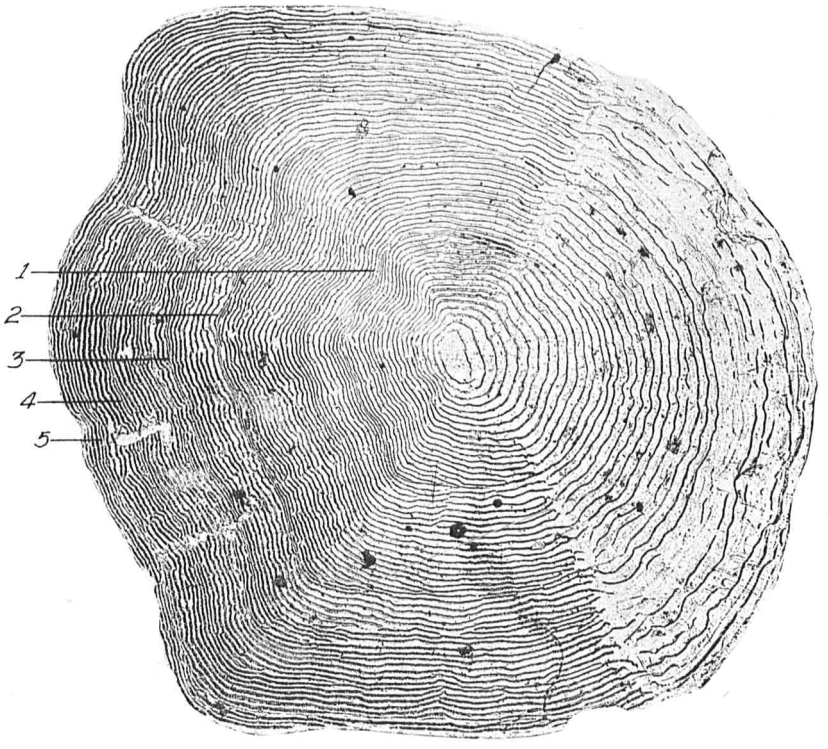

FIG. 29.—Scale of Lake Huron herring (*L. artedi*) taken November 1, 1922, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 58693. Length, 281 millimeters. Weight, 10 ounces. Mature female. Age VI. Scale shows five completed annuli and a marginal growth

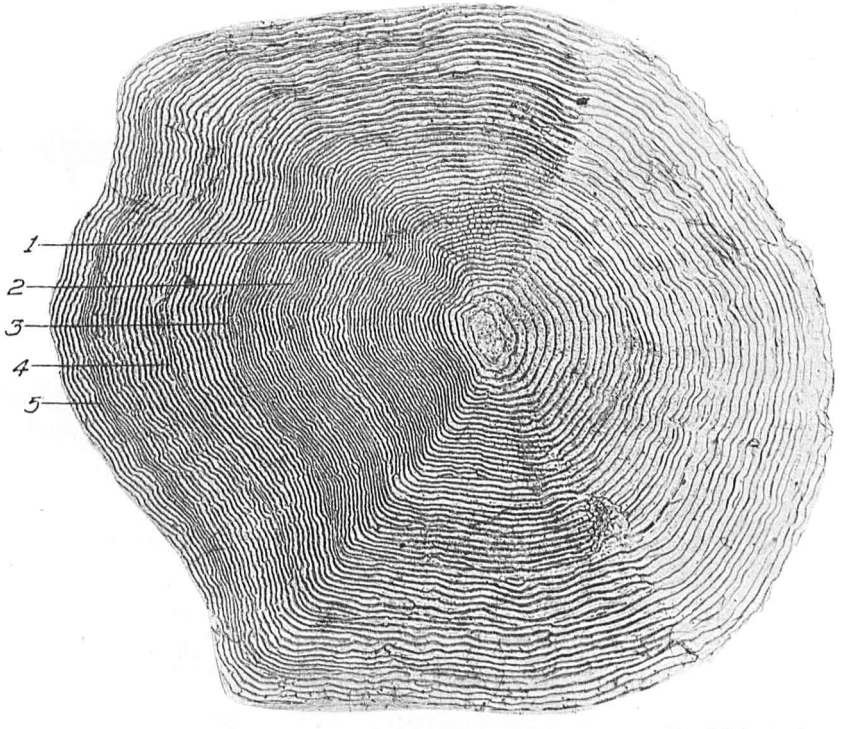

FIG. 30.—Scale of Lake Huron herring (*L. artedi*) taken October 29, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54662. Length, 295 millimeters. Mature female. Age VI. Scale shows five completed annuli and a marginal growth

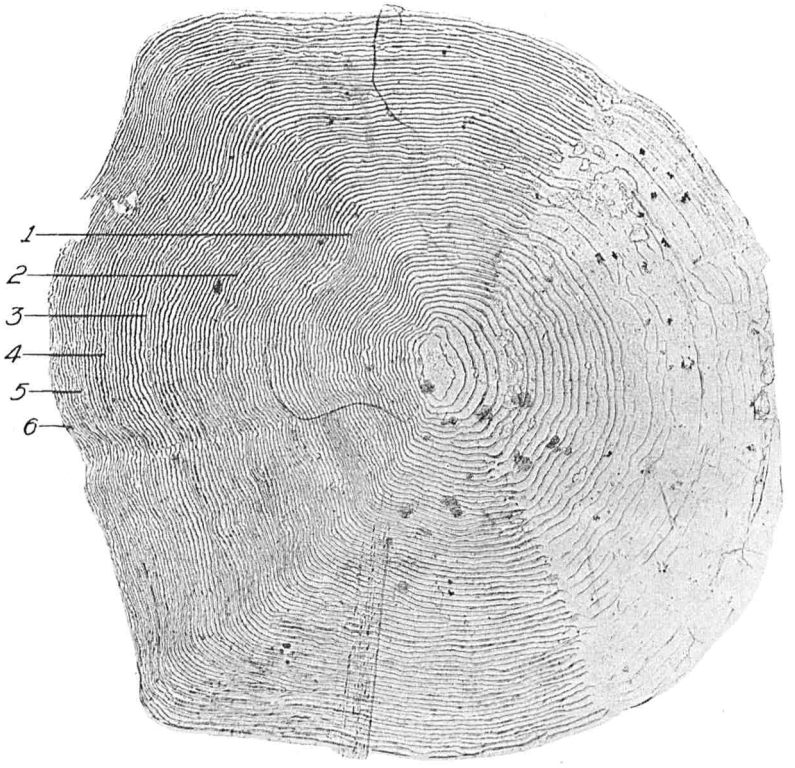

FIG. 31.—Scale of Lake Huron herring (*L. artedi*) taken October 27, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54478. Length, 272 millimeters. Mature male. Age VII. Scale shows six completed annuli and a marginal growth

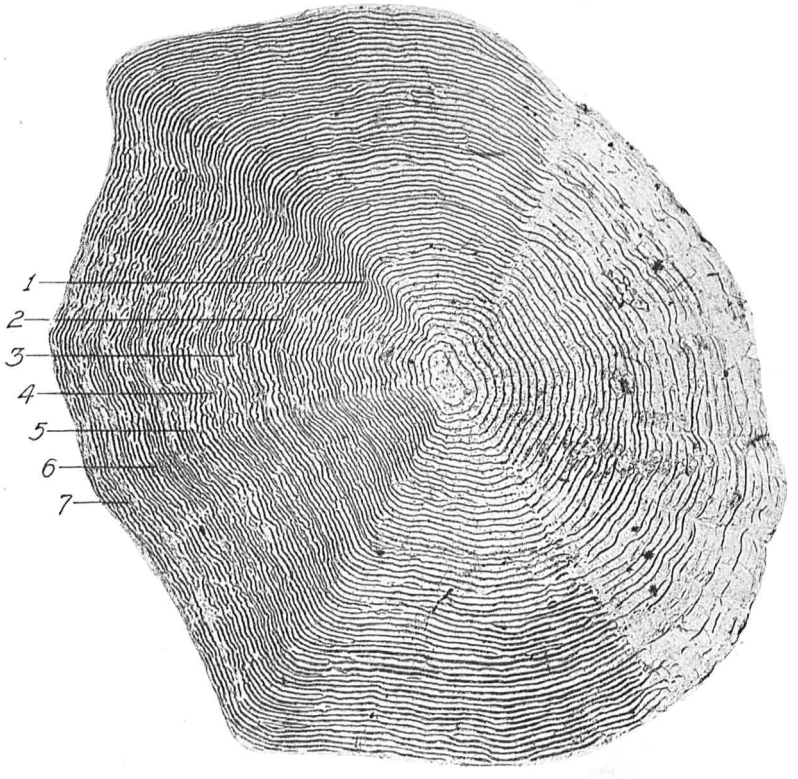

FIG. 32.—Scale of Lake Huron herring (*L. artedi*) taken October 27, 1921, at Bay City, Mich. (Saginaw Bay). University of Michigan Museum No. 54470. Length, 263 millimeters. Male. Age VIII. Scale shows seven completed annuli and a marginal growth

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

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

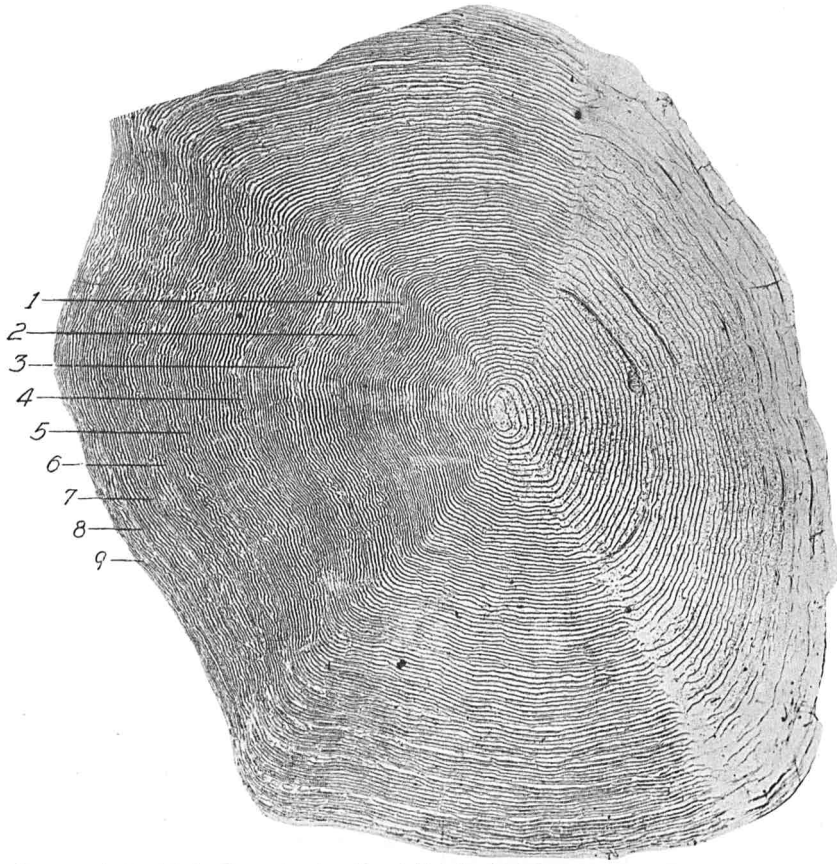

FIG. 35.—Scale of Lake Huron herring (*L. artedi*) taken October 22, 1917, at East Tawas, Mich. University of Michigan Museum No. 52272. Length, 377 millimeters. Weight, 2 pounds. Age X. Scale shows nine completed annuli and a small marginal growth

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

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

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

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

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

AVERAGE AND EXTREME LENGTH AND WEIGHT OF HERRING

FISH OF DIFFERENT SCHOOLS

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

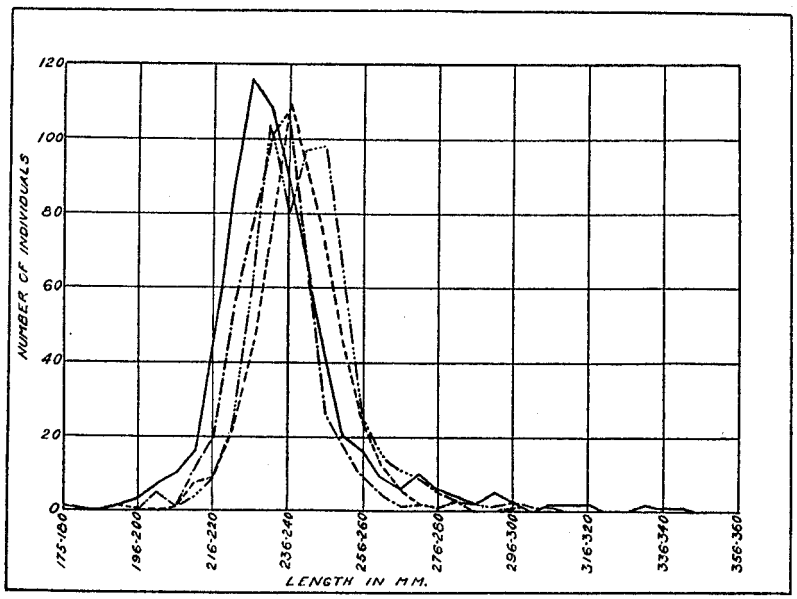

FIG. 37.—Frequency polygons showing for each sample of herring taken in 1921, 1922, 1923, and 1924 the number of individuals in each size group at 5-millimeter intervals. The data are shown in Table 29. — — —, 1921; — · —, 1922; — — — —, 1923; — · · · —, 1924 (Tobico and Nayanquing samples combined)

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

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

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

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

As shown in Table 31, the smallest 2-year herring measured 177 millimeters in length; the lightest 2-year fish weighed 2 ounces. The largest 2-year herring measured 229 millimeters in length; the heaviest weighed 5 ounces. The smallest sexually mature male measured 160 millimeters in length; the smallest sexually mature female 190 millimeters. The youngest sexually mature male and female were in their second year. The largest sexually mature male was in its eighth year and measured 365 millimeters in length. The largest sexually mature female measured 335 millimeters in length and was in its sixth year (Table 32). The largest sexually immature or nonspawning male was 238 millimeters long; the oldest was in its fifth year. The largest sexually immature or nonspawning female was 257 millimeters long; the oldest was in its fifth year. The heaviest male weighed 16.5 ounces, the heaviest female 13.0 ounces. The oldest male and female were in their

eighth year of life. The oldest herring I have ever seen was a female in its eleventh year, taken in 1917 from a pound net at Blind River in Georgian Bay. The largest herring I have ever seen was a female 395 millimeters (15.6 inches) long, weighing 2 pounds and 3 ounces. It was taken in 1924 from Saginaw Bay. The largest herring of which I have a record was captured at Brighton, Ontario (Lake Ontario), in 1921; it measured 412 millimeters in length and was in its eleventh year (see fig. 36).

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

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

AGE GROUPS

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

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

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

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

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

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

MALES AND FEMALES

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

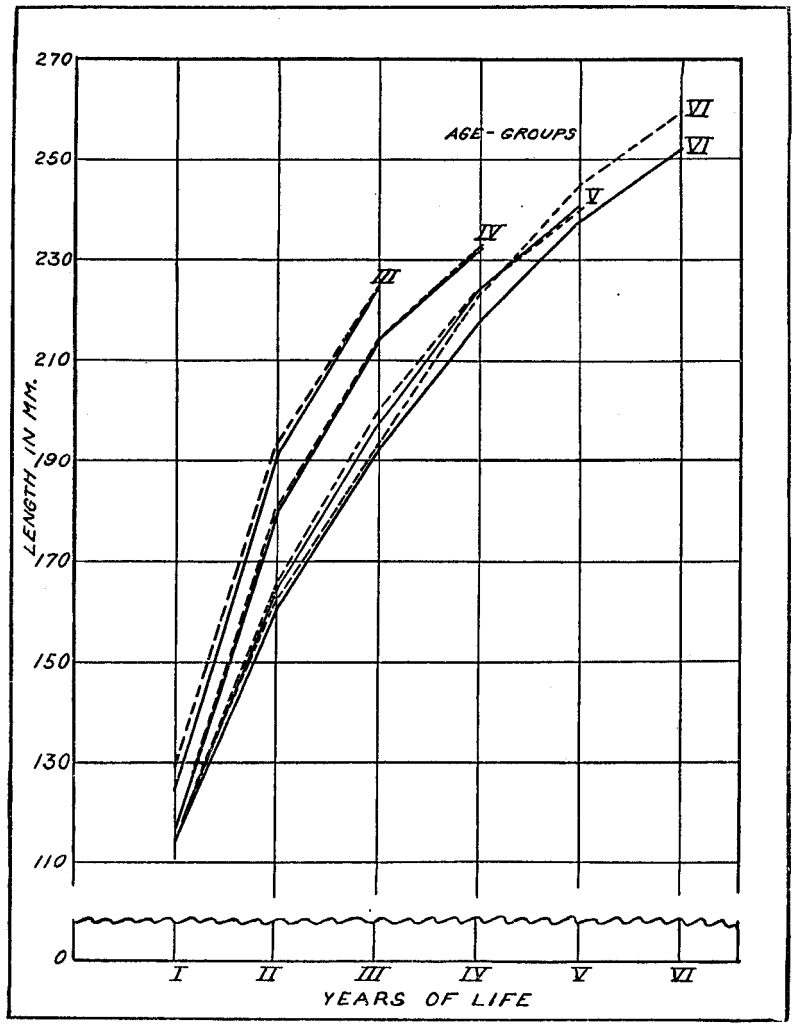

FIG. 38.—Average total length (for Saginaw Bay herring taken in 1921) attained by the male and female of an age group at the end of each year of life. The data are shown in Table 33. — — — —, male; — — — —, female

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

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

[1] Actual length when captured in November.

RATE OF GROWTH

METHOD OF DETERMINATION

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

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

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

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

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

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

[4] Male and female.

UNCORRECTED AND CORRECTED COMPUTED LENGTHS

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

GROWTH OF AGE GROUPS AND YEAR CLASSES

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

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

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

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

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

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

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

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

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

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

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

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

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

Summarizing this detailed analysis, we find that the 1915 and 1916 year classes grew at corresponding rates throughout life. Although the fish used for calculating the lengths of these two year classes were respectively 7 and 6 years old, the difference in age is so little that there is no evidence of apparent change in growth rate. We find that the 6-year fish of the 1917 year class grew at the same rate as the two previously mentioned year classes during the first two years of life (1917 and 1918), then reached a greater length in the third year in 1919 and in the corresponding later years of life. The 1918 year class (age groups V and VI) reached about the same

length in the first year of life as the three preceding year classes but exceeded them in length in corresponding later years. The 1919 year class (age groups IV,V, VI), however, in general reached greater average lengths at corresponding ages than its predecessors in all years of life. The same tendency to attain greater lengths than its predecessor at corresponding ages is found among the remaining year classes considered. Two exceptions are noted—the rates of growth are approximately the same in the 5-year fish of the 1919 and 1920 year classes and in the 4-year herring of the 1920 and 1921 year classes. It is to be noted, then, that an acceleration in growth occurred in 1919 in the third year of life in the fish of the 1917 year class, in the second year in the fish of the 1918 year class, and in the first year in the fish of the 1919 year class, but apparently not in the fourth year in the 6-year individuals of the 1916 year class; and that the herring of all age groups attained greater lengths in the early years of life after 1919 than before this year. As comparisons are made between fish of the same age groups, the increases in length are believed to be actual and not Lee's "apparent change in growth rate." It appears, then, that the year 1919 introduced a period favorable for the growth of herring.

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

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

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

[3] See footnote 4, p. 368.

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

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

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

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

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

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

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

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

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

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

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

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

Age group	Year of life	Average computed increments of length, in millimeters, attained during the year—										
		1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924
VIII	IV				30 (3)							
VII	IV					30 (12)		26 (2)				
VI	IV						28 (67)	26 (9)	25 (15)	28 (18)		
V	IV							25 (205)	24 (95)	24 (90)	25 (74)	
IV	IV								[b] 18 (291)	[b] 19 (245)	[b] 19 (240)	[b] 20 (356)
VIII	V					33 (3)						
VII	V						21 (12)		24 (2)			
VI	V							21 (67)	18 (9)	19 (15)	21 (18)	
V	V								[b] 16 (205)	[b] 12 (95)	[b] 14 (90)	[b] 18 (74)
VIII	VI						20 (3)					
VII	VI							18 (12)		14 (2)		
VI	VI								[b] 14 (67)	[b] 10 (9)	[b] 16 (15)	[b] 19 (18)
VIII	VII							18 (3)				
VII	VII								[b] 15 (12)		[b] 15 (2)	
VIII	VIII								[b] 15 (3)			

[b] Increment up to November when captured.

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

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

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

LAW OF GROWTH COMPENSATION

Gilbert (1914) concludes from a study of the computed growth increments of some 4-year sockeye salmon (*Oncorhynchus nerka*) that a compensation in growth occurred in the third and fourth years of life. That is, salmon that were large at the end of the second year grew, on the average, more slowly in succeeding years than the salmon that were small at the end of the second year, so that eventually all indi-

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

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

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

If we rearrange the increments of length of Table 38 in such a way that those of the same age groups are brought together as shown in Table 40 they may be compared more rapidly. An examination of this table shows that the 6-year herring hatched in 1916—that is, during a period of slow growth—grew slightly faster in the fourth and

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

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

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

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

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

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

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

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

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

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

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

NORMS OF GROWTH

Lengths.—As suggested at the beginning of this section, in order to obtain the norm of growth in a long-lived species, which is not influenced by seasonal cycles of growth or annual fluctuations in it, we must combine the rates of growth for corresponding ages of all year classes. Such an incomplete general norm, based on direct measurements of fish, is shown near the bottom of Table 34. A complete one, based on the measurements of scales, is shown at the bottom of Table 26. A third, based on both uncorrected computed averages and actual averages, is shown in the grand averages of Table 43. The grand averages of Tables 26, 34, and 43, both total lengths and increments of length, are plotted in Figure 39. Those of Table 43 really

represent the average growth rate for the whole period covered by the years 1915 (1914) to 1924, inclusive. The curve plotted from the grand averages of Table 43 shows graphically the average growth of the lake herring during the last 10 years.

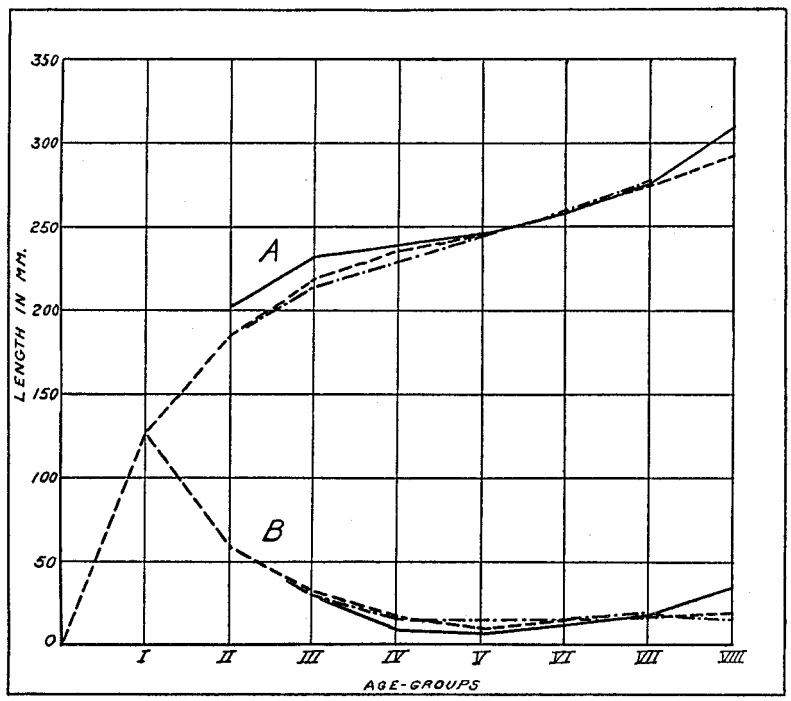

FIG. 39.—Total length and increment in length attained by Saginaw Bay herring at the end of each year of life. **A**, curves based on grand averages of total lengths: — — —, curve plotted from the grand averages obtained by combining the actual lengths of all fish belonging to the same age group. (See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

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

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

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

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

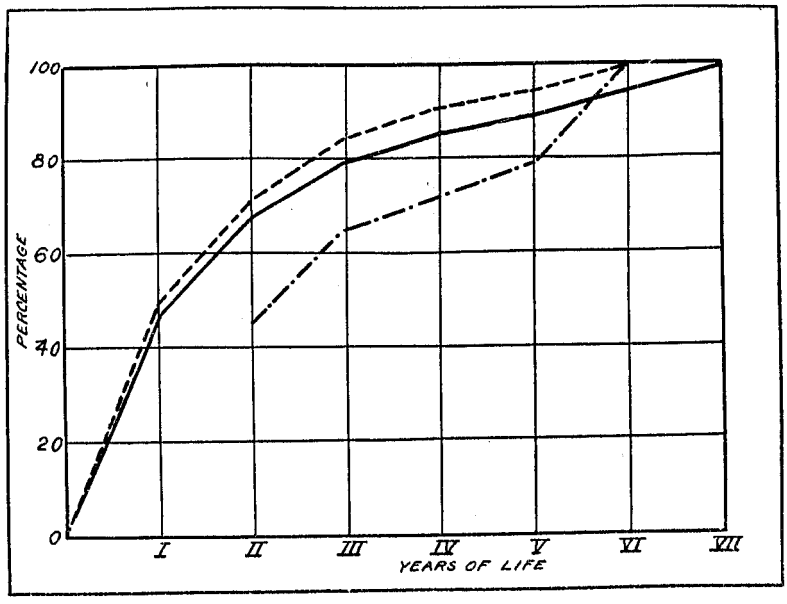

FIG. 40.—Percentage of total growth in length and weight completed at the end of each year of life. The percentages of length are shown on pages 375 to 376 and are derived from the grand averages of Table 43. The percentages of weight are shown on page 376 and are derived from the grand averages of Table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

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

Weights.—Table 34 furnishes growth data of the herring in terms of weight. The general average weight for each sex is given near the bottom of each column. Curves based on these values are shown in Figure 41. If the total weight at the end of the sixth year is taken as 100 per cent, then at the end of the second year 50.3 per cent, at the end of the third year 64.2 per cent, at the end of the fourth year 73.9 per cent, and at the end of the fifth year 83.9 per cent of the average total weight is attained by the males, while in the females the corresponding values are 46.7, 63.4, 69, and 77 per cent. When the weights of the males and females are combined

the percentages at the end of each year are as follows: Year II, 45.4 per cent; year III, 64.7 per cent; year IV, 72.1 per cent; and year V, 79.4 per cent. (Corresponding figures for length, based on year VI are: year I, 49.2 per cent; year II, 71.7 per cent; year III, 84.5 per cent; year IV, 91.1 per cent; and year V, 94.6 per cent; see fig. 40.)

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

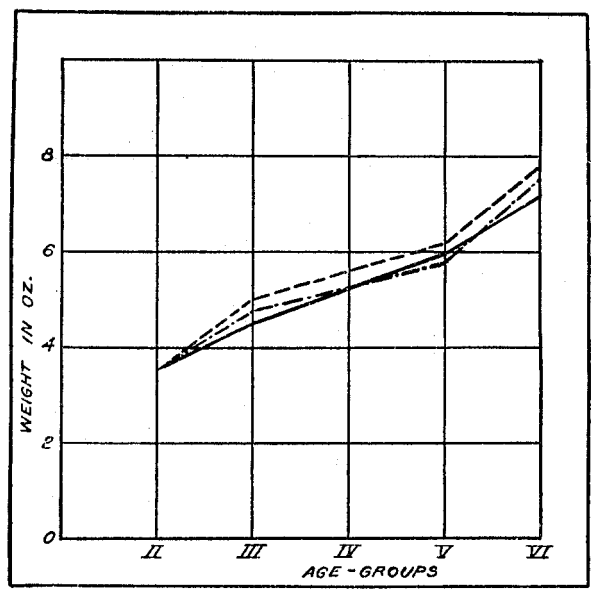

FIG. 41.—Average weight, in ounces, reached by male (— — —) and female (— · —) Saginaw Bay herring in different years of life. The curve based on males and females (— — — —) involves larger numbers of specimens. Curves are plotted from the grand average weights of Table 34

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

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

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

RELATIONSHIP BETWEEN LENGTH AND WEIGHT

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

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

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

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

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

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

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

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

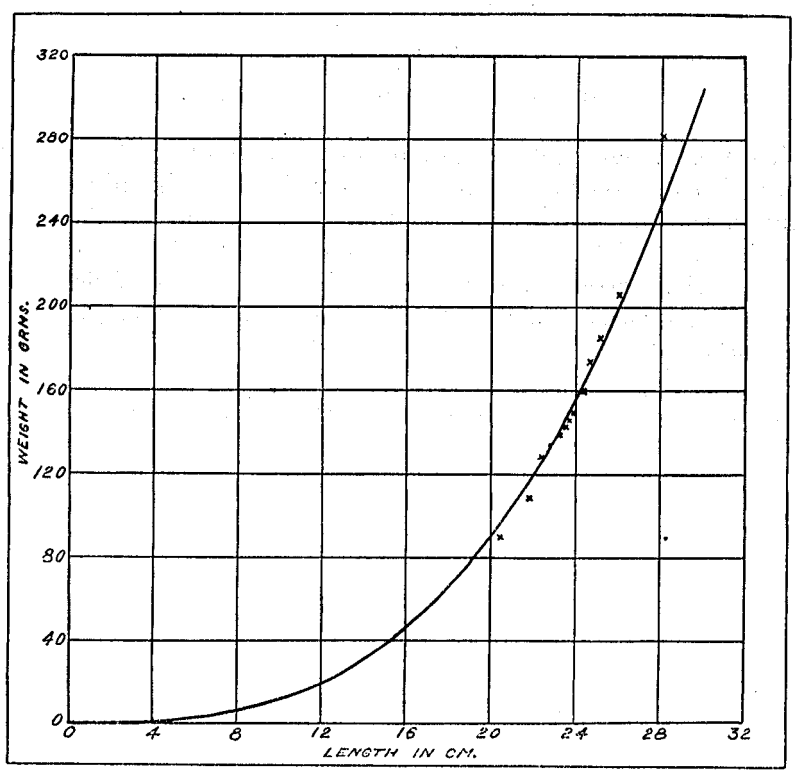

FIG. 46.—Length-weight relationship of Saginaw Bay herring taken in the fall just before spawning. The curve is plotted from theoretical weights computed by means of the length-weight formula $W=k.L^3$, in which $k=0.01126$. The crosses represent actual weights (see Table 46).

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

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

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

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

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

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

RELATIVE ABUNDANCE OF MALES AND FEMALES

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

and to predominate in the annual run. He found that "the relative numbers of males and females in the different year groups is a comparatively constant feature in each river basin" and "thus rises to the dignity of a racial character [p. 17]."

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

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

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

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

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

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

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

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

The percentages of Table 47 show that the relative abundance of males and females also varies with the age groups. The grand averages at the bottom of the

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Examination of Tables 53 and 54 shows that beyond any question the Tobico and Nayanquing herring belong to the same general population. The range in length, the average size of the sample, and the average actual and computed lengths of the age groups are virtually identical in the two collections. The modal and the average length of the Au Gres and the Gravelly Point herring are somewhat less than those of the Tobico and the Nayanquing fish. Examination of the actual lengths of Table 53, however, shows that this decrease in size is due entirely to the small average size of the 3-year fish. Those of Gravelly Point are noticeably small. As stated on page 385 the small size of these fish is due to the 3-year individuals taken November 30 (Table 51). The 3-year herring taken at Gravelly Point on December 4 reached about the same average length as those taken at Tobico, Nayanquing, and Au Gres (Tables 51 and 53). Mr. Brackenbury, a fisherman who has fished at Gravelly Point for the last 32 years, states that large numbers of small herring come on late in the fall after the main run of herring is over. This late run, he states, is composed principally of males. Our November 30 sample may include part of such a late run, although the 3-year fish of this sample are mostly females (75.6 per cent). The differences in length between the 3-year herring from Gravelly Point and those

from the other localities considered are no greater than these differences between the 3-year fish taken at Gravelly Point on different dates.

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

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

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

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

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

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

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

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

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

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

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

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

The Oscoda sample evidently represents an earlier stage in the spawning run than does the sample from Bay City, although both collections were made at approximately the same time. The schools of herring at Oscoda apparently had not yet been as completely segregated into spawning and nonspawning fish by November 1 as those found at Tobico. On this basis it is to be expected that the 2 and 3 year fish would be more abundant in the Oscoda collection than in the Tobico sample. Most of the Oscoda nonspawning fish whose sex could be determined were females (70.8 per cent). This probably explains, at least in part, why the females were so preponderant in the Oscoda age groups. Computations show that the non-

spawners of an age group average less in length than the spawners of that age group. I found for the Oscoda herring that in the third age group 54 immature individuals averaged 222 millimeters in length, while 83 mature specimens averaged 228 millimeters, and that in the fourth age group 18 nonspawning fish averaged 220 millimeters in length, while 131 spawners averaged 233 millimeters. A priori, the Oscoda herring should then have a greater range in length but smaller average lengths than the Tobico fish. Tables 55 and 56 show this to be true. In the Oscoda fish the range in length is greater, but the modal and average lengths of the sample as well as the average actual and computed lengths of the age groups are less than in the Tobico fish. The increments of Table 56 show that these smaller total lengths of the Oscoda herring are due to the growth rate of either the first or second year of life. The 5-year specimens of the two samples did not grow at very different rates (the 6-year fish are too few in number to be considered). The nonspawners were too few in number to affect the growth rates of these age groups. The 4 and 3 year fish of Oscoda grew less in the first year of life but as rapidly as or faster in the later years of life than the corresponding age groups from Tobico. The 2-year herring, which in both samples were principally immature fish, grew at the same rate in the first year; in the second year the Oscoda fish grew the more slowly.

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

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

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

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

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

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

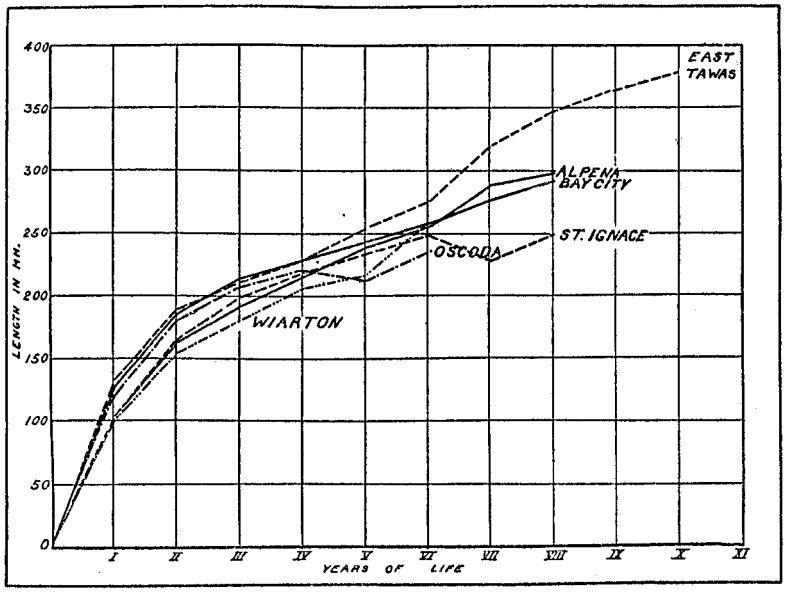

FIG. 43.—Showing the total length attained at the end of each year of life by lake herring taken at various ports on Lake Huron. The curves are plotted from the computed lengths of Table 59

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

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

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

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

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

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

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

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

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

This incomplete comparative study shows at least two things: (1) That there may be distinct races of herring in Lake Huron or, at any rate, that there are distinct differences between the growth rates of the herring of certain localities in Lake

Huron, and (2) that Saginaw Bay produces, so far as known, the most rapidly growing herring in Lake Huron.

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

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

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

RÉSUMÉ OF THE GROWTH HISTORY OF SAGINAW BAY HERRING

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

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

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

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

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

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

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

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

[6] For each statement refer to Table 39.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

TEMPERATURE AND SUNSHINE AS FACTORS

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

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

[8] Italics are mine.

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

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

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

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

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

We know nothing specifically about the relation of temperature to growth rate in the herring or about optimum temperatures for the growth of the herring; but if we assume that, other factors remaining constant, the year with the warmest growth season produces the largest and fastest growing fish, we ought, then, to find that the herring in Saginaw Bay grew most rapidly in 1921 and least rapidly in 1917, and that the growth rates of the other years fluctuated in general as the average temperatures

or heat budgets (Table 63) of these years; that is, that the growth rates of a relatively cool year were lower than those of a relatively warm year, and vice versa. At first glance there appears to be some correlation between temperature and the growth rate of the Saginaw Bay herring. We see from Tables 62 and 63 that the years 1919, 1921, and 1922 were the warmer years of the series, and from Table 39 that during these years and 1920 growth was more rapid than during the years 1915 to 1918. In the years 1915 to 1918 chemical substances undoubtedly were present in Saginaw Bay water that were not present before or after that period. Their effect on growth rate is discussed in another place. Assuming that they had an effect, the relation of temperature and growth rate might be obscured by it if years when the chemicals were present were compared with other years. It is best, therefore, to compare the years 1915 to 1918 one with another and the years subsequent to 1918 one with another to see whether in either period any relation is revealed between fluctuations in temperature and those in growth rate.

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

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

FISHING INTENSITY AS A FACTOR

One of the best and most convincing demonstrations of the effect of intensive fishing on the rate of growth of fishes is that afforded by the work of the Danish biological station at Copenhagen, carried on under the direction of Doctor Petersen (1922). In his survey of the plaice fisheries, covering the years 1893 to 1922, Doctor

Petersen reports some interesting facts on the relation between these fisheries and the stock of plaice. I can do no better than quote him verbatim. On page 9, he writes:

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

Again, page 18:

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

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

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

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

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

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

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

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

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

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

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

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

TEMPORARY CHEMICAL POLLUTION OF SAGINAW BAY AS A FACTOR

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

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

Paradichlorobenzol ($C_6 H_4 Cl_2$), a white crystal, is derived from chlorobenzene ($C_6 H_5 Cl$), a heavy, clear liquid, and, unlike the latter, is very soluble in water. "The

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

The computed lengths attained by the herring at various ages at the end of the growth year of 1920 are shown in Table 37. Those of different age groups belonging to the same year class were combined into one average. These combined averages

(see Table 43) and the theoretical average weights of the fish of each age group are given below:

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

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

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

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

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

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

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

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

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

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

GENERAL SUMMARY

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

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

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

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

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

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

7. An attempt has been made to review all the criticisms that have been directed against the age hypothesis and the nature and extent of all the evidences, direct and indirect, that support or contradict the hypothesis. The review indicates that the large majority of the experiments on the scales of fishes are fragmentary but favor, as far as they go, the theory that the annuli on the scales of a fish are a reliable guide to its age. This assumption has not been tested experimentally for the lake herring. I have tested it, however, by experimentation for the whitefish (*Coregonus clupeaformis*), a coregonid closely related to the lake herring. The whitefish employed were reared in the New York Aquarium and were known to be in their eighth or ninth year of life. (Van Oosten, 1923.)

8. A review of the most important papers devoted to a study of the body-scale growth relationship shows that the question of the validity of growth calculations based on the scales of fishes is still a disputed one. The direct experimental evidences are very fragmentary, but show, as far as they go, that calculated and empirical measurements of growth agree almost exactly. An attempt has been made to ascertain the exact growth relationship between the scales and the body of the lake herring, to determine the accuracy of the calculated measurements of growth, and to analyze the factors involved in the apparent discrepancies in the calculated measurements of growth.

9. In lake herring scales of the same individual may grow at different relative rates.

10. In lake herring the various areas of a single scale may increase in length at different relative rates.

11. Lake herring scales taken from the same area on the body grow more nearly at the same rate than those taken from various parts of the body.

12. The body-scale length ratios (K/V) of lake herring of age groups III and older decrease slowly but consistently with each older age group, irrespective of whether selected corresponding scales (X scales) or unselected scales (non-X scales or those actually used for the life-history work) are employed. That is, the percentage of increase in length with age is greater in the scale than in the body of the herring.

13. The decrease in the body-scale length ratios with age is not due to the age variations in head length, for the length of the head in proportion to that of the body remains virtually constant with age in herring 3 years of age and older.

14. The body-scale length ratios (K/V) of juvenile coregonids decrease very rapidly with age and growth in the first year of life.

15. The scales of lake herring increase in length comparatively faster than the body until a body length of approximately 260 millimeters (age group VI) is reached, when the scales increase proportionately more slowly. In early life the scales increase in length much faster relatively, than the body; in later life (third year and thereafter throughout the sixth year) only a little faster.

16. In both lake herring (*Leucichthys artedi*) and whitefish (*Coregonus clupeaformis*) scale formation begins when the fish has attained a length of approximately 35 to 40 millimeters.

17. The diameter of a herring scale increases in length more nearly proportional to the increase in the length of the body than does the anterior radius.

18. The diameter dimension of the scales of an individual herring varies less than the anterior radius dimension.

19. In lake herring the computed lengths based on the diameter dimension of scales are always higher for corresponding years of life than those based on the anterior radius. The difference between the two increases consistently with each earlier year of life for which calculations are made, so that the maximum average difference is found in year I.

20. In lake herring the computed lengths based on the diameter measurements of scales are in general lower than the corresponding lengths obtained from direct measurements of fish of the same year class. The differences between the actual and computed lengths are in general greatest for the early years of life.

21. The length value computed for a particular year of life generally decreases as the age of the herring whose scales are employed increases. (Lee's "phenomenon of apparent change in growth rate".)

22. The decrease with age in the computed length values of corresponding years of life (Lee's "phenomenon") occurs when the calculated length values of herring of different age groups and of different year classes are compared.

23. The decrease with age in the computed length values of corresponding years of life (Lee's "phenomenon") also occurs when the calculated length values of herring of different age groups but of the same year class are compared.

24. A phenomenon similar to that of Lee occurs when the "annular" scale-diameter measurements of herring of different age groups but of the same year class are

compared. The "annular" scale-diameter measurement of a particular year of life decreases as the age of the herring whose scales are employed increases.

25. The scale (and body) increments of the first and second growth years of a year class of the lake herring generally decrease as the age of the fish whose scales are studied increases; but the scale (and body) increment of the third growth year increases or remains constant with age, while the scale (and body) increments of the fourth and fifth growth years increase with age.

26. Every factor that could possibly explain conclusions 20 to 25, inclusive, in the lake herring was critically considered. It was concluded that these facts may be interpreted best as the results of the following three natural events in the life history of the herring: (*a*) Herring that reach sexual maturity late in life are the more slowly growing individuals of their year class; (*b*) sexual maturation usually is accompanied by a retardation in the growth of body and scale; (*c*) a compensation in growth occurs in lake herring; that is, herring that grow slowly during the earliest years of life grow rapidly during the later years of life, and vice versa. According to this view, then, Lee's "phenomenon" is largely a natural event and should occur to some extent in calculations of growth based on the scales of adult herring. The disproportionate growth rate of body and scale may be an additional factor for the "phenomenon" in the computed lengths. It is believed that late scale formation, which is usually considered to be the cause of Lee's "phenomenon," is not such a factor, for (*a*) computations of growth are based on the assumption that the lengths of the body and scales maintain a fixed relationship after the first year of life; that the body-scale ratio of a fish at death is the same as it was at the time of the completion of each annulus on the scale, irrespective of the actual growth relationship during the first year or during the intervals between the periods of annuli formation, for lengths are calculated back to the periods of annuli formation (p. 320); (*b*) the rapid proportional increase in the length of the scale during the first year of life counteracts late scale formation in its effect on the computations of length (p. 340); (*c*) late scale formation can not be a factor in the "phenomenon" found in direct measurements of scale diameters (p. 341); (*d*) corrections for late scale formation do not eliminate the "phenomenon" from computations of growth; corrected computations of length tend to be too high for the early years of life (p. 339).

27. The life history of the lake herring described in this paper is based on four large collections made at Bay City, Mich., on Saginaw Bay in the fall of 1921, 1922, 1923, and 1924.

28. No 1-year herring and relatively few 2, 6, 7, or 8 year fish were found in the commercial herring catches of Saginaw Bay. The 3, 4, and 5 year fish composed 87.2 to 97.4 per cent of the commercial catches. The fourth age group was always dominant, its individuals comprising 42.8 to 58.3 per cent of the total catch. The oldest lake herring I have ever seen was in its eleventh year.

29. The percentage of 3-year herring in the commercial catches of Saginaw Bay increased each year during the period 1921 to 1923, then remained stationary in 1924. This increase in the number of 3-year fish occurred at the expense of the 5-year fish mainly, which each year became progressively less abundant.

30. A year class predominated for one year only in the commercial catches of the Saginaw Bay lake herring. Each year class dropped off rapidly in the years following the year of its dominance—the fourth.

31. The biological data suggest that commercial fishing for herring is very intense. The symptoms of heavy fishing are: The paucity of old individuals (28), the shifting in the age composition of the samples (29), and the one-year dominance of a year class (30).

32. In lake herring males and females of an age group grow at the same rate in all years of life.

33. The sexually mature female herring weigh, on the average, slightly more than the sexually mature male herring of the same age group.

34. In the Oscoda sample of 1922 the nonspawners of an age group average less in length than the spawners of that age group.

35. The lake herring grows most rapidly in length during the first two years of life; nearly 50 per cent of the length reached in the sixth year is completed at the end of the first growth year. The data indicate that the growth rate of the first year of life determined largely the size, and indirectly the weight, of most of the individuals of the commercial catches studied (p. 369). From the point of view of the fisheries, the growth history of the 1-year fish is of extreme significance. The first prominent break in the curve of total growth in length occurs in the third year—the year during which sexual maturity is first attained by many individuals. The lake herring reaches at the end of the second year nearly 50 per cent of the weight attained in the sixth.

36. From the point of view of the commercial fisheries, it is not profitable to allow the herring at their present rate of growth to become much older than 3 or 4 years, for the increase in weight in the fourth and fifth years together is less than that of the third year alone. If the nets are so regulated that they take no fish under 4 years of age (235 millimeters, or 9.3 inches long, measured snout to base of caudal, and 5.61 ounces in weight), then many herring can spawn twice and a greater number can spawn once, thus insuring the perpetuation of the species, provided the number of spawners is not reduced below the number required for the maintenance of the species.

37. In lake herring the big yearlings of a year class are, on the average, the big fish in all succeeding years of life, but the differences between the small and large yearlings diminish each year of age—that is, the small yearlings are rapid growers, the large yearlings slow growers. (Gilbert's law of growth compensation.)

38. The length-weight relationship of lake herring taken just before spawning in the fall can be expressed satisfactorily by the formula $W=k.\ L^3$, in which k has a value of 0.01126.

39. Of the 2,950 lake herring taken in Saginaw Bay 49.5 per cent were males and 50.5 per cent females.

40. The relative abundance of male and female herring varies during the course of the spawning run. Males are more numerous than females early in the season but less numerous late in the season.

41. The relative abundance of male and female herring varies with the age groups. In general the males become relatively more numerous than the females with each higher age group. It is believed that this indicates that a bigger percentage of the

females than of the males of a year class reach sexual maturation for the first time in the third year—that is, the females mature earlier in life than the males.

42. About 3 per cent of all the herring taken in the samples from Saginaw Bay were sexually immature or nonspawning fish.

43. The majority of the lake herring attain sexual maturity in the third and fourth years of life. Fewer reach it in the fifth year. Very few individuals reach sexual maturity in their second year. All herring of the sixth and older age groups are sexually mature.

44. The lake herring taken in 1924 at the same locality in Saginaw Bay but on different dates show no consistent differences in size, rate of growth, and age composition. These facts indicate that the character of the herring stock of one locality in the bay does not change during the spawning run.

45. The herring population of Saginaw Bay can not, on the basis of growth rate, be separated into distinct races.

46. Distinct differences exist between the growth rates of the herring of some localities in Lake Huron. This suggests that there may be distinct races of herring in Lake Huron and that the migrations of the herring are more or less local.

47. Saginaw Bay produces, so far as known, the most rapidly growing herring in Lake Huron. Of the various localities in Lake Huron considered, the herring of Oscoda rank second in rate of growth, those of Alpena, St. Ignace, and Killarney third, and those of Wiarton fourth. The different growth rates of the herring of these localities possibly may be correlated with the different conditions of life.

48. The average measured length of the herring schools of Saginaw Bay tended to increase each year during the period 1921 to 1924.

49. The average measured length and weight of herring of corresponding age groups increased progressively each year during the period 1921 to 1924.

50. A study of the computed lengths and increments of the Saginaw Bay herring shows: (*a*) that in each of the years 1915 to 1918, inclusive, the rate of growth of herring in the first year of life was the same; (*b*) that in the year 1919 the growth rate was increased in herring 1, 2, and 3 years of age; (*c*) that neither in 1919 nor subsequently did the growth rate of fish older than 3 years increase; (*d*) that the acceleration of growth rate initiated in 1919 in fish 3 years of age and younger continued in the years 1920, 1921, and 1922; (*e*) that in the period 1919 to 1922, inclusive, fish in their first year of life, in general, grew more rapidly each successive year (during this period there was progressive increase of growth rate in 1-year fish, although in 1922 the increase was very slight—1 millimeter); (*f*) that during the period 1919 to 1923, inclusive, the growth rate of the second and third year fish did not increase in successive years but remained virtually constant at the increased rate attained in 1919; (g) that the growth rate for the fourth and later years likewise tended to remain constant in the years 1919 to 1924, inclusive; (*h*) that all fish 3 years of age and younger in general reached progressively greater lengths each successive year after 1918, while the 4-year fish did likewise after 1919; and (*i*) that fish older than 4 years, hatched after 1917 attained greater average lengths at the same age than those hatched before or in 1917, the fifth age group of year class 1918 excepted.

51. The low growth rates that prevailed among the herring of Saginaw Bay during the period 1915 (1916) to 1918 were abnormal; in general, higher rates prevailed before 1915 (1916) and were resumed in 1919.

52. The low growth rates of the Saginaw Bay herring during 1915 (1916) to 1918 were due to some unfavorable local conditions of growth in Saginaw Bay.

53. The growth alteration of the Saginaw Bay herring during the period 1915 to 1922 is explained best as due to the temporary chemical pollution in 1915 to 1917 by the Dow Chemical Co., of Midland, Mich., by wastes containing dichlorobenzol. Temperature, light, and fishing intensity as factors of growth do not explain all the data satisfactorily and therefore do not appear to have been the controlling factors in the growth of these fish.

54. Rough computations based on growth data and herring statistics show that the indirect economic losses, due to retardation in growth, in the herring fisheries for the years 1917 to 1923, inclusive, totaled 4,450,224 pounds, with a value to the fishermen of $135,753. These indirect losses are believed to have been occasioned principally by the chemical pollution of 1915 to 1917.

CONCLUSIONS

This study shows that the structural characters of the scales of the coregonoid fishes of Lake Huron are so clearly recognizable as to permit their use by the scale method. It shows, further, that the fundamental assumptions underlying the scale method are warranted in so far as they apply to the lake herring (*Leucichthys artedi* Le Sueur). The scale method is therefore valid when applied in a study of the life history of the lake herring. The life history of the lake herring that occur in Lake Huron is described in detail in this paper for the first time.

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INVESTIGATION OF THE PHYSICAL CONDITIONS CONTROLLING SPAWNING OF OYSTERS AND THE OCCURRENCE, DISTRIBUTION, AND SETTING OF OYSTER LARVÆ IN MILFORD HARBOR, CONNECTICUT

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INTRODUCTION

The primary purpose of this investigation is to show the close relationship that exists between physical conditions and the success or failure of oyster production in inshore waters. It is hoped that the analysis of conditions in Connecticut waters and the determination of the predominating factors that control oyster propagation there may serve as the basis for the development of scientific oyster culture in our extensive coastal waters. To accomplish this, it is essential that we have a thorough knowledge of the oyster in every stage of its development and a greater understanding of the influence of each physical and biological factor on the egg, embryo, larvæ, spat, and adult. In the cultivation or control of an aquatic animal such as the oyster, the response of the organism to changes that occur in its environment is not only of scientific interest but may be of great practical importance. The plan of the investigations carried out at Milford, Conn., during the summers of 1925 and 1926 was to study the effect of the physical conditions on the oyster and oyster larvæ in this typical location, the results of which would serve as the basis for analyzing and understanding the conditions found in other oyster-growing regions.

The most important problem that presented itself was the analysis of the causes of the great variations that occur in the annual production of seed oysters on an entire natural bed as well as on the cultivated oyster beds. A good example of this is the Bridgeport natural bed, which, according to Collins (1889), produced 115,000 bushels of oysters in 1887, 31,000 in 1888, and 3,500 in 1889, most of which

were seed oysters. On the cultivated beds of Connecticut similar fluctuations in seed production during the last three years are representative of the experiences of the industry since the initiation of oyster culture. For instance, the production of seed oysters here ranged from over 1,000,000 bushels in 1925 to virtually none in 1926 and 1927. Through a detailed study of the conditions in Milford Harbor, it was hoped that an understanding of this phenomenon might be obtained. The objects of this investigation were to determine—

1. The principal factors that influence and control the spawning of oysters.
2. The occurrence and distribution of the oyster larvæ.
3. The zones in which setting or attachment of the larvæ takes place.
4. The conditions responsible for the occurrence of great annual fluctuations in the intensity of setting or production of seed oysters.

These studies were conducted under the direction of Dr. Paul S. Galtsoff, in charge of oyster investigations, to whom the author is deeply indebted for advice in the course of the work and for criticism of the manuscript.

The author wishes to acknowledge his appreciation of the valuable and cordial cooperation rendered by the North Atlantic Oyster Farms (Inc.) in carrying on these investigations, and especially the help, suggestions, and information given by W. H. Raye, Capt. Charles E. Wheeler, and A. E. Loring, of that company, relative to various studies of the oyster situation and for generously supplying oysters, laboratory facilities, men, and boats for this work. Valuable assistance was received from H. A. Marmer, of the United States Coast and Geodetic Survey, in the studies of the tides and currents, and from the United States Weather Bureau and Geological Survey in supplying climatological and river-discharge data.

METHODS AND EQUIPMENT

A small laboratory was established at the plant of the Connecticut Oyster Farms Co., at Milford, Conn., where suitable arrangements could be made for setting up tide and temperature recording apparatus and for boating operations. In Milford Harbor and the adjacent inshore waters of Long Island Sound six stations were established, as shown in Figure 1. These were visited regularly with a small cruiser equipped for the collection of water and plankton samples and for making observations of general physical conditions.

Water temperatures at the surface and bottom were taken at each cruising station by means of a Negretti and Zambra deep-sea reversing thermometer, and, in addition, a long-distance thermograph was set up at Station 2, which recorded continuously the water temperatures on the bottom in the harbor.

In collecting water samples for the determination of salinity and pH, a Greene-Bigelow water bottle was lowered over the side by means of a meter wheel and Lucas sounding machine. The samples were titrated in the usual way, using silver nitrate against the international standard sea water and calculating the salinities by means of Knudson's (1901) hydrographical tables. For the determination of the hydrogen-ion concentration of the water, the colorimetric method was employed, using cresol red and brom-thymol blue as indicators. No correction for salt error has been made for the figures that are given. All the observations fall within the range of the indicator cresol red.

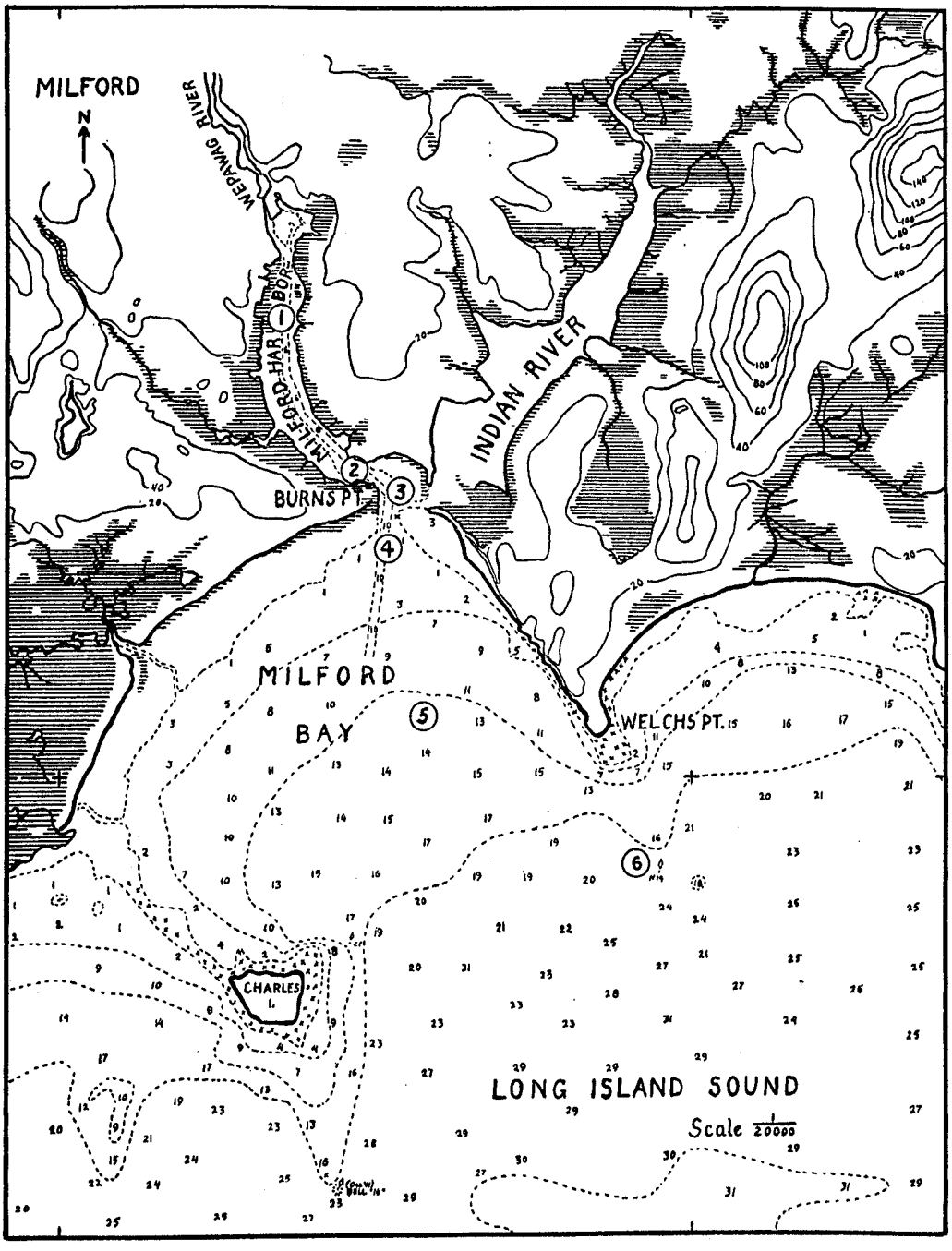

FIGURE 1.—Location of stations and hydrographical features of Milford Harbor and vicinity

In studying the tides and currents several devices were used. At Station 2 an automatic tide gauge was put in operation, whereby a continuous record of the rise and fall of tide in Milford Harbor was obtained. The velocity and direction of the tidal currents at various depths and stages of the tide were determined by means of Eckman and Price current meters. In order to determine the drift or general movement of the water along the Connecticut shore of Long Island Sound, 500 drift bottles with drags were released from several localities, and of these, over 300 have been recovered.

The most important procedure was the collecting and examining of plankton collections to determine the presence of oyster larvæ. The method employed was essentially the same as that used by Churchill and Gutsell (1920; unpublished manuscript, United States Bureau of Fisheries) for determining the abundance of oyster larvæ. The results obtained by this method are quantitative and of much greater value than those obtained by drawing a tow net through the water.

At each station, 50-gallon samples were taken at the surface and bottom and occasionally at various depths. By means of a rotary bronze pump with 50 feet of rubber hose weighted at the intake end a definite quantity of water was pumped on deck and strained through a net of No. 20 bolting silk. The plankton collected was washed down into a quart jar, labeled, and preserved in 10 per cent formalin. In the laboratory, the contents of each jar was washed through a series of sieves covered with Monel-metal wire of Nos. 80, 100, 150, 200, and 270 mesh. This procedure served to classify the oyster larvæ according to their size and greatly simplified microscopic examination of the samples by dividing them into several portions. The plankton collected in each sieve was washed into watch glasses, and the number of oyster larvæ was determined by direct count under the microscope.

The setting of the oyster larvæ was studied in 1925, 1926, and 1927 by arranging several types of stationary and floating spat collectors in various positions, according to the depth of water, tides, and currents. For spat collectors, brush, glazed tiles, tar paper, clam, scallop shells, and oyster shells were used, the latter being set out in lath crates and wire baskets.

TOPOGRAPHY

Milford Harbor is situated on the Connecticut shore of Long Island Sound and lies about halfway between two great oyster-producing centers—Bridgeport and New Haven. The general topographic and hydrographic features of the harbor and surrounding territory are shown in Figure 1. In this discussion, the term "Milford Harbor" is applied only to the area above the stone breakwater at Burns Point, which, on the hydrographic charts, is labeled "Wepawaug River." This small body of water covers approximately 80 acres, about half of which is exposed at low tide. It is a small but typical oyster-producing harbor, and in former times the entire area was a natural bed of oysters. In this nearly inclosed basin, the brackish water of Long Island Sound mixes with the fresh water from two small streams—the Wepawaug and Indian Rivers—producing ideal conditions for oyster growth and propagation.

As a result of overfishing, the harbor was found to be virtually devoid of oysters, so that it was necessary to restock it before carrying on the experiments. The

Connecticut Oyster Farms Co. generously supplied a sufficient quantity of large oysters to establish two spawning beds, one of which was located on the flats and the other in the channel. Since at present these waters are unpolluted to any serious degree, it was possible, by the rehabilitation of this small harbor, to study the oyster in an environment very similar to that in which it thrived in years past.

Milford Harbor is but one of the many inshore areas that border and empty into Long Island Sound, and its topography would not be complete without a description of this adjoining large body of water.

Long Island Sound is a partially inclosed basin having a length of about 80 nautical miles and a depth averaging 65 feet. Its general shape is that of a double convex lens with the broadest portion at a point just southeast of New Haven, where its width is about 16 miles. From this point to the eastward the width of the Sound decreases gradually until it is about 8 miles wide at its mouth, where it receives the water from Block Island Sound and the Atlantic Ocean. To the westward of New Haven the shore lines also converge until they are less than a mile apart at the head of the Sound or upper entrance to New York Harbor.

The longitudinal axis of the Sound lies in a northeast and southwest direction and is about at right angles to the rivers emptying into it from the north. The two principal drainage basins discharging into the Sound are those of the Connecticut and Housatonic Rivers, the valley of the former extending about 250 miles to the north and of the latter, 90 miles.

The water in the Sound is a mixture of the salt water brought in by the tides from the ocean with the fresh water discharged by the rivers, its average salinity for the year, as determined by Galtsoff (unpublished report), ranging from about 24 parts per thousand at Hell Gate to 29 at its mouth. As a result of the tides, the level of the Sound changes constantly, and large inshore areas, covering thousands of acres, are regularly flooded and exposed at times of high and low water. The location, extent, and contour of these flood grounds determines, to a noticeable degree, the differences that are found in the physical conditions in each of the various inshore areas, such as Milford Harbor, and in the various parts of the Sound.

PHYSICAL CONDITIONS

GENERAL

A study of the early location of the natural oyster beds and shell deposits along the coast of Long Island Sound clearly indicates that certain regions were more favorable than others for the growth and propagation of the oyster. The favorable regions, for the most part, were found to lie in the coves, bays, and estuaries and were all similar in structure, consisting generally of a partially inclosed basin, which received fresh water from the land and salt or brackish water from the place into which it emptied. In these bays and harbors the natural beds extended from nearly the upper limit reached by the brackish water to some distance outside of the entrances. This is well illustrated in Figure 2, which is taken from an old map of the oyster grounds of Connecticut published in 1889. The location and extent of the natural beds clearly defines the regions in which the physical conditions were most favorable for the growth and propagation of the oyster. If we examine these areas carefully,

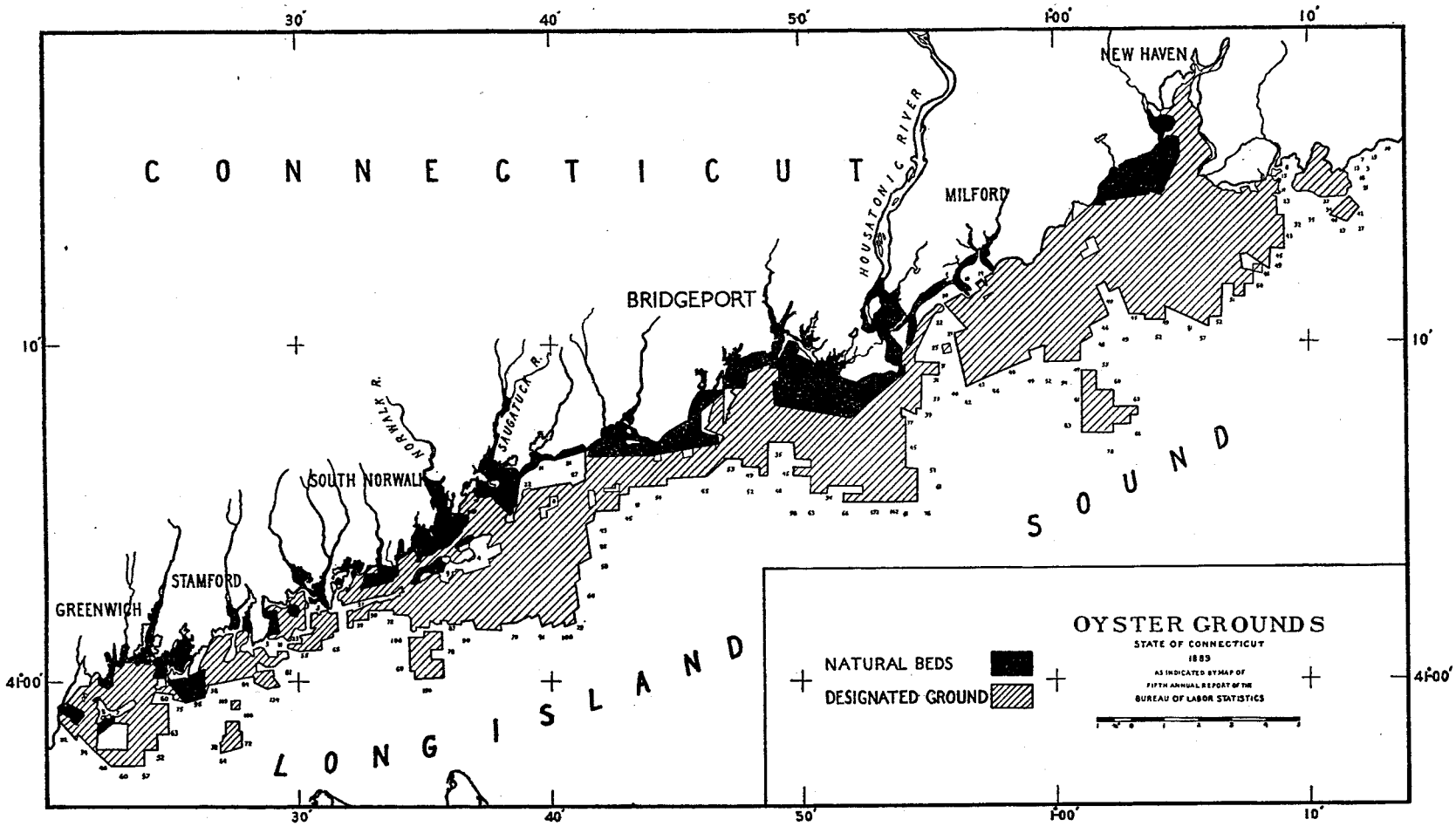
CONNECTICUT
LONG ISLAND SOUND
NEW HAVEN
MILFORD
BRIDGEPORT
HOUSATONIC RIVER
SAUGATUCK R.
NORWALK R.
SOUTH NORWALK
STAMFORD
GREENWICH
30'
40'
50'
1°00'
10'
41°00'
OYSTER GROUNDS
STATE OF CONNECTICUT
1889
AS INDICATED BY MAP OF
FIFTH ANNUAL REPORT OF THE
BUREAU OF LABOR STATISTICS
NATURAL BEDS
DESIGNATED GROUND

FIGURE 2

we find that at several points between the upper and lower boundaries of the natural beds in each section the productivity and abundance of the oysters show wide variations. As a general rule, oyster growth and seed production are best in a zone about halfway between the upper and lower limits of a natural bed and least at the extremes, which can be correlated with variations in the physical conditions found in different parts of the bed. However, if we take the natural beds as a whole, or the cultivated beds, we find great fluctuations in the quantity of seed oysters that they produce from year to year. Their production often ranges from over 1,000,000 bushels, as was the case in 1925, to virtually none, as in 1926 and 1927. The study and comparison of the physical conditions in 1925 and 1926 was made in order to determine the factors responsible for these annual fluctuations in seed-oyster production.

The potential value of any body of water for the propagation, growth, or fattening of oysters is determined largely by the physical and chemical conditions that exist there. In some localities these conditions are more or less constant, while in others they undergo considerable variation. Each region, however, has certain physical characteristics of its own, and these are representative of the combined influence of the climatological, hydrographical, and physiographical conditions found there. In Milford Harbor and vicinity there is a great range of variation in a comparatively short distance; and since it is a favorable location for the production of three important shellfish—the oyster, quahaug, and soft clam—the various factors will be discussed in detail in order that they may serve as the basis for comparison with other regions.

TEMPERATURE

In the environment of the oyster, water temperature is the most important factor, as it controls, either directly or indirectly, the growth and reproduction of the organism. It directly affects the physiological processes of the oyster, such as feeding, respiration, development of the gonads, spawning, etc., while indirectly it influences, to a great extent, the growth and abundance of the microscopic forms that constitute the food of the oyster and oyster larvæ.

The water temperature in Milford Harbor is the resultant of the interaction of the various factors that can be placed in two major groups—the climatological and the hydrographical. The chief climatological factors affecting water temperature are (1) solar radiation, (2) air temperature, (3) precipitation, (4) wind, and (5) percentage of sunshine. The chief hydrographical factors, in order of their importance, are (1) tide, (2) river discharge, (3) tidal currents and circulation, and (4) depth of water.

The relative importance of any one of these factors can be discussed only in a general way because its effect on water temperature depends largely on its relation to one or more of the remaining factors.

In Figure 3, the mean daily temperatures of bottom water are shown for July and August of 1925 and 1926 and cover the period when spawning and setting of oysters occur in Connecticut waters. The figures are taken from the records of the thermograph placed in the harbor at Station 2, the average for each day being determined by means of a planimeter. The fluctuations in water temperature that occurred during these two summers are typical for estuaries and shallow inshore

bodies of water, where there is considerable variation according to the day and even the hour.

In beginning our analysis of the data, we find that the mean temperature for the 2-month period was 20.3° C. for 1925 and 19.7° C. for 1926, showing a slight annual difference of less than 1°. The monthly and daily averages, however, show greater differences between the two years and are of greater importance, as will be shown later because of the effect of temperature on (1) the ripening of the gonads and (2) the spawning reaction of the oyster. In 1925 the mean monthly water temperature during July was 19.7° C., while in 1926 it was 17.8° C., or 1.9° lower. During August, 1925, the monthly mean was 20.8° C. and in 1926, 21.6° C. As can be seen from Figure 3, the water temperature on certain days was above 20° C., and we are interested in discovering the difference between the two years in relation to this point, because it has been found by previous observation that spawning of the oysters occurred after the water had reached this temperature. In July, 1925, there were

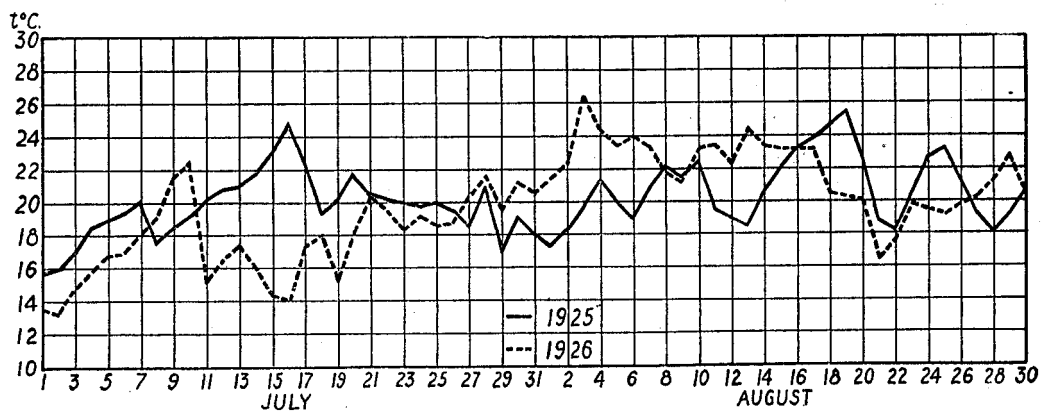

FIGURE 3.—Mean daily bottom temperature, ° C., at Station 2, Milford Harbor. Computed from thermograph records

15 days when the temperature was above 20° C. and 16 when it was below, while in 1926 there were only 7 days when it was above and 24 days when it was below. In August, 1925, there were 19 days when the water temperature was above 20° C. and 12 when it was below, while in 1926 it was above this point for 24 days and below only 7 days. These data are presented in the following table, together with the highest and lowest water temperatures for each month.

TABLE 1.—*Fluctuations in daily water temperature from 20° C.*

Month	Number of days		Highest daily temperature	Lowest daily temperature
	20° C. and above	Below 20° C.		
July, 1925	15	16	24.8	15.8
July, 1926	7	24	22.4	13.2
August, 1925	19	12	25.4	17.4
August, 1926	24	7	26.4	16.5

Although these data refer to the inshore areas, they reflect the trend of conditions in the Sound, where the water generally is from 2 to 3 degrees lower than the daily average in the harbor. This decrease in temperature, which is found as we leave Station 1 in the upper part of the harbor and go out to Station 6 in the Sound, is shown clearly by Figure 4. In this figure the distribution of temperature is shown for July 15, 1925, when the water in the harbor and Sound was unusually warm for this time of the year. The temperature records at Station 2 in the harbor are the most complete, however, and have been analyzed and are presented in Tables 2 and 3, which give the maximum, minimum, mean, and range of temperature for each day of the summers of 1925 and 1926.

TABLE 2.—*Water temperatures at Station No. 2, 1925, in °C.*

Date	July				August			
	Extremes		Daily		Extremes		Daily	
	Maximum	Minimum	Mean	Range	Maximum	Minimum	Mean	Range
1	17.5	15.0	15.8	2.5	19.0	15.0	17.4	4.0
2	19.5	15.0	16.0	4.5	19.5	17.0	18.2	2.5
3	21.0	16.0	17.0	5.0	23.0	18.0	19.8	5.0
4	21.5	17.0	18.5	4.5	24.5	19.0	21.4	5.5
5	22.0	17.5	19.0	4.5	20.5	18.5	20.0	2.0
6	23.0	15.5	19.4	7.5	20.0	18.5	19.0	1.5
7	22.5	17.5	20.2	5.0	22.5	20.0	20.8	2.5
8	20.0	17.0	17.6	3.0	25.0	21.0	22.2	4.0
9	21.5	17.5	18.5	4.0	22.0	21.0	21.5	1.0
10	20.0	18.5	19.2	1.5	25.0	20.5	22.4	4.5
11	22.5	19.5	20.2	3.0	22.0	18.0	19.5	4.0
12	22.5	18.0	20.8	4.5	20.5	18.0	19.0	2.5
13	23.0	18.0	21.0	5.0	20.5	18.0	18.5	2.5
14	25.0	18.0	21.8	7.0	23.0	19.0	20.6	4.0
15	25.0	20.0	23.0	5.0	23.0	21.0	22.0	2.0
16	27.0	20.5	24.8	6.5	25.5	22.0	23.2	3.5
17	26.5	20.0	22.5	6.5	27.0	23.0	23.8	4.0
18	24.0	17.0	19.4	7.0	28.5	22.0	24.6	6.5
19	24.0	16.5	20.2	7.5	29.0	23.0	25.4	6.0
20	26.0	19.0	21.8	7.0	27.0	20.0	22.8	7.0
21	21.5	20.0	20.5	1.5	19.5	15.5	18.8	4.0
22	22.0	19.5	20.2	3.5	20.0	16.0	18.2	4.0
23	23.5	19.0	20.0	4.5	21.0	19.0	20.2	2.0
24	22.5	19.0	19.8	3.5	23.0	21.0	22.6	2.0
25	22.5	18.5	20.0	4.0	24.0	21.5	23.2	2.5
26	21.0	18.5	19.6	2.5	24.5	18.0	21.4	6.5
27	20.5	18.0	18.5	2.5	20.0	16.0	19.2	4.0
28	23.0	19.0	21.0	4.0	20.5	15.5	18.0	5.0
29	21.5	16.0	17.0	5.5	23.0	17.0	19.2	6.0
30	20.0	17.5	19.2	2.5	23.0	19.0	20.6	4.0
31	20.0	16.5	18.0	3.5	24.0	19.0	21.8	5.0
Monthly mean	22.3	17.9	19.7	4.4	22.9	19.0	20.8	3.8

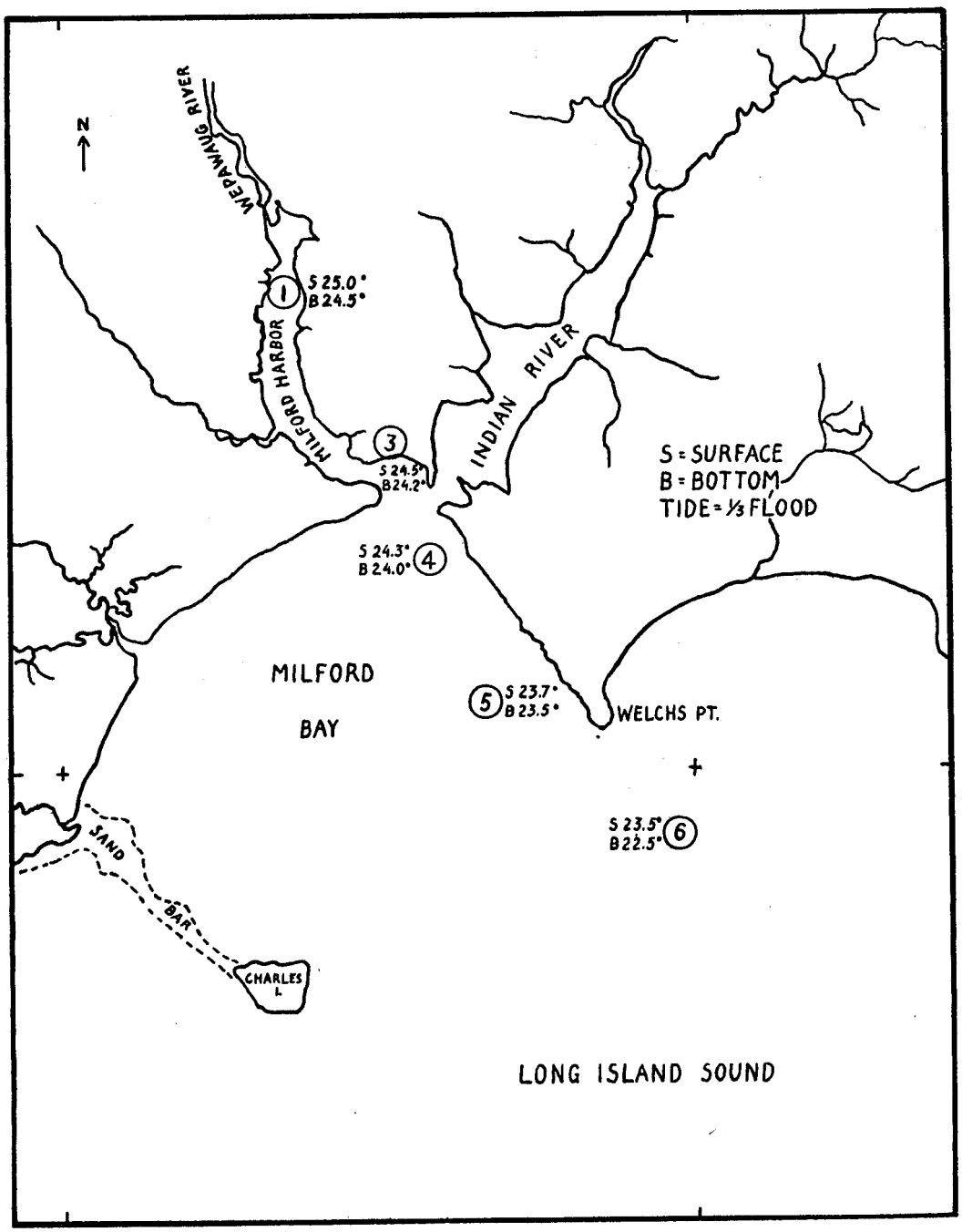

FIGURE 4.—Distribution of surface and bottom temperatures, July 15, 1925

TABLE 3.—*Water temperatures at Station No. 2, 1926, in ° C.*

Date	July				August			
	Extremes		Daily		Extremes		Daily	
	Maximum	Minimum	Mean	Range	Maximum	Minimum	Mean	Range
1	17.5	10.5	13.5	7.0	23.5	19.0	21.5	4.5
2	15.5	11.5	13.2	4.0	24.0	20.0	22.4	4.0
3	17.0	13.0	14.8	4.0	28.5	23.0	26.4	5.5
4	19.0	13.5	15.8	5.5	31.0	21.5	24.4	9.5
5	20.0	14.5	16.8	5.5	27.0	21.5	23.4	5.5
6	18.5	14.5	17.0	4.0	25.0	21.0	24.0	4.0
7	23.0	15.5	18.0	7.5	25.0	22.0	23.4	3.0
8	23.0	16.0	19.2	7.0	25.0	13.5	21.8	11.5
9	25.0	17.0	21.5	8.0	26.0	18.0	21.2	8.0
10	27.0	17.5	22.4	9.5	26.0	19.0	23.2	7.0
11	20.0	12.5	15.2	7.5	26.0	19.5	23.4	6.5
12	19.0	13.0	16.5	6.0	23.5	21.0	22.2	2.5
13	20.0	16.0	17.4	4.0	29.0	22.0	24.4	7.0
14	18.0	14.5	16.0	3.5	27.0	20.5	23.4	6.5
15	16.5	12.0	14.4	4.5	25.5	20.5	23.2	5.0
16	16.5	13.0	14.0	3.5	24.0	22.0	23.2	2.0
17	20.5	15.0	17.4	5.5	23.5	22.0	23.2	1.5
18	20.5	16.0	18.0	4.5	22.0	18.0	20.5	4.0
19	19.5	13.0	15.2	6.5	21.5	18.5	20.4	3.0
20	21.0	15.0	18.2	6.0	23.0	17.0	20.0	6.0
21	25.0	15.0	20.4	10.0	18.0	14.0	16.5	4.0
22	26.0	15.0	19.6	11.0	19.0	16.0	17.6	3.0
23	24.0	15.0	18.4	9.0	23.0	17.0	19.8	6.0
24	23.0	16.0	19.2	7.0	20.5	19.0	19.5	1.5
25	26.0	16.5	18.6	9.5	20.0	19.0	19.2	1.0
26	23.0	16.0	18.8	7.0	22.0	18.0	19.8	4.0
27	23.0	18.0	20.4	5.0	21.5	19.0	20.2	2.5
28	24.0	19.5	21.6	4.5	23.0	19.5	21.2	3.5
29	20.0	19.0	19.5	1.0	25.0	20.0	22.8	5.0
30	23.5	20.5	21.2	3.0	23.0	17.5	20.4	5.5
31	22.0	20.5	20.6	1.5	20.0	16.0	18.0	4.0
Monthly mean	21.7	15.3	17.8	5.9	23.9	19.2	21.6	4.7

The daily range of water temperature varies from 1 to 11.5 degrees and is indicative of the continuous fluctuations that occur in these inshore waters. It also shows very well how little value can be given to occasional water-temperature observations in such localities. The records given in these tables have been plotted in Figure 5 so as to show more clearly the extremes of water temperature for each day together with the daily mean. The maximum, in virtually every instance, corresponds to the water temperature at the time of low water, while the minimum invariably occurs at high water, when the greatest quantity of water has been brought in by the flood tide from the Sound. It is apparent from these graphs that at certain times the daily range of temperature was much greater than the average monthly range, as, for example, on July 6 and 19 and August 20, 1925, and on July 10 and 22 and August 4, 1926, when the daily range of temperature was from 7.5° to 11° C. These periods were found to correspond to the times when there were certain tidal conditions, which are discussed in detail in the paragraph on the effect of tide on temperature.

In order to understand and make clear the causes of the changes in temperature that have been discussed, it is necessary that each important climatological and hydrographical factor be taken up separately with regard to the effect it produces.

As a basis for discussion, the normal climatological data for this region are shown in Figure 6. The monthly means are taken from the records of the United States Weather Bureau station at New Haven, Conn., which is but 9 miles east of Milford.

The water temperature in Long Island Sound and especially its inshore waters are dependent upon the local weather conditions and those in adjacent regions and will follow them quite closely in their general trend.

SOLAR RADIATION

The sun is the primary source from which the water derives its heat. The quantity of heat that the water absorbs is proportional to the intensity of solar radiation, which varies during the months of the year, as shown in Figure 6. Its

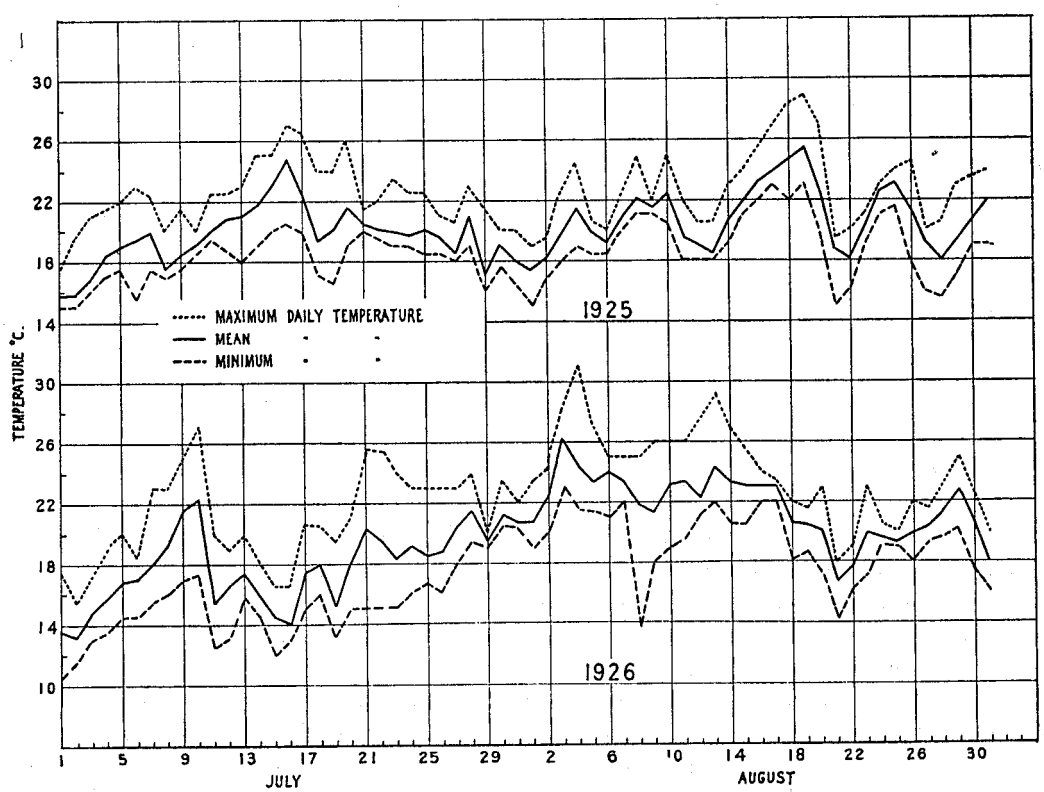

FIGURE 5.—Daily water temperatures, Milford Harbor, 1925 and 1926

intensity is greatest during the latter part of July and is responsible for the maximum air and water temperatures that occur at that time of the year. Although the water is warmed considerably by direct absorption, the greatest effect of sunlight on water temperature is the heating of the air and the land with which the water comes in contact.

Solar radiation has a pronounced effect upon the temperature of the water in Long Island Sound because of its configuration and tidal conditions. As a result of these conditions, the water is kept in constant motion and brought into contact with large land areas or tidal flats, which have a temperature much higher than that of the air because of the absorption of a greater proportion of the sun's heat. The effect of solar radiation on air, land, and water temperature will vary according to

the clearness of the day and the number of hours of sunshine that are possible at that time of the year. During July the total number of hours of possible sunshine for this latitude is 458.3, and there is a gradual decrease in the number of hours per

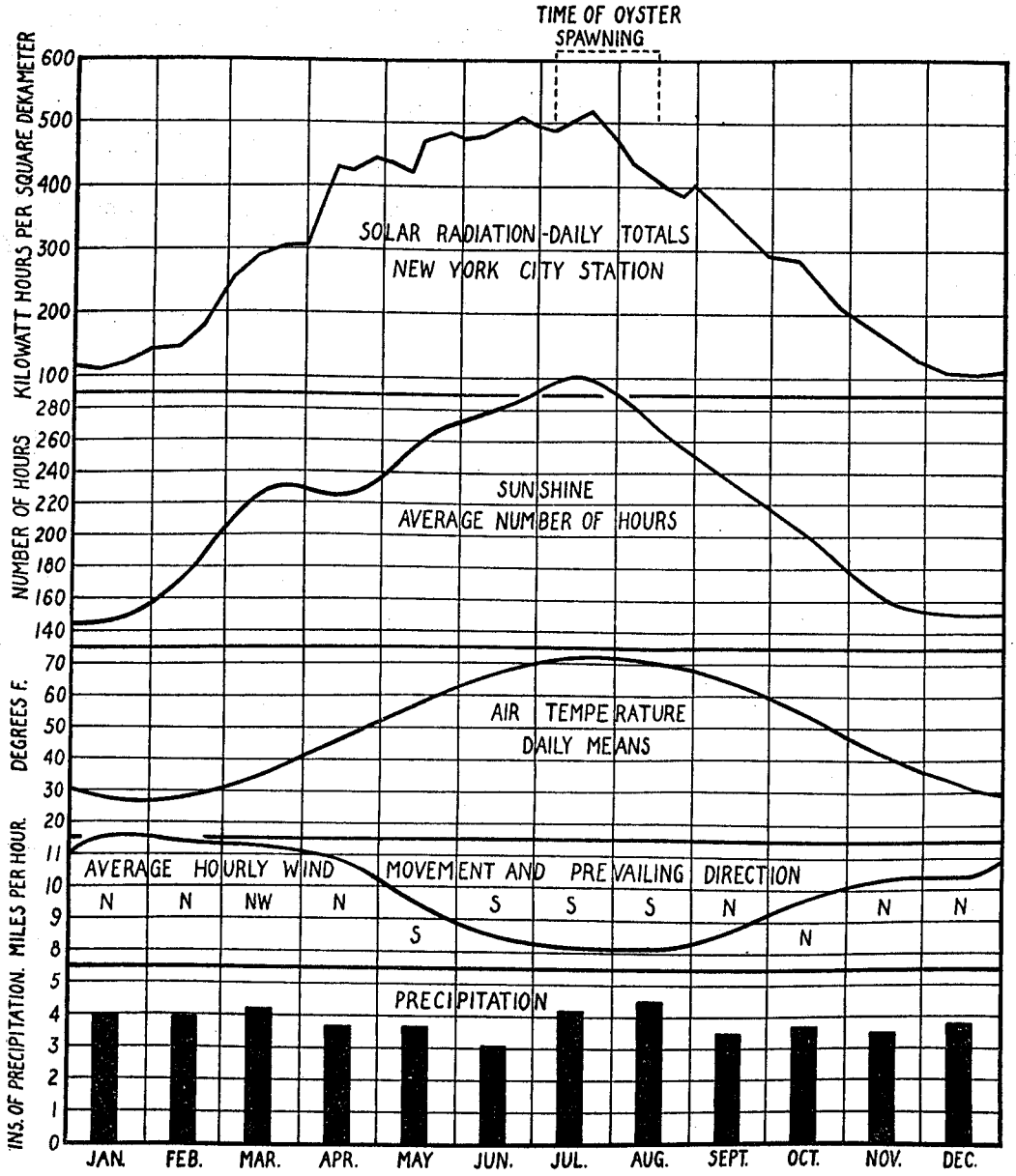

FIGURE 6.—Normal climatology for New Haven, Conn., taken from records of the United States Weather Bureau

day from 15.1 on July 1 to 14.4 on July 30. For the month of August the total number of hours is 426.9, and there is a gradual daily decrease from 14.3 on the 1st to 13.2 on the 30th. In July we normally have sunshine for 302 hours, or 66 per ent of the total possible number for this month, and in August for 265 hours, or 62 per cent.

In July, 1925, there was sunshine for 276 hours and in August for 308 hours, while in 1926 there was sunshine for 320 hours in July and for 256 hours in August. Comparing both years, we find only 8 hours' difference between the two during this 2-month period and, similarly, less than 1° difference in the mean air and water temperatures. When the number of hours of sunshine and its intensity are above or below the normal mean for the month, there is invariably a corresponding departure in air and water temperatures.

The number of hours during which solar heating of the water takes place will be found to vary from 0 to approximately 15 per day, and these variations are the fundamental causes of the daily and hourly fluctuations in water temperature that occur during the summer. A good example of the effect of solar radiation on air and water temperatures and the changes it produces are shown in the following table.

TABLE 4.—*Effect of solar radiation on air and water temperatures, August 1 to 3, 1926*

Date	Hours of sunshine	Daily mean air temperature, ° C.	Water temperature, ° C.			
			Daily mean	At 6 a. m.	At 6 p. m.	Daily increase
Aug. 1	2.3	18.9	21.5	20.5	21.0	0.5
Aug. 2	7.5	23.3	22.4	21.0	23.0	2.0
Aug. 3	14.2	28.3	26.4	23.0	28.5	5.5

On these three days the factors of wind and range of tide were virtually constant, while the chief variable was the number of hours of sunshine per day. On August 1, when there was the least amount of sunshine, the increase in water temperature was exceedingly slight, while on August 3 there was sunshine for 99 per cent of the possible number of hours, which resulted in an increase in water temperature of 5.5° C. during the day.

AIR TEMPERATURE

A close relationship exists between the air and water temperatures in inshore coastal areas and the river waters emptying into them. Although the range of water temperature is considerable, it is much less than the range in air temperature. In the following table, a comparison of the characteristics of the two for the summers of 1925 and 1926 is given.

TABLE 5.—*Comparison of air and water temperatures, monthly data, ° C.*

Monthly data	July, 1925		July, 1926		August, 1925		August, 1926	
	Air	Water	Air	Water	Air	Water	Air	Water
Mean	21.8	19.7	22.0	17.8	21.6	20.8	21.8	21.6
Mean maximum	26.2	22.3	27.0	21.1	26.8	22.9	25.9	23.9
Mean minimum	17.2	17.9	17.0	15.3	16.4	19.0	17.8	19.2
Highest	33.3	27.0	38.3	27.0	32.8	29.0	34.4	31.0
Lowest	12.8	15.0	12.8	10.5	9.4	15.0	12.2	13.5
Greatest daily range	13.3	7.5	16.1	11.0	15.6	7.0	13.3	11.5
Least daily range	3.9	1.5	4.4	1.0	3.3	1.0	3.9	1.0

The relationships between the mean air and water temperatures for July, 1925 and 1926, apparently are contradictory in view of the fact that the water was 1.9° C. lower in 1926, though the air temperature was actually higher than in 1925. However, under the circumstances this is what we would expect because of the difference in the water temperatures on July 1, which were 2.3° C. higher in 1925.

The influence that the air temperature exerts on the temperature of the water is modified to a great extent by wind, precipitation, river discharge, range of tide, and

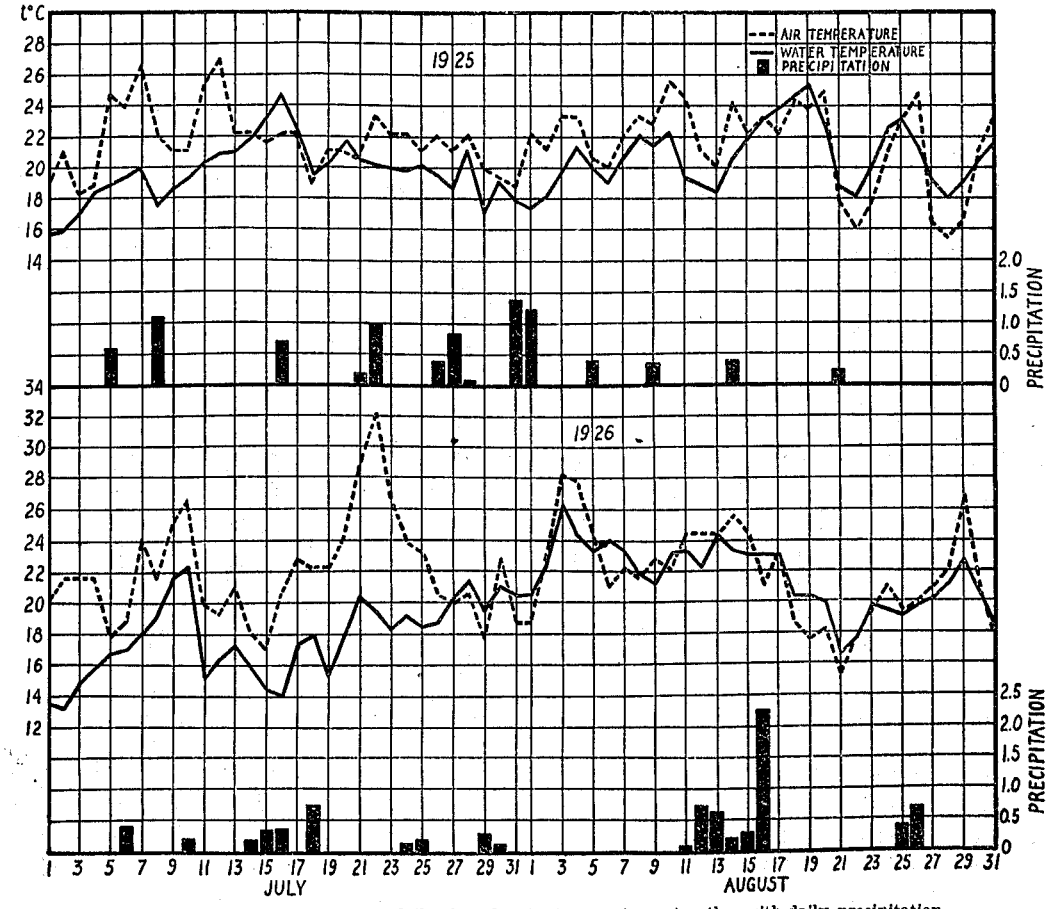

FIGURE 7.—Comparison of mean daily air and water temperatures, together with daily precipitation

the area of tidal flats. The relationship between the air and water temperatures for the summers of 1925 and 1926 is shown clearly in Figure 7. The two curves do not coincide, but, as one would expect, the water curve follows the air curve with a slight lag and less amplitude. A rise in air temperature is followed about 24 hours later by a less prominent rise in water temperature. This is due largely to the fact that the thermal capacity of water is about three thousand times that of the air. Records of the New Haven station of the United States Weather Bureau show that the mean

daily air temperature reaches its annual maximum during the period from July 10 to August 5. This is true for the water temperatures, also, as the trend of the two is approximately the same during the annual cycle.

In comparing the monthly mean temperature of the air with that of the water in Milford Harbor, we find that during the summer months the air ranges only from 1 to 2 degrees higher. This relationship can be used as the basis for estimating the approximate water temperatures over a period of six years (from 1922 to 1927) when thermograph records were not available. Obviously, when air temperatures are above normal the water is correspondingly warmer, and when they are below normal the water temperatures are noticeably lower. Thus, analysis of

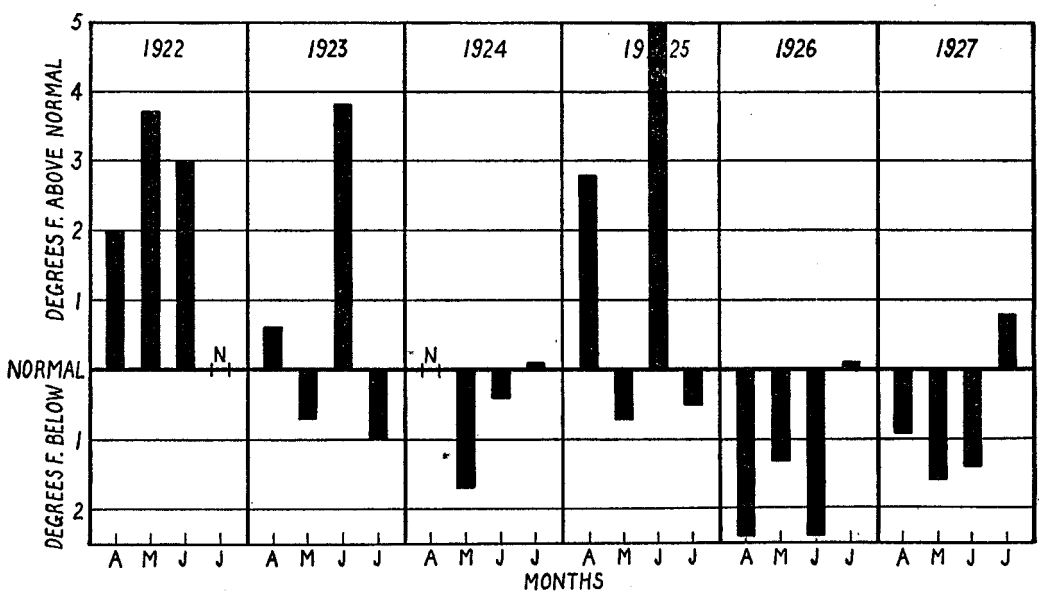

FIGURE 8.—Monthly departure of air temperature from normal, as shown by records of the United States Weather Bureau, New Haven, Conn. The normal mean temperature, in ° F., for April is 46.9; May, 57.8; June, 66.6; and July, 72

the mean monthly air temperatures for any year will indicate the probable water temperatures that occur in small, partially inclosed basins. For this purpose the departure of the air temperature from normal can be used as an index to the prevailing conditions. The monthly departures of air temperature for April, May, June, and July of each year from 1922 to 1927 are presented in Figure 8. In April the water temperature reaches a degree at which the oyster resumes feeding after having been in hibernation since November, and, consequently, we are interested in temperature conditions from this time until spawning occurs in the latter part of July. The monthly differences in air temperatures occurring during this period in each of these years are at once apparent, and when they are summarized for the entire period we find that for three of the years the temperature was above normal and for the other three below. The significance of these departures is discussed later in connection with their effect on spawning and setting.

PRECIPITATION

In rainfall or precipitation we have another important climatological factor that should be considered with air temperature. The quantity of fresh water discharged into the harbors depends largely upon the intensity and amount of precipitation, while its temperature is determined by the temperature of the air and land in this particular drainage basin. The effect of precipitation on harbor-water temperatures depends, therefore, on the quantity and temperature of fresh water discharged into it. When both air temperature and precipitation are above normal, as they were in 1922 and 1925, their combined influence on the physical condition of the

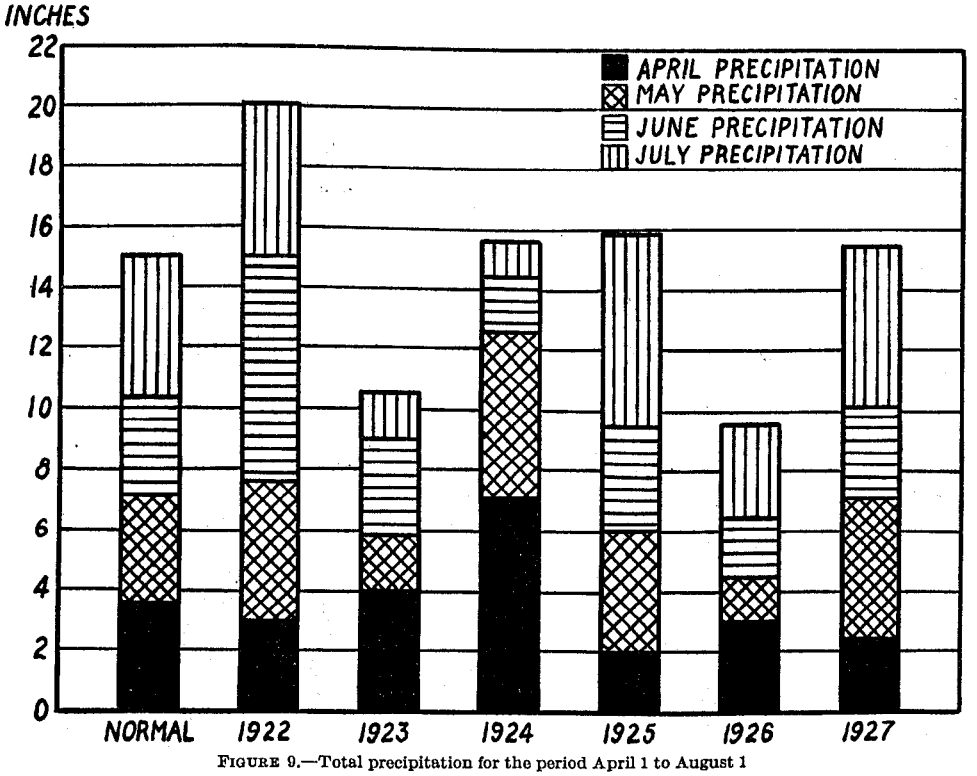

FIGURE 9.—Total precipitation for the period April 1 to August 1

water in the harbor is considerable, as there is not only an increase in water temperature but also a decided change in the chemical composition of the water. The daily precipitation, in inches, for July and August, 1925 and 1926, is presented in Figure 6, together with the water temperatures. In Figure 9 the normal and monthly amounts of the total precipitation for the period April 1 to August 1 is shown for the six years and clearly demonstrates the variations in rainfall that have occurred each spring and summer. According to Hoyt and Grover (1916), in this region approximately 40 per cent of the rainfall reaches the streams as run-off during these months, and its importance can hardly be overlooked in view of the fact that Long Island Sound receives the drainage of virtually all of the State of Connecticut and a large portion of Massachusetts, Vermont, and New Hampshire. In the

chapter on river discharge the monthly variations in precipitation are discussed in relation to their effect on the quantity of fresh water emptied into Long Island Sound.

WIND

Another climatological factor that should be mentioned briefly with regard to its effect on water temperatures is wind. The nearest Weather Bureau station from which detailed wind records could be obtained was at Sandy Hook, N. J.

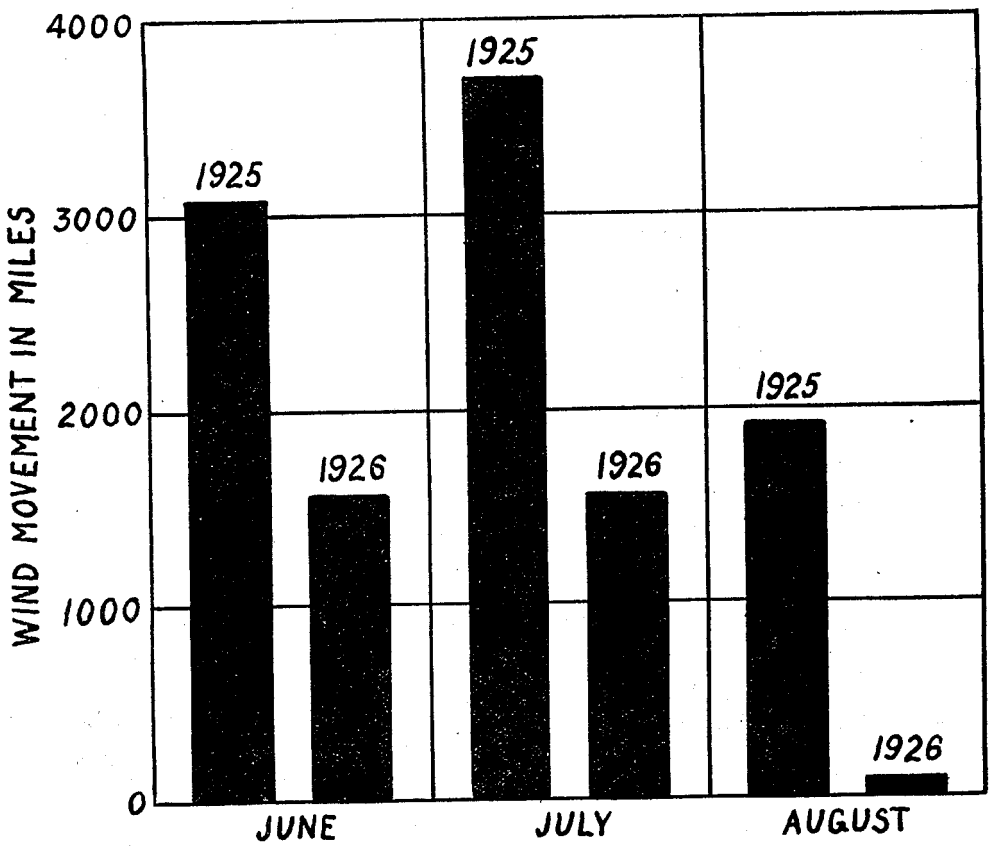

FIGURE 10.—Excess of south component wind movement over north for 1925 and 1926

Taking the two years 1925 and 1926, we find a marked difference in the total monthly wind movements and its direction for the summer months—June, July, and August. For these months the movement of the south wind is invariably greater than the movement of the wind from the north, and the prevailing direction is from the south. In comparing the movement of the south component winds (southeast, south, and southwest) with the north component winds (northwest, north, and northeast), we find a noticeable variation in the number of miles excess of south winds over north winds. As shown by Figure 10, in 1925 the wind movement from the south was 1,487 miles greater than that in 1926 for June, 2,113 miles for July, and 1,848 for August. In other words, for this period the resultant wind movement

from the south in 1925 was 5,448 miles greater than it was in 1926. The effect of wind on air and water temperatures depends largely on the original source of the winds, which, in the case of the south component winds, for this region is both land and marine. The southwest winds come from the adjacent Atlantic Coast States lying in that direction, while the south and southeast winds come from over the Gulf Stream.

The wind has great effect on water temperatures in this region because of the exposure of extensive tidal flats, where rapid changes in temperature were found to occur with strong north or south winds. A good example of the effect of a north wind was found on August 8 and 9, 1926, when the temperature dropped from 25° C. at low water at 6 p. m. to 13.5° C. at low water 12 hours later. During this time, the most sudden drops in temperature occurred on the 9th from 4.30 a. m. to 5.15 a. m., when the water cooled from 20° C. to 13.5° C., a decrease of 6.5° in 45 minutes. Although the opposite effect is produced by the south wind, the increase in temperature is not as great because of a certain amount of cooling by evaporation. The wind is an important factor in changing inshore water temperatures, especially in regions where the tidal movement and area of flats is considerable, because the rate of exchange of heat between the air and water depends largely on the area of the surfaces that are brought into contact and the extent of circulation of each medium.

INFLUENCE OF TIDE ON WATER TEMPERATURE

The tide is an important hydrographic factor indirectly affecting the temperature of inshore waters. As a result of the tide, the water undergoes considerable vertical and horizontal movement, thereby coming into contact with the tidal flats, which greatly increases the effect of climatological conditions on its temperature.

In Milford Harbor the mean range of tide is 6.6 feet and the spring range 7.7 feet. The water temperature showed marked variations according to the range and stage of tide and the time of high water in relation to the time of day. Besides solar radiation and air temperature, the magnitude of the hourly and daily variations in temperature was found to depend also upon the range of tide.

The principal purpose in studying the tides was to determine their influence on the development of the maximum temperatures that affect many physiological activities of marine organisms. In comparing 1925 and 1926 water temperatures, it has been found that during the periods of full-moon spring tides there occurred a definite upward trend in the daily mean water temperature.

During the spring and early summer, the ocean water that is brought into Long Island Sound with the tides has a low temperature, while that from the rivers and shallow tidal flats is considerably warmer. In the fall conditions are reversed, the ocean and Sound waters persisting as a warm influence, while those from the land rapidly become colder. The quantity of ocean water coming into the Sound varies from day to day in accordance with regular changes that occur in the range of tide. With spring tides, when the range is greater than the average, we have the maximum inflow of cool ocean water; and with neap tides, the minimum, as at this time the range is less than the average.

In comparing conditions that exist at different tides, we find that during the period of the full-moon spring tides, in July and August, the hourly water-temperature

fluctuations are greatest, and the daily average shows a steady increase. We can define the full-moon tidal period as the interval between the first increase in tidal range following first quarter of the moon to that which follows the third quarter of the moon. The length of this period is approximately 15 days, half of which occurs before the time of full moon and the other half after full moon. During the first half of the full-moon tidal period, the tide in Milford Harbor gradually increases in range from approximately 6 feet to 8.5 feet, while during the second half it gradually decreases from day to day until the range is again approximately 6 feet.

The area of tidal flats that are flooded at the time of high water or exposed at low water is smallest at the beginning and end of this period and largest at the middle, when the range of tide is greatest. Similarly, the effect of solar radiation and air temperature on temperature of the water is greatest when the range of tide is highest, because of the greater surface that is exposed.

The rate of increase in the daily water temperature and the maximum degree attained during the full-moon tidal periods in July, 1925 and 1926, are shown graphically in Figure 11. During this period in 1925, the water temperature increased from 15.8° C. at the beginning to 24.8° C. at the end, a rise of 9° in 15 days. Under virtually the same conditions in 1926, the water temperature increased from 18.2° C. to 26.4°, a rise of 8.2° in the same period of time. The similarity of the changes in the daily temperature as recorded by the thermograph at the beginning and end of this period in 1925 and 1926 is also shown in Figure 11. The maximum temperature reached by the water during the full-moon tidal periods depends upon three general conditions, namely, (1) the temperature of the inshore water at the beginning of full-moon tides, (2) the temperature of the ocean water brought in by the tides, and (3) weather conditions during this period. The first two conditions can be determined by direct observations and will vary from year to year in accordance with weather conditions in the preceding spring months. The temperature of the ocean at the mouth of the Sound attains its maximum, which is approximately 18.5° C., from about the 15th of July to the 15th of August. There are, however, noticeable annual differences, of which the 1925 and 1926 records, shown in Figure 12, are good examples. When the ocean temperature has attained 18° or 20° C., its cooling effect on the waters of Long Island Sound during spring tides is not very great and is more than counteracted by the flooding and warming of the water on a much greater area of tidal flats. The third factor, weather conditions, can not be predicted definitely, but an analysis of the meteorological data for many years, as presented in Figure 5, shows that during this period one should expect maximum intensity of solar radiation, maximum number of hours of sunshine, and the maximum air temperatures for the entire year. The influence of intense solar radiation and high air temperatures combined with greatly increased tidal range is responsible for the heating of the water to a temperature of 20° C. and above during this period. Though the water in the Sound does not warm as rapidly nor reach as high a temperature as that in the harbors, it follows closely the trend of the inshore-water temperatures.

In studying the hourly fluctuations in water temperature, we can readily see the actual changes that occur with spring and neap tides and at different stages of the tide, examples of which are given in Figure 13, for the periods July 24 to 26, 1926, and August 2 to 4, 1926. The greatest hourly fluctuations occur with spring

tides and the least at the time of neap tides. The lowest water temperatures in the harbor were found to occur at the time of high water and the highest at low water, the difference sometimes being as great as 10 or 12 degrees.

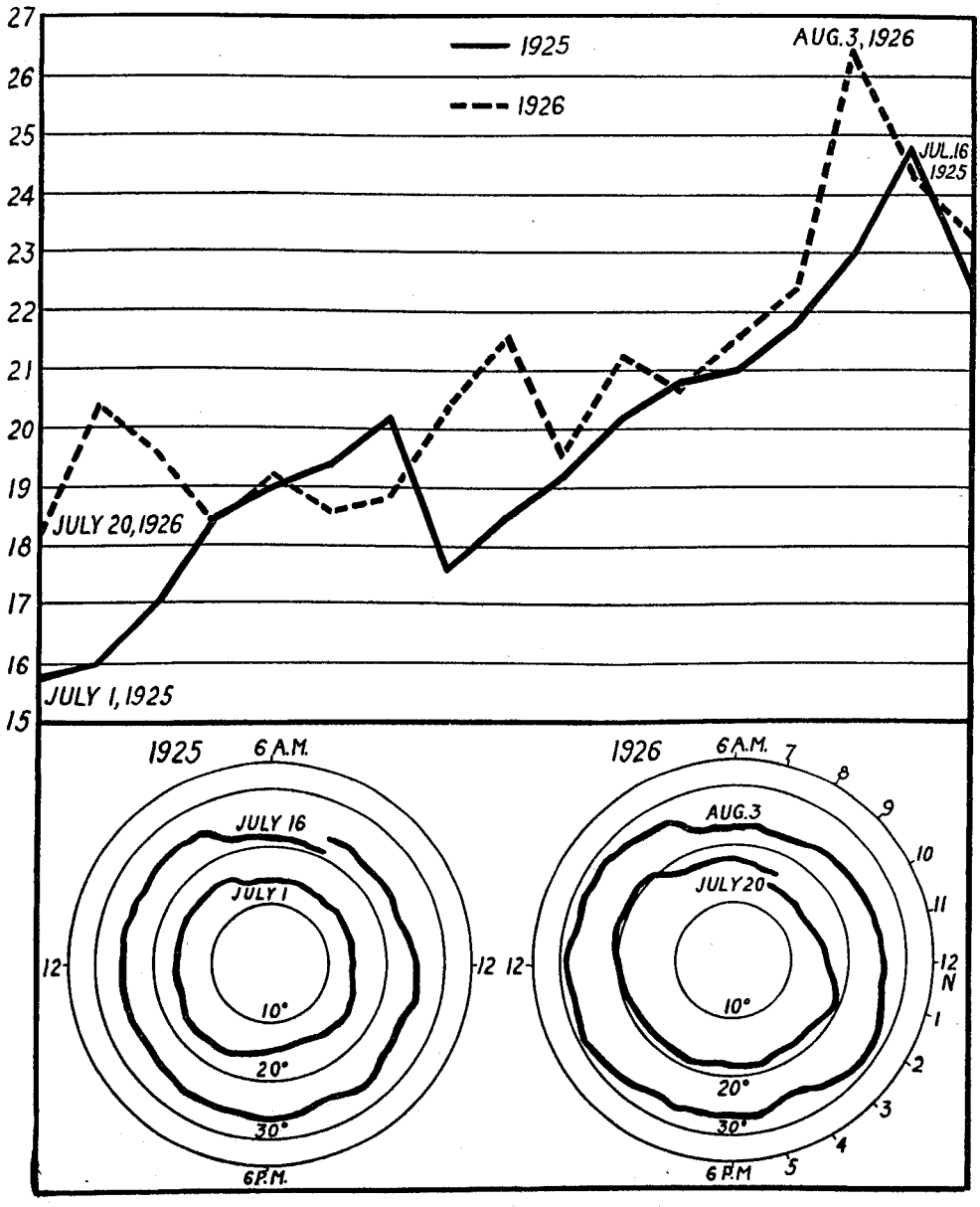

FIGURE 11.—Mean daily water temperature during "full-moon tidal period" in July, 1925, and July, 1926. Copies of thermograph records show the change in the daily temperature from the beginning to the end of this period

The influence of the tide on water temperature may be summarized as follows:

1. The vertical and horizontal movement of the water, as a result of the tide, increases the area of water surface that is brought into contact with the air and land.

2. The magnitude of this movement varies with the range of tide, and both are greatest when the moon is full and in perigee.

3. Since the temperatures of the air and land are highest in July and August, their effect on water temperature will be greatest during the periods of maximum range of tide.

4. Taking into consideration meteorological conditions, the daily and hourly temperature fluctuations can be correlated closely with changes in the stage and range of tide.

TIDE AND CURRENT

In discussing tidal phenomena, the term "tide" is used to designate the vertical movement of the water and "tidal current" to designate the horizontal movement.[1] In the various bays and estuaries along the coast the tidal movement is determined

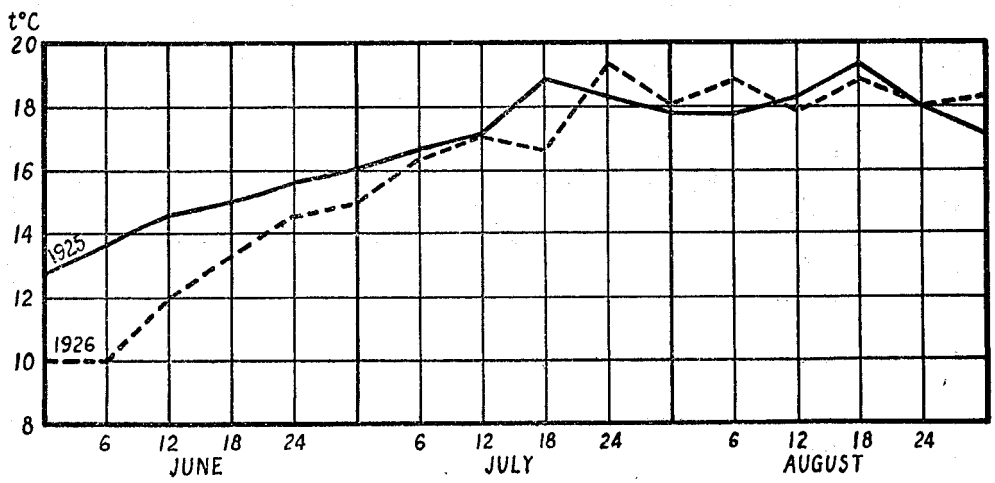

FIGURE 12.—Comparison of the water temperature at the mouth of Long Island Sound in 1925 and 1926

largely by the type of ocean tide that enters them and is modified by the configuration and hydrographic features of the coast in each locality. On the Atlantic coast of the United States the ocean tide is of the semidiurnal type, the chief characteristics of which are that (1) two high and two low waters occur during each tidal day, and there is but little difference between morning and afternoon tides; (2) the rise and fall of the tide varies from day to day according to the position and phase of the moon; (3) spring tides follow full and new moon by one day and are 20 per cent greater than the average, while neap tides follow first or third quarters of the moon by one day and are 20 per cent less than the average; and (4) the duration of rise and the duration of fall of tide are equal, each being about 6 hours and 12 minutes. These are also the general characteristics of the tides in Long Island Sound and Milford Harbor. As the ocean tide enters a partially inclosed basin along the coast, it produces considerable variation in the physical conditions existing there, such as salinity, temperature, H-ion concentration, etc. The hydrography of the region and the range of tide determine largely the extent of variation that is produced. From

[1] In this discussion of tide, statements frequently are taken from "The Tide," by H. A. Marmer, 1926.

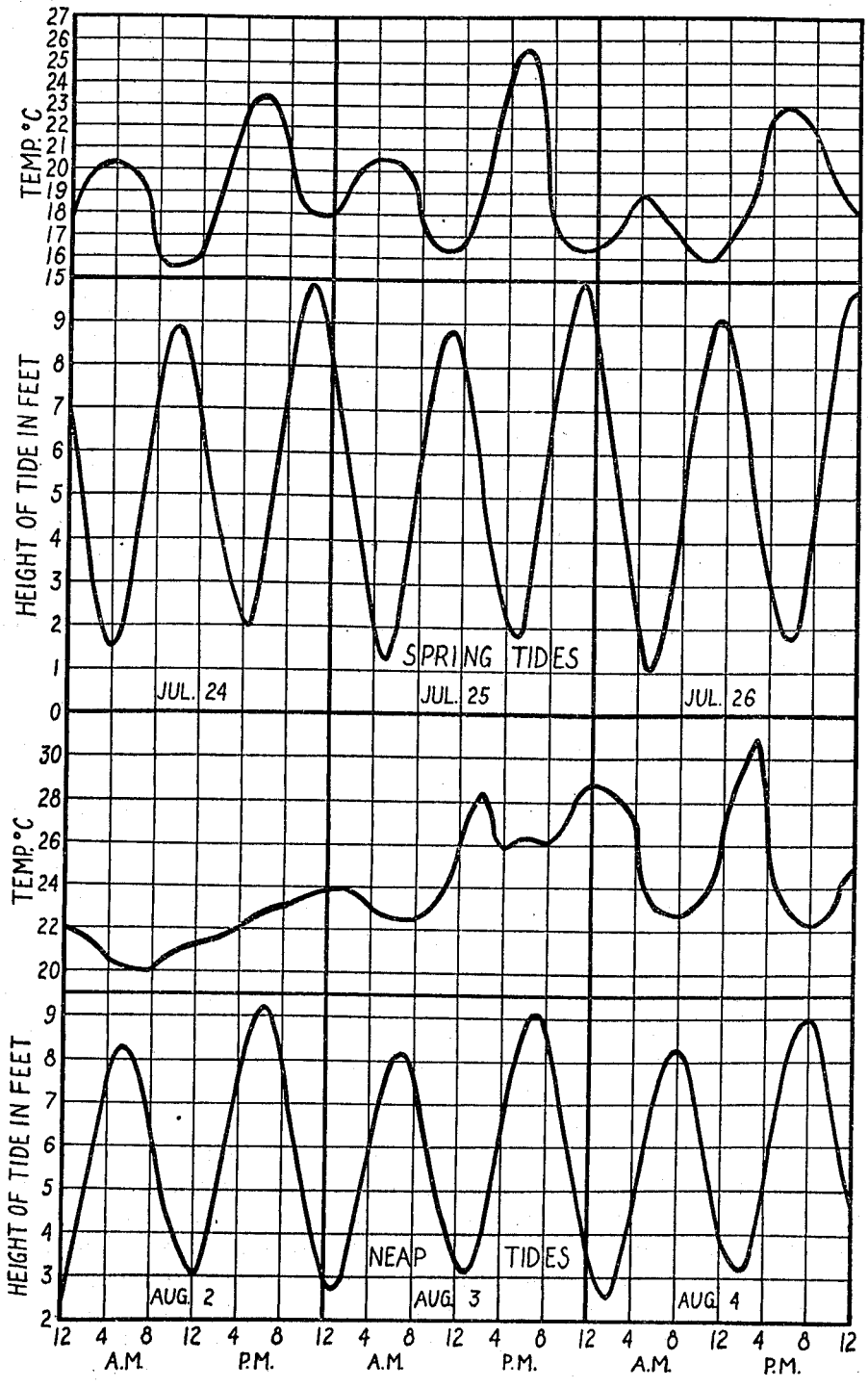

FIGURE 13.—Hourly fluctuations in water temperature during spring tides and neap tides

a biological standpoint both intimately related features of the tidal movement—the rise and fall of the water and the horizontal movement or tidal current—are of considerable importance.

According to Marmer (1925), in most bays and rivers of the Atlantic coast the tide enters as a progressive wave, the characteristics of which are that the strength of the tidal current is greatest at the times of high and low water while the slack of the current comes midway between the times of high and low water. However, in Long Island Sound and its inshore waters we find a different kind of movement, which is of the stationary-wave type. With this type of wave movement the strength of the current comes midway between high and low water, while the slack of the current comes near the times of high and low water. This difference is illustrated by Figure 14, in which the tide and current curves are plotted for Milford Harbor entrance, where the movement is of the stationary-wave type, and for New York Harbor (Marmer, 1925), as determined by the Coast and Geodetic Survey, where we have progressive wave movement.

In each locality the tidal currents vary in strength from day to day in accordance with the changes in the range of tide. The strongest currents come with the spring tides of full and new moon, and the weakest currents with the neap tides of the moon's first and third quarters. During the spring tides the flood current in Milford Harbor attains a maximum velocity of 1.1 feet per second, and the ebb current, 1.5 feet per second. With neap tides considerably less water passes in and out of the harbor, and the velocity of the flood current at strength is 0.8 per second and the ebb current 1.3 feet per second. The tidal current in Milford Harbor is of the rectilinear or reversing type—that is, the flood current runs in for a period of approximately 5 hours and 30 minutes and the ebb current runs out for a period of 6 hours.

In studying the tidal current and its possible effect on the occurrence and distribution of the oyster larvæ a complete understanding of the direction as well as the velocity of the current at each stage of the tide is necessary. For this purpose the Eckman current meter and several sets of drift bottles were used. The direction of flow during flood and ebb is shown in Figure 15 for Milford and vicinity. During a complete tidal cycle the distance traveled by an object floating in the water or by a buoyant microorganism is equal to the product of time multiplied by the average velocity during this interval. For a normal flood or ebb period of 6.2 hours, the approximate distance a tidal current with a velocity, at strength, of 1 knot will carry a floating object is 3.95 nautical miles or 24,000 feet. (Marmer, 1925.)

As a result of river discharge the ebb current has a greater velocity and duration than the flood, and currents of such strength as those at the entrance of Milford Harbor would transport a floating object approximately 21,100 feet during the ebb flow and return it but 15,600 feet during the flood. The currents inside and outside of the harbor are not as strong as those at the narrow entrance, so, in order to determine the actual direction and drift of the currents, several observations were made with floats. In each case two pairs of floats were used and were released at Station 2, in the harbor, and their course charted for several hours. When the floats were released, at the beginning of ebb tide, they followed the channel to Station 5 and then swung east, passing the red buoy near Station 6 in approximately 2½ hours, and finally came to a stop about 1,000 yards offshore at Pond Point. The distance the

floats were transported by the ebb current was over 15,000 feet in a period of 6 hours. With the change of current from ebb to flood the floats were carried west nearly to Welchs Point, and then swung in toward shore and into the rotating current in this little bay. When the floats were released on the last of ebb tide from Station 2, they

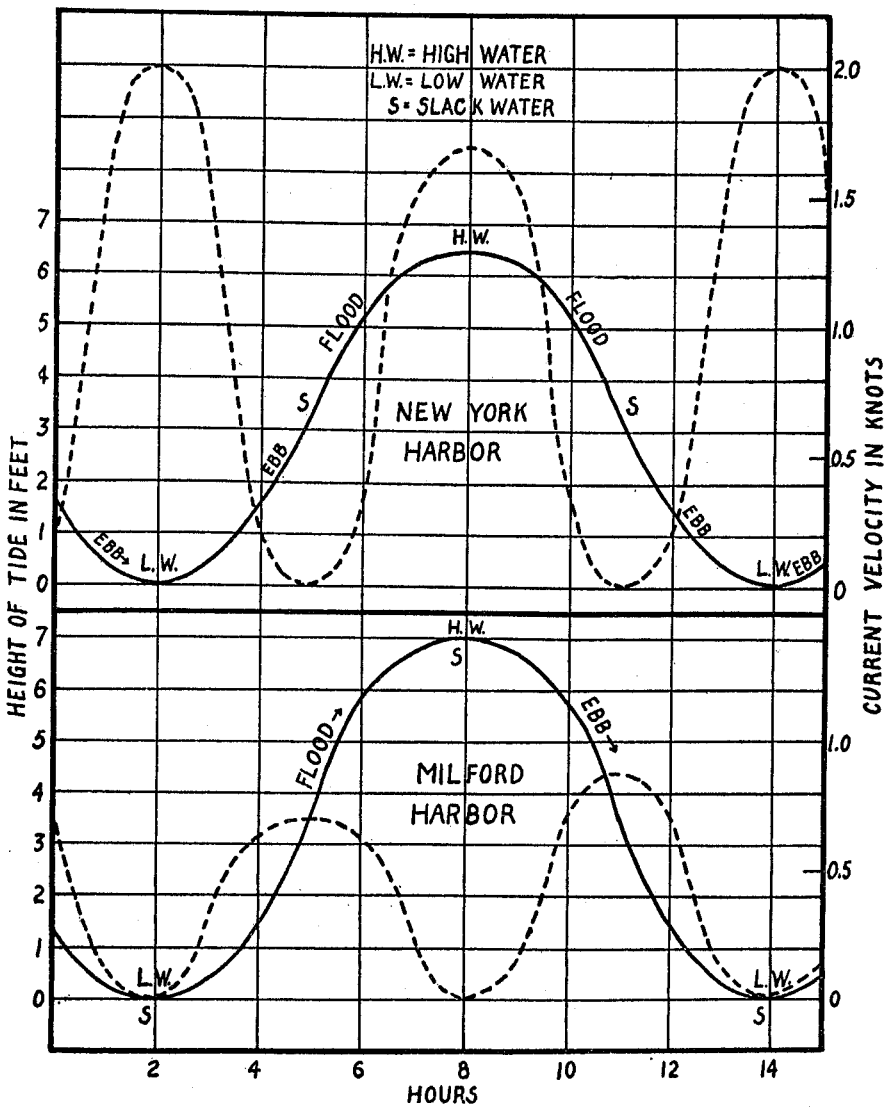

FIGURE 14.—Comparison of tide and current relationships in Milford and New York Harbors

were carried out of the harbor as far as Station 5, and there met the first part of flood tide in the Sound, which carried them to the west in a large circle, finally washing them ashore about 1 mile from the harbor entrance.

From these observations it is apparent that any object floating freely in the water will be carried out of the harbor by the tidal currents in the first day and never

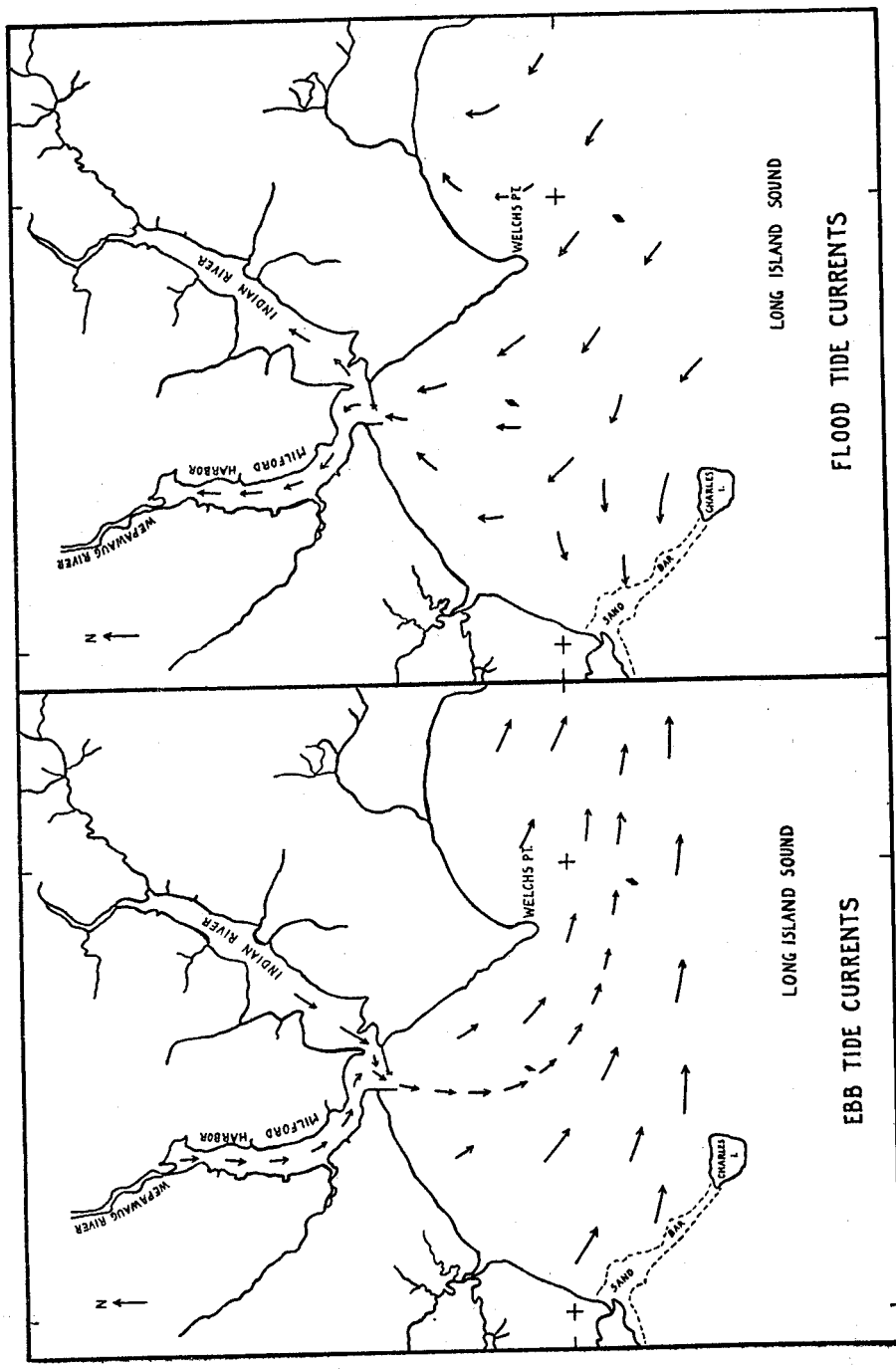

FIGURE 15.—Direction of flood and ebb tide currents in Milford Harbor and vicinity

will be transported back to it. This consideration has a bearing on the distribution and occurrence of oyster larvæ in the harbor and Sound, which will be discussed later.

Briefly summarized, the chief characteristics of the tides and currents in Milford Harbor are as follows:

1. The mean range of tide is 6.6 feet.
2. With spring tides the maximum range recorded during the summer was 9 feet, while with neap tides the minimum range was 4.2 feet.
3. The tide is of the semidiurnal type and possesses the general characteristics of the Atlantic Ocean tide, as described previously.
4. The tidal currents are of the rectilinear or reversing type.
5. The duration of the flood current is approximately 5½ hours, and of the ebb current 6 hours.
6. The currents attain their greatest velocity when the tide is halfway between high and low water mark.
7. The velocity of the ebb current is approximately one-third greater than the velocity of the flood current.
8. The period of slack water, or zero velocity, occurs at the times of high and low water. With neap tides, slack water lasts for an interval of about 1 hour, and with spring tides only 20 minutes.

TIDES AND CURRENTS IN LONG ISLAND SOUND

Studies of the tides and currents were not confined entirely to Milford Harbor but were carried on in Long Island Sound also, as this is the largest and most important seed-oyster producing region in the north. Here the tidal currents are rather complex, and, in order to study them, several experiments were made with drift bottles in addition to the current-meter observations.

The current-meter observations consisted of determinations of the velocity and direction of the current at various stages of the tide and were made at two stations off Milford. Observations made during ebb tide showed that the predominant direction of the current during this period was E. 20° S., and that the maximum velocity was 0.9 foot per second. During the flood tide the current does not run in one general direction but swings to the right through an arc of 140° from low water to high water. The direction and velocity at four stages of the flood tide are as follows:

TABLE 6

Stage	Predominating direction	Velocity (knots)
First-quarter flood	W. 20° N.	0.25
Second-quarter flood	W. 40° N.	.85
Third-quarter flood	N. 40° E.	1.15
Fourth-quarter flood	N. 70° E.	.30

The veering of the current to the right during this flood cycle can be attributed to two chief causes: (1) The rotation of the earth, in consequence of which all moving bodies are impressed with a force that, in the Northern Hemisphere, deflects them to the right of the direction in which they are moving. The water

on the flood tide would be deflected to the Connecticut shore and that on the ebb to the Long Island shore. Evidence of such deflection is found in the difference in range of tide on the two shores, high water being higher and low water lower on the Connecticut shore than on the Long Island shore. (2) The configuration and hydrographic features of the Sound. The convergence of the shore lines between Stratford Point and Oldfield Point and between Norwalk and Eatons Point confines the tidal wave as it advances up the Sound, forcing the water to expand into the bays and estuaries. Virtually all such areas are on the Connecticut shore, and the large quantity of water that passes into them results in changing the course of the flood tide during the latter period of rise. A similar rotation of the flood current, but in an anticlockwise direction, has been reported for the Long Island shore, between Herods Point and Ortons Point, by people long familiar with this region.

Summarizing the current-meter observations, it can be stated that though the tidal currents in Long Island Sound are chiefly of the rectilinear or reversing type, there is a clockwise rotation along the Connecticut shore during the last half of the flood tide.

This rotary movement, combined with the greater velocity and duration of the ebb current, results in a dominant drift over the Connecticut oyster grounds in approximately an ENE. direction. The observations indicated that during a tidal cycle a floating object released at the beginning of ebb tide will travel toward the entrance of the Sound with the ebb current, and on the change to flood will retrace its path for about 3 hours and then swing in a large arc to the right toward the shore, finally arriving at high water at a point about 2 miles ENE. from where it was released. The actual course traveled by the floating object will vary somewhat according to the range of tide, river discharge, and point of release.

DRIFT-BOTTLE EXPERIMENTS

On September 18 to 21, 1926, 500 drift bottles with drags attached were released in groups at various places off Stratford Point and Milford. In Table 7 the general record of release and recovery is given, and in Table 8 is shown the percentage recovered during the first month in each of the three major regions—Connecticut, entrance of the Sound, and Long Island.

TABLE 7.—*Drift-bottle record*

Experiment	Group	Locality	Tide	Number released	Total number recovered	Recoveries, according to months						Per cent recovered
						1	2	3	4	5	6 to 10	
A	1	Stratford Point to Stratford Shoal.	High water	100	38	24	5	3	3	1	2	38
	2	do	Low water	100	60	41	9	3	5	1	1	60
B	3	Housatonic River	¼ ebb	50	24	16	4	1	1	0	2	48
	4	do	¾ ebb	50	30	24	5	1	0	0	0	60
C	5	Charles Island	¼ ebb	25	18	15	3	0	0	0	0	72
	6	do	½ flood	50	36	24	5	1	1	3	2	72
	7	Milford Harbor	½ ebb	25	17	11	0	1	0	0	5	68
	8	Welchs Point	½ flood	100	67	48	7	0	3	5	4	67
Total				500	290	203	38	10	13	10	16	58

TABLE 8.—*Per cent of drift bottles recovered during the first month, according to location*

Experiment	Group	Connecticut	Entrance of Sound	Long Island
A	1	50	33	17
	2	70	3	27
B	3	88	6	6
	4	67	0	33
C	5	67	0	33
	6	83	0	17
	7	99	0	1
	8	90	1	9
Total		76.7	5.3	18

In a period of 10 months, 290, or 58 per cent, of the bottles were recovered. Taking the groups as a whole, we find that 70 per cent of the recovered bottles were collected during the first month, 13 per cent in the second month, and the remainder, about equally divided over the next eight months. The records of the bottles recovered during the first month are of greatest significance, and, in analyzing them the factors of time, distance, and points of release and recovery have been considered carefully. In discussing the results it is necessary that each experiment be taken up separately because of the different conditions in each locality.

Experiment A.—(See figs. 16 and 17.) This experiment was planned so as to cover the most valuable oyster-seed producing region in Connecticut. The drift bottles were released in groups of 10 from the northeast corner of oyster lot No. 771, at Stratford Point, out to Stratford Shoal Lighthouse, a distance of approximately 6 miles. The bottles in Group 1, which were released at the time of high water, were transported first by the ebb current in the Sound, while those released in Group 2 were carried first by the flood current. The recoveries in Group 1 were all made to the eastward, and in no instance were bottles recovered west of the line of release. In Group 2 the effect of the flood current is shown by the recovery of 16 bottles to the west of the line of release, though as a whole the bottles of this group were carried eastward also. The fact that 60 per cent of Group 2 were recovered and only 38 per cent of Group 1 is due chiefly to two factors—(1) the shoreward movement of the flood tide, which deposited a greater number on the Connecticut coast, and (2) the discharge of the Housatonic River, which caught the bottles as they were moving eastward and forced them over to the Long Island shore. Further influence of these two factors is shown in the difference in distribution of the bottles by the currents and the percentage recovered in each region. If we analyze the results over shorter periods of time, as, for example, by weeks, we find that during the first two weeks the majority were found on the Connecticut shore, the third week at the entrance of the Sound, and during the fourth week on the north shore of Long Island. Only 1 of the bottles of Group 2 succeeded in getting out of the Sound, while 5 of Group 1 were recovered outside, 3 of which went to the Green Hill Coast Guard Station in Rhode Island, a distance of 80 miles from the point of release, in approximately 14 days.

In Group 2, the farthest distance covered by a bottle drifting to the east was 50 miles and to the west, 14 miles. In this experiment the general distribution of the drift bottles in relation to time, tide, and point of recovery also indicates a clockwise rotary circulation of the water in the Sound.

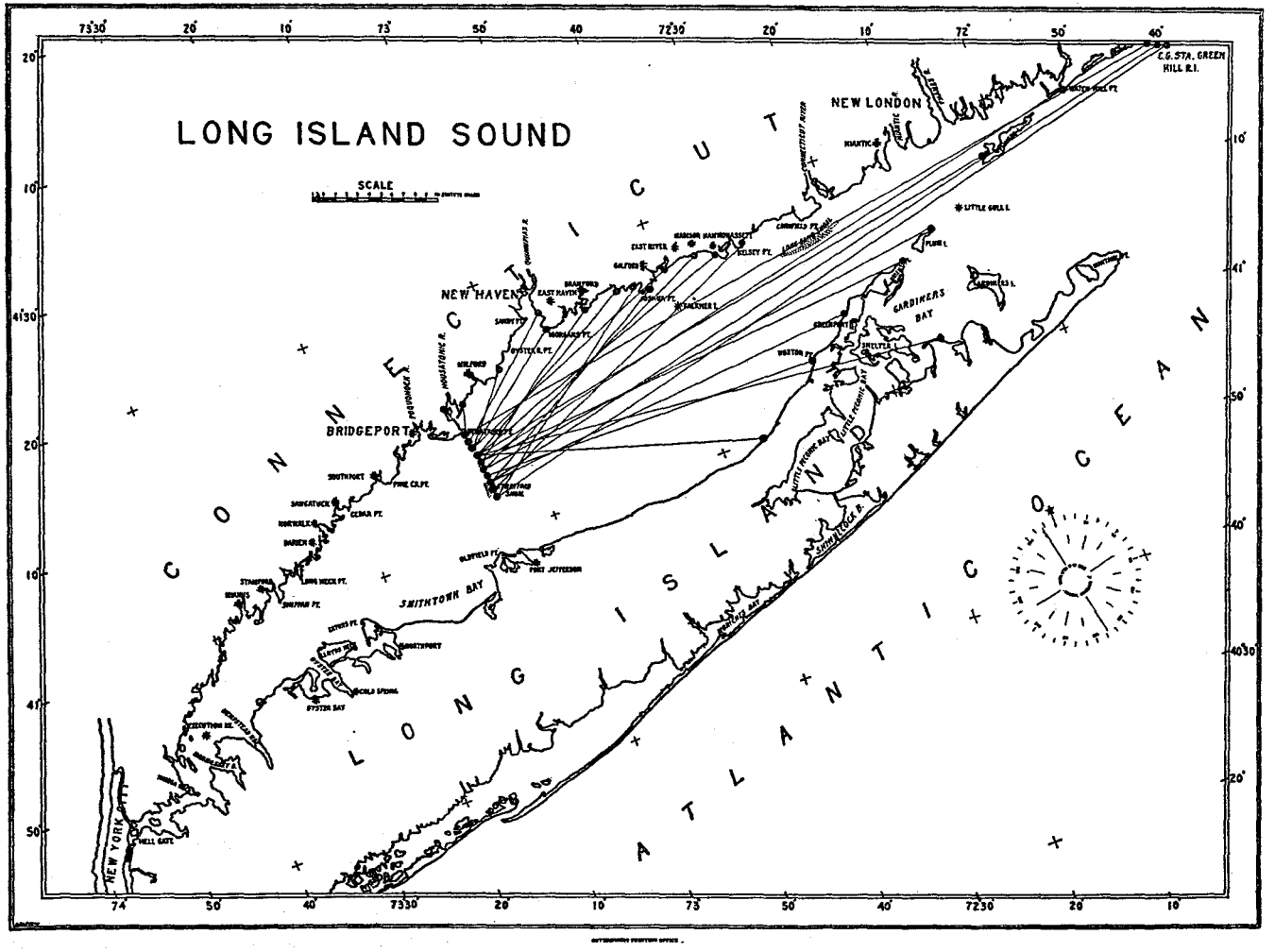

FIGURE 16.—Experiment A, Group 1. Place of release and recovery of bottles put out at high water

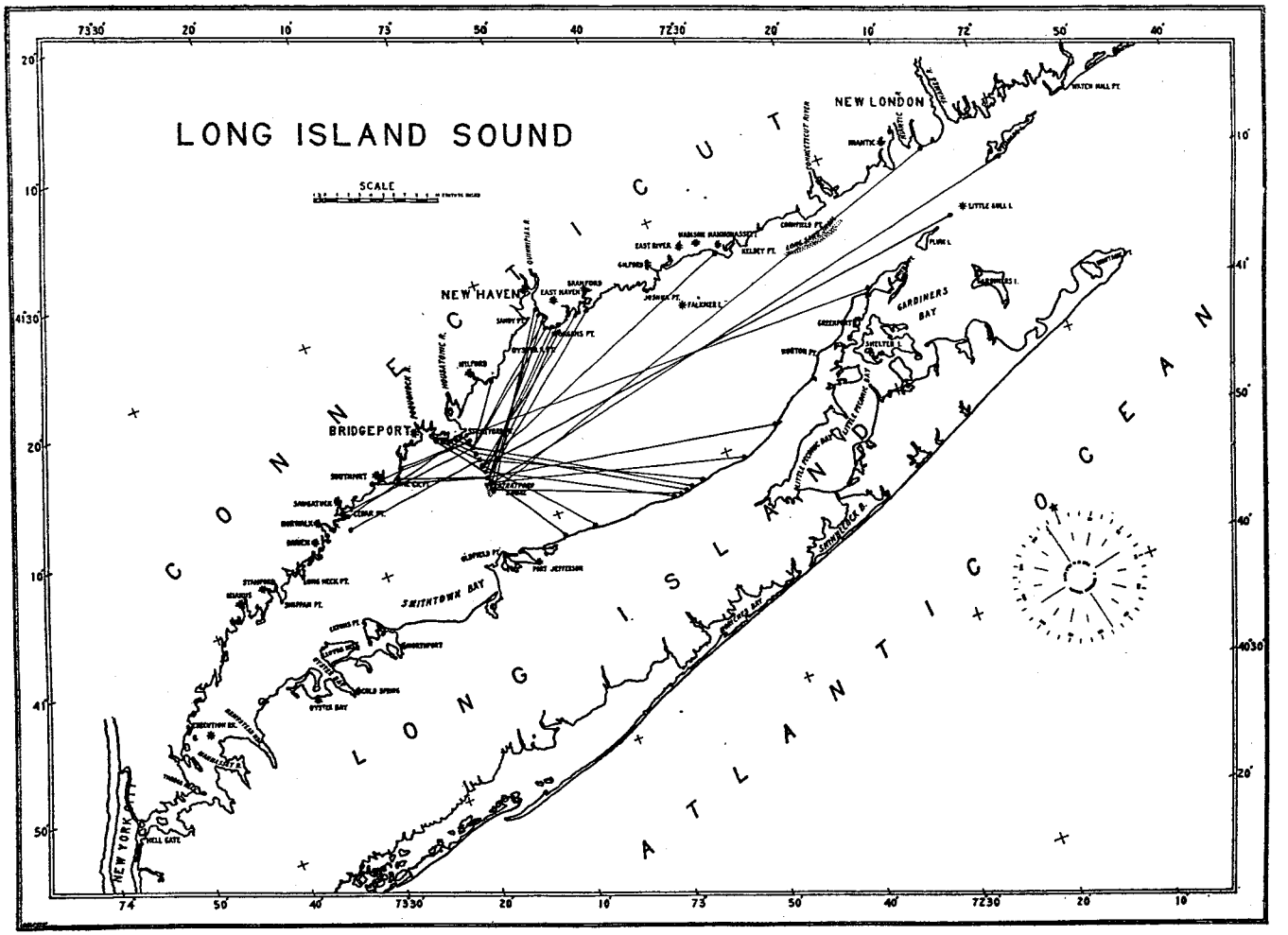

FIGURE 17.—Experiment A, Group 2. Place of release and recovery of bottles put out at low water

Experiment B.—The purpose of this experiment was to determine the drift of the water discharged by the Housatonic during the first and last stages of the ebb tide. Two groups of 50 bottles each were released in the channel at black buoy No. 3. When the bottles of Group 3 were put out at the beginning of ebb tide, the velocity of the current was 1.2 feet per second, and when Group 4 was released at three-quarters ebb the current had attained a velocity of 2.5 feet per second. The distribution of the bottles during the first month is shown in Figures 18 and 19. The majority of Group 3 were recovered to the eastward along the Connecticut shore, from Stratford Point to Joshua Point, a distance of about 20 miles. One of these bottles was the only one of the 500 that succeeded in getting out into the Atlantic Ocean and was recovered on the southern shore of Long Island near Amagansett Lighthouse. The bottles of Group 4 were distributed more widely, and during the first two weeks the majority went to the Connecticut shore and for the most part were found west of Stratford Point as far as Darien, a distance of 17 miles.

Another outstanding difference of this group is the recovery of about one-third of the bottles on the Long Island shore 3 and 4 weeks after they were released. The chief cause of the difference in the distribution of the bottles of Groups 3 and 4 is the velocity and direction of discharge of the Housatonic River at different stages of the ebb tide. At the first quarter of ebb tide, though the current from the river is quite strong, it is met at the entrance by an equally strong ebb current in the Sound, with the result that the river water is carried in an ESE. direction. At the period of about three-quarters ebb, the current from the river has attained considerable strength, while in the Sound we have comparatively slack water. Under these conditions, the river water is discharged straight out into the Sound, oftentimes reaching as far as Stratford Shoal. As the tide in the Sound begins to run flood, this water is forced to the westward and toward the Connecticut shore and is distributed much the same as the drift bottles of Group 4. In the spring and summer the water discharged by the river during the last of ebb tide has a high temperature and low salinity, and its distribution to the westward is responsible, to a great extent, for producing suitable water conditions over this area for the production and setting of oysters.

Experiment C.—(See figs. 20 and 21.) This experiment was planned so as to study the drift of the water close inshore, where the influence of river discharge is negligible. Groups 6 and 8, which were released with the flood tide, were recovered during the first week along the Connecticut shore *east* from Stratford Point to New Haven, in the second week *west* from Stratford Point to the Norwalk Islands, and in the third week on Long Island from Hortons Point to Roanoke Point. In Groups 5 and 7 the distribution of the bottles was very similar, the recoveries having been made a little more to the eastward because they were released with the ebb current. The place and time of recovery of the bottles in experiment C indicate the same general clockwise circulation of the water in Long Island Sound as is shown in experiments A and B.

SUMMARY

The results of the drift-bottle experiments may be summarized as follows:

1. Five hundred bottles were released and of these, 290, or 58 per cent, were recovered in a period of 10 months.

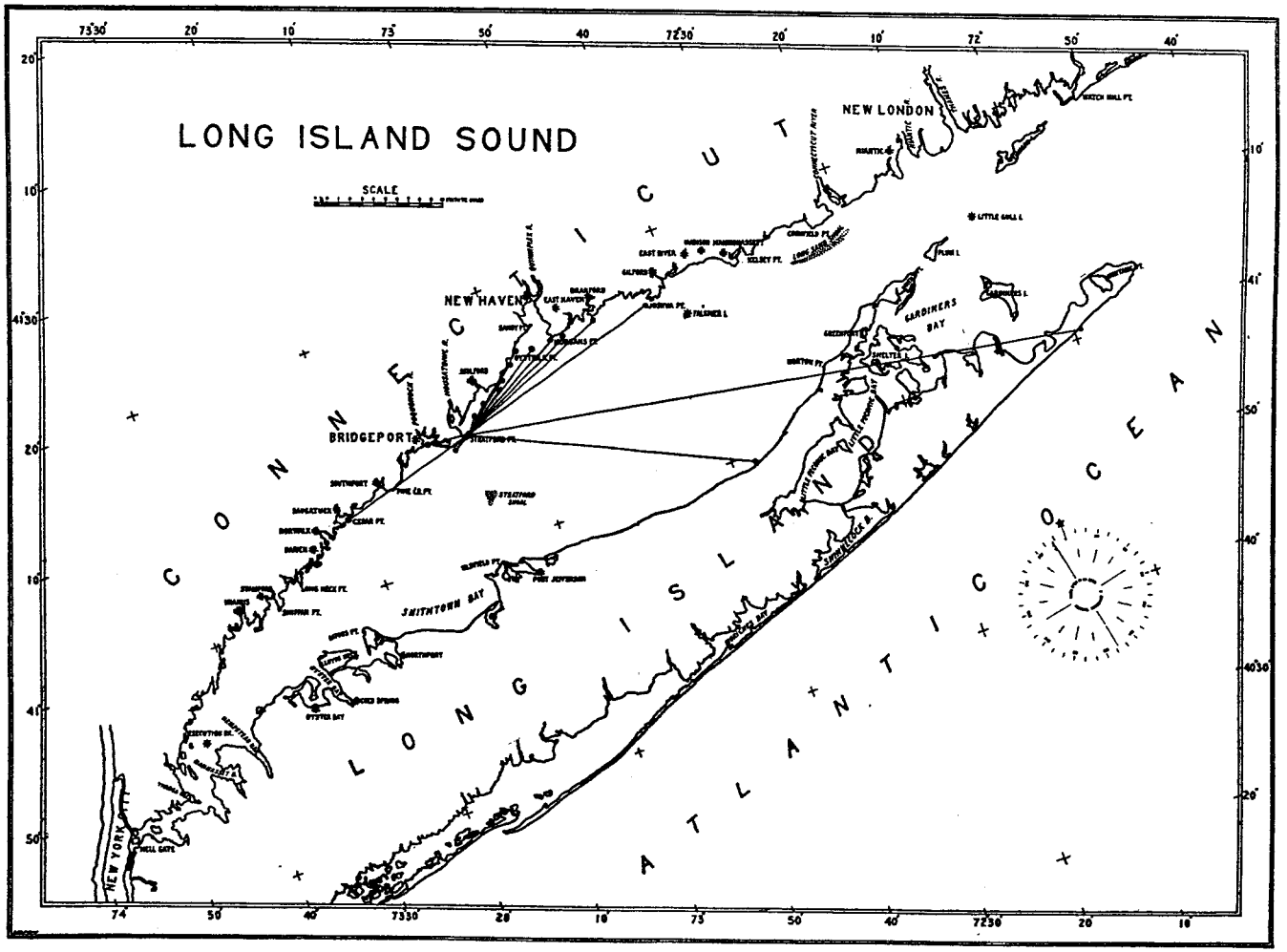

FIGURE 18.—Experiment B, Group 3. Place of release and recovery of bottles put out in the mouth of the Housatonic River at first of ebb tide

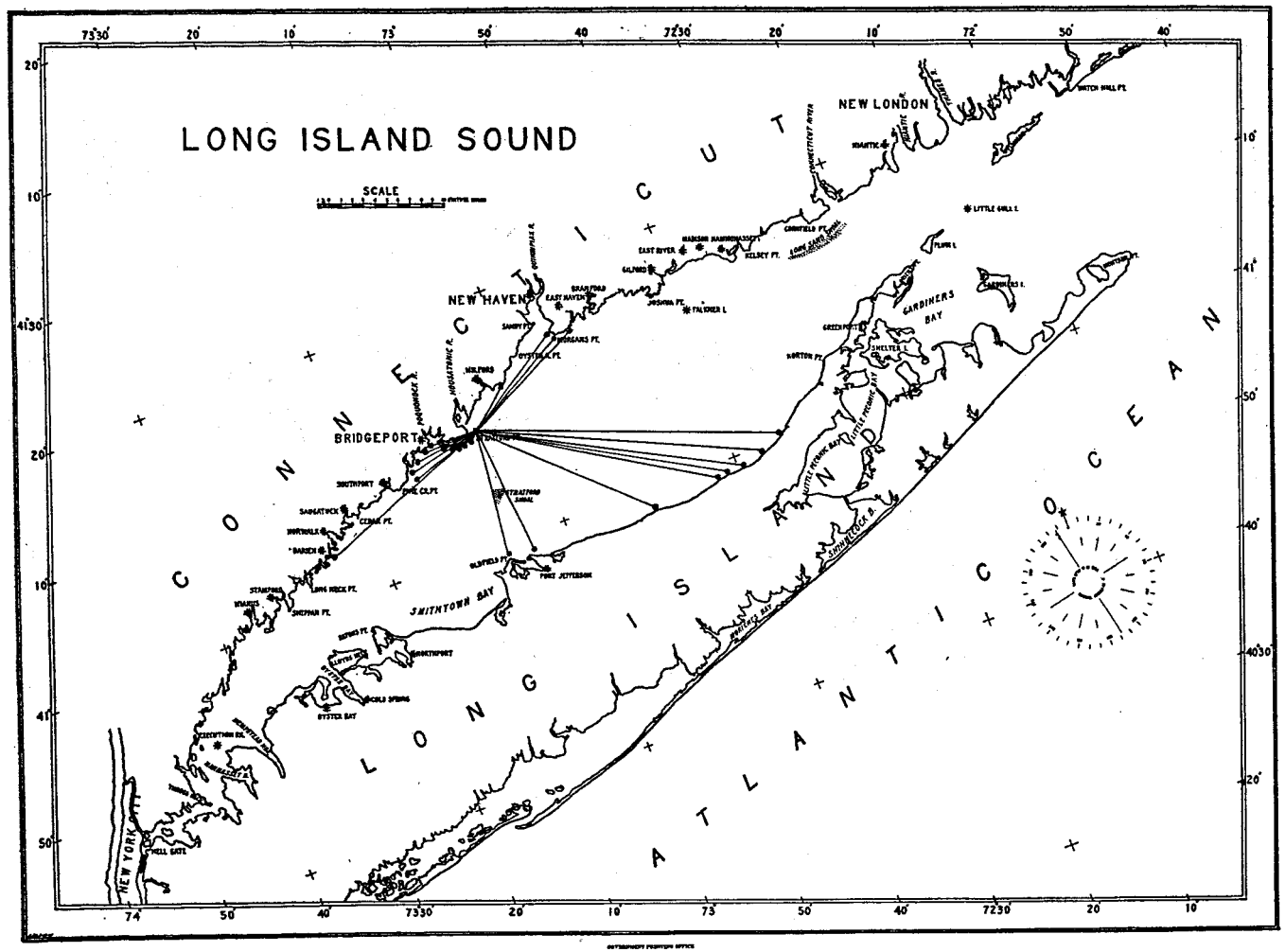

FIGURE 19.—Experiment B, Group 4. Place of release and recovery of bottles put out in the mouth of the Housatonic River at three-fourths ebb tide

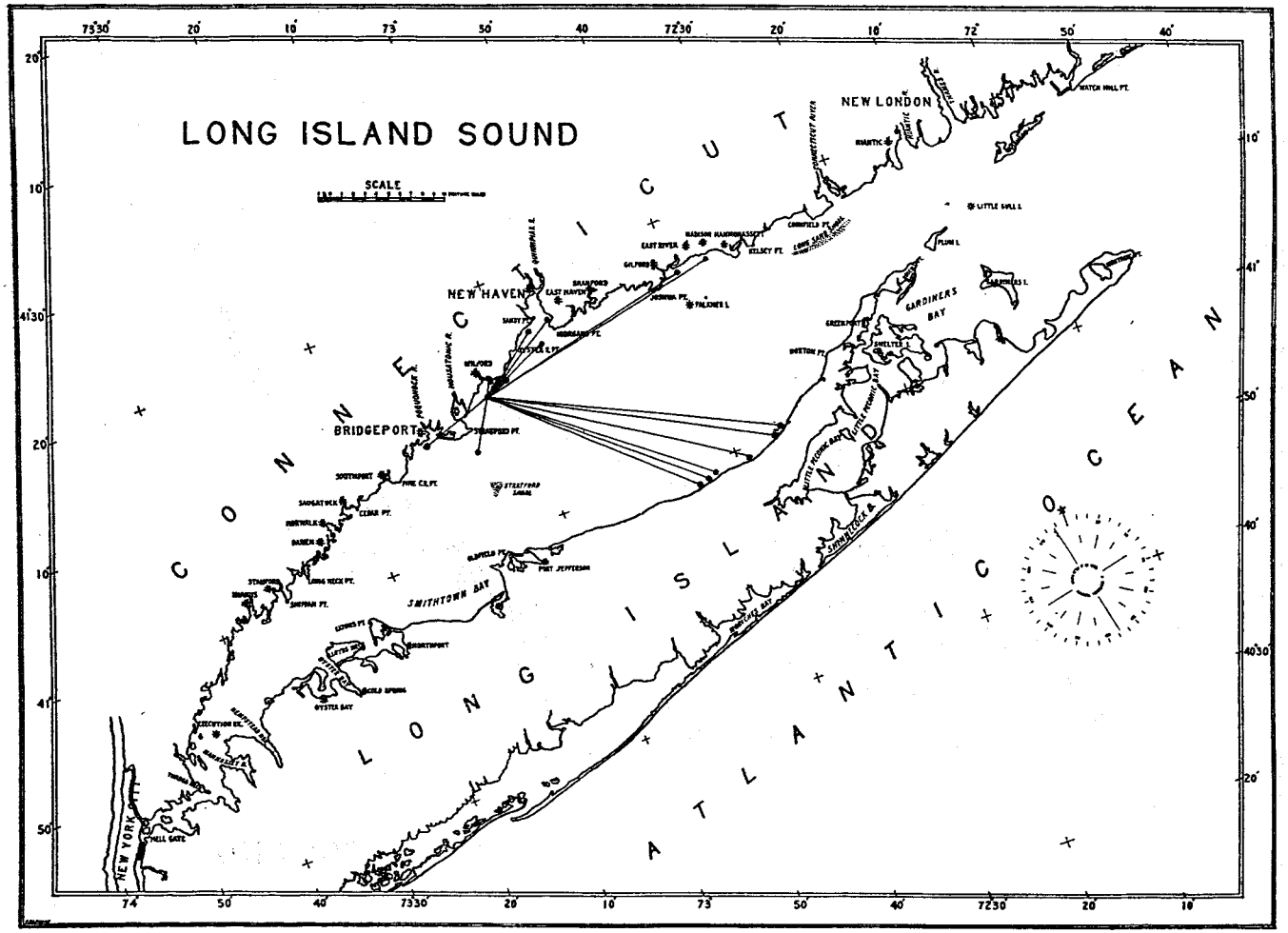

FIGURE 20.—Experiment C, Group 5. Place of release and recovery of bottles put out at Charles Island at one-fourth ebb tide

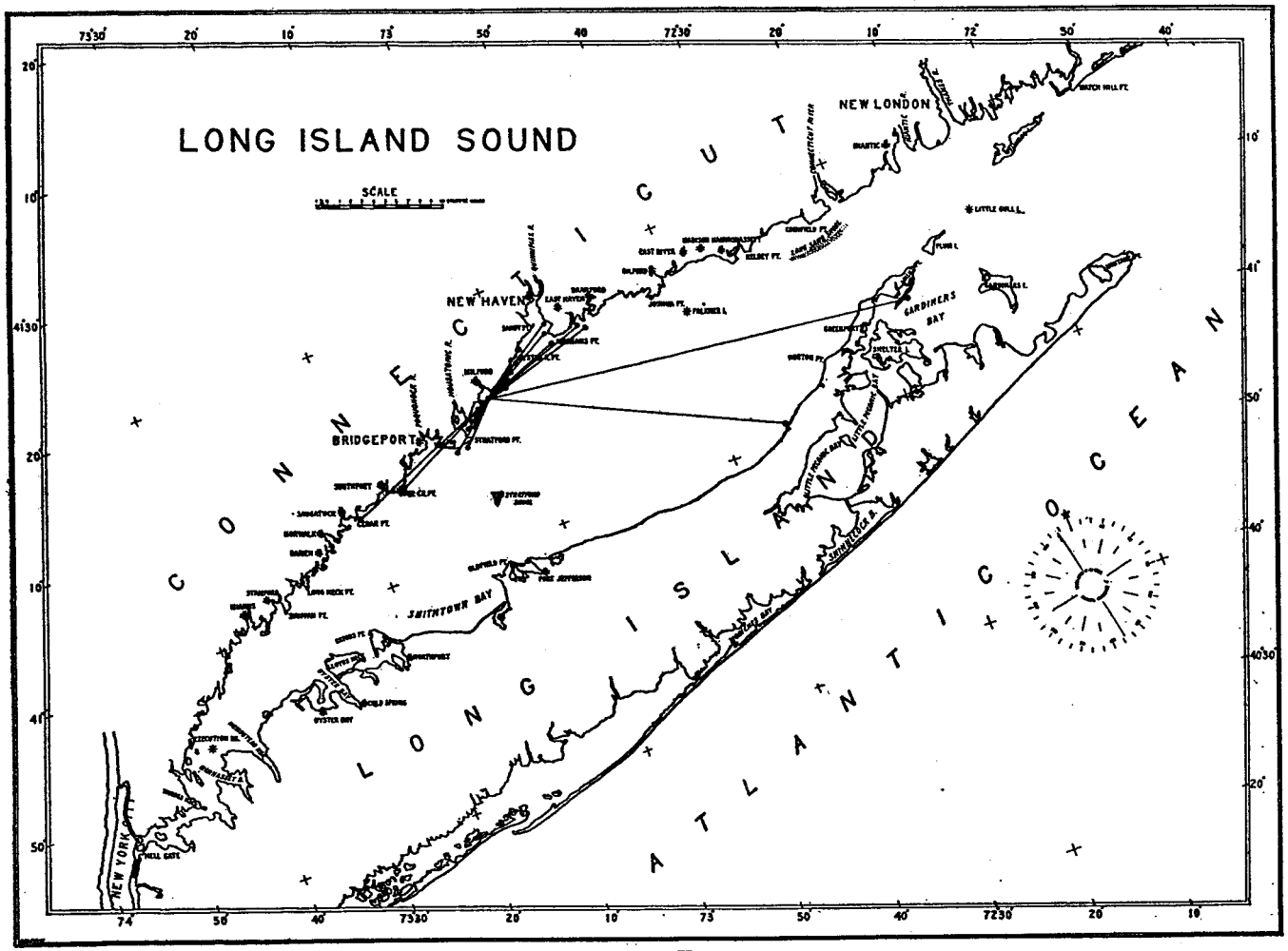

FIGURE 21.—Experiment C, Group 6. Place of release and recovery of bottles put out at Charles Island at one-half flood tide

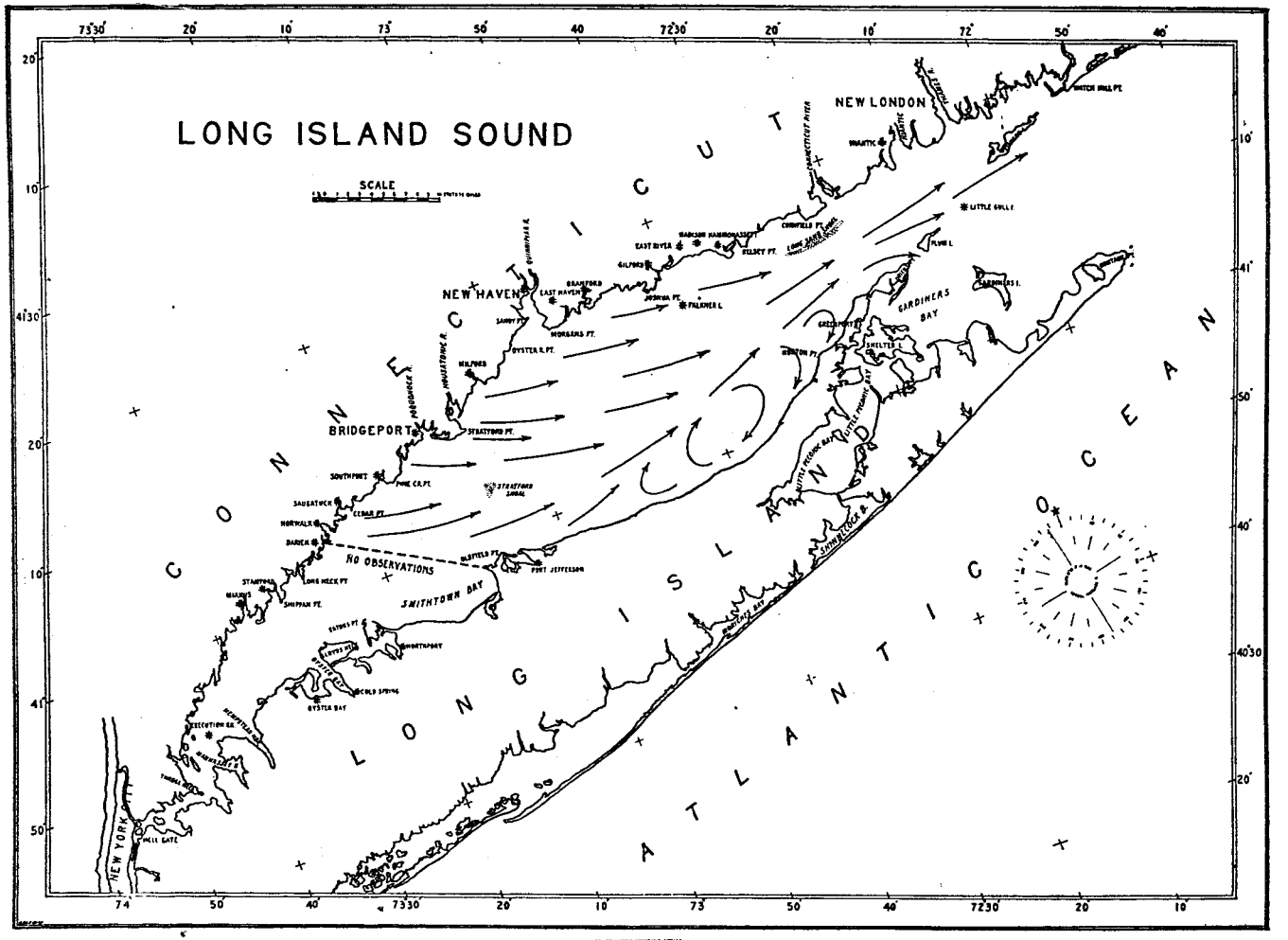

FIGURE 22.—Schematic representation of ebb-tide movement in Long Island Sound as indicated by drift-bottle and current-meter observations

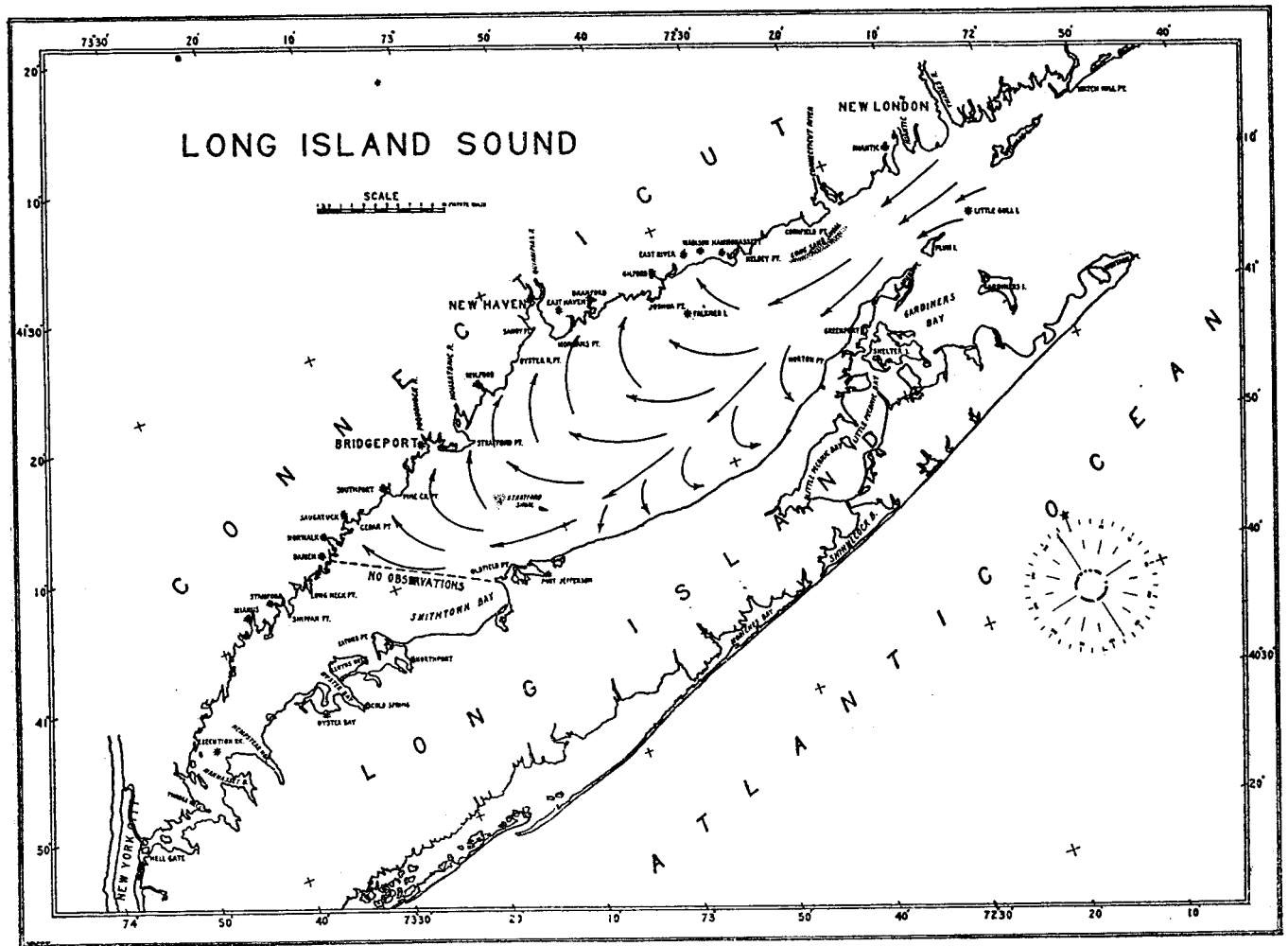

FIGURE 23.—Schematic representation of flood-tide movement in Long Island Sound

2. Seventy per cent of the recovered bottles were collected during the first month, 13 per cent during the second month, and the remainder about equally divided over the next eight months.

3. The bottles recovered during the first month were distributed as follows: 76.7 per cent to the Connecticut shore, 5.3 per cent at the entrance or outside of the Sound, and 18 per cent on the Long Island shore.

4. On the Connecticut shore the bottles were recovered from the Norwalk Islands to Goshen Point, a distance of 65 miles, 15 of which were to the west of the points of release and 50 to the east.

5. In the region at the entrance of the Sound and outside, only 12 bottles were recovered.

6. On the Long Island shore, bottles were recovered from Oldfield Point to Orient Point, a distance of 45 miles.

7. The greatest distance covered by a drift bottle was approximately 150 miles.

8. The fastest recorded drifts were 45 miles in 9 days and 80 miles in 15 days, which give average drifts of 5 and 5.3 miles per day, respectively.

9. A greater percentage of bottles was recovered from the groups released at low water, or with the flood tide, than from those released during the ebb tide.

10. The recovery of the bottles, in relation to time and position, showed a clockwise distribution along the shores of the Sound.

The general movement of the water in Long Island Sound is primarily tidal, resulting in a dominant clockwise circulation, as represented in Figure 24. The rate of movement, as indicated by the drift-bottle records, is approximately 5 nautical miles per day. The existence of such a circulation is of great importance in producing favorable conditions for the growth and propagation of oysters in Connecticut waters. The water coming from the harbors and estuaries on the last of ebb tide is of much lower salinity than that in the Sound and in the spring and summer is considerably warmer. Instead of being carried out to the ocean, it meets the tidal current in the Sound, which has already changed to flood, and is carried to the westward and then spread to the north over the vast oyster region, creating conditions that are favorable for growth and propagation of oysters. In the dumping of mud, sludge, or other refuse, even in the designated areas in the Sound, strict attention must be paid to the stage of tide or the material is liable to be carried and deposited on the oyster grounds and beaches. In all cases dumping should be done preferably at the time of high water in the Sound or during the first 2-hour run of the ebb current. This suggestion is made at this time in view of the recent heavy mortality of oysters that occurred on the beds off Bridgeport as the result of dumping mud from the harbor.

SALINITY

The salinity of the water in Long Island Sound and its estuaries and harbors is determined by two main factors—namely, the discharge of fresh water by the rivers and the inflow of salt water from the ocean. In the Sound the salinity is highest and decreases gradually as we approach the sources of fresh water along the shore. We have a typical example in Figure 25, in which the general distribution of salinity is shown for Milford Harbor and vicinity. The figures are based on the average of

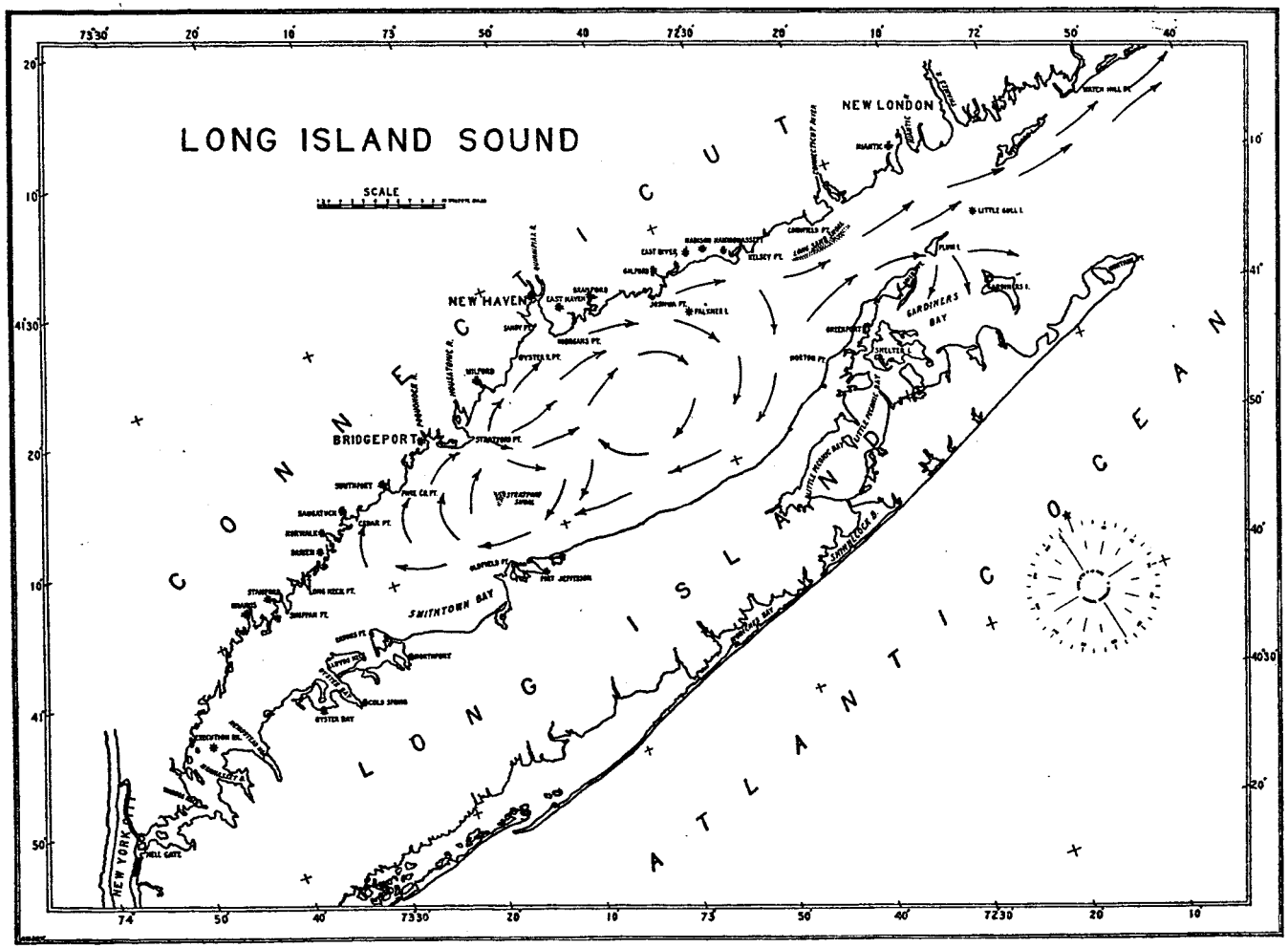

FIGURE 24.—Schematic representation of the dominant circulation in Long Island Sound, as indicated by drift-bottle and current-meter observations

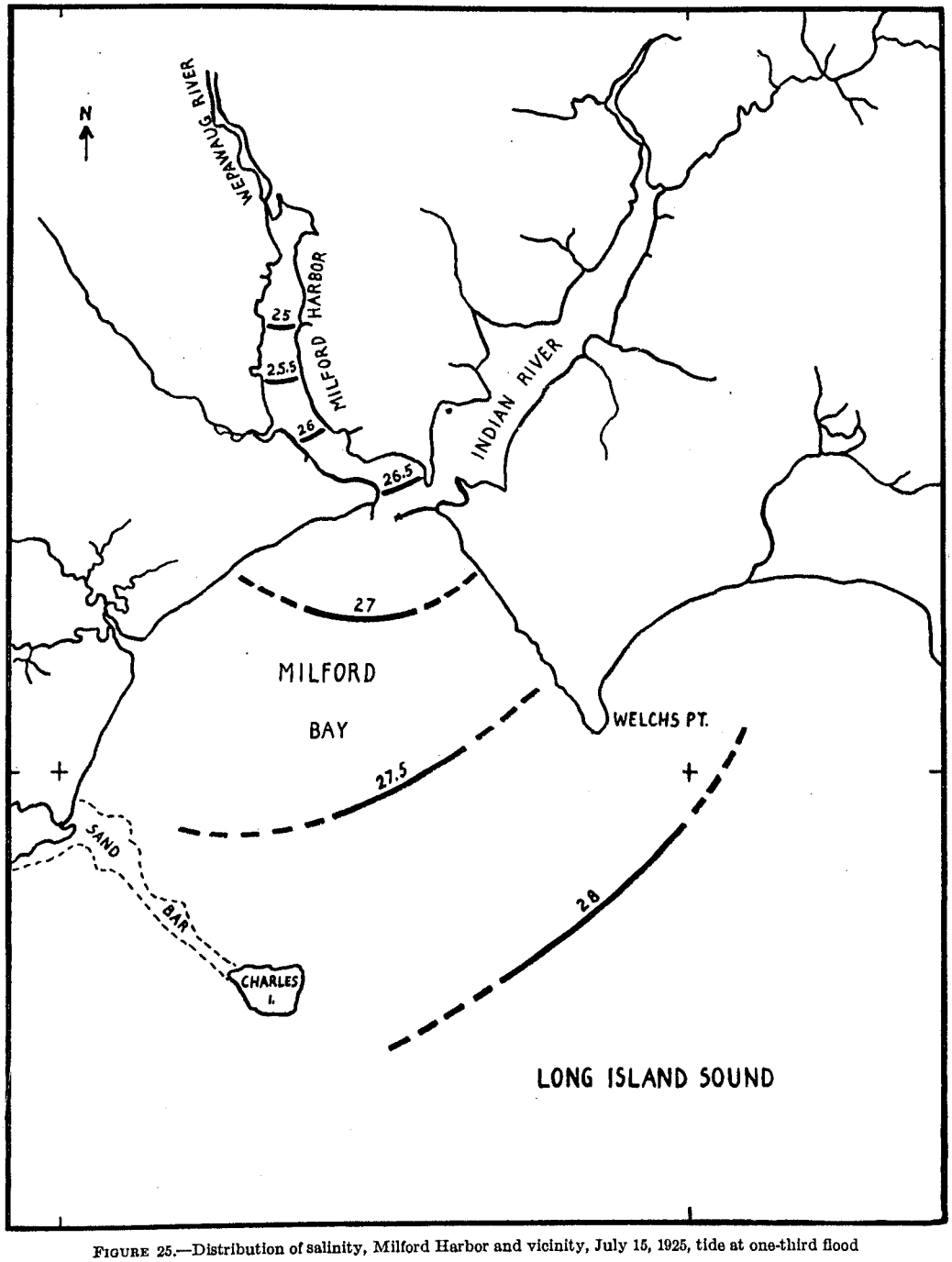

FIGURE 25.—Distribution of salinity, Milford Harbor and vicinity, July 15, 1925, tide at one-third flood

surface and bottom samples taken at each station on July 15, 1925, between 3 and 4 p. m., when the tide was one-third flood. The greatest number of salinity determinations was made at harbor Station No. 2 and at the inshore Sound Station No. 6 at various stages of the tide. The monthly averages at these Stations for July and August of both years are shown in the following table.

TABLE 9.—*Salinity of the water*

Station	Month	Year	Salinity per mille	
			Surface	Bottom
Harbor station No. 2	July	1925	26.32	26.77
Do	August	1925	26.93	27.87
Do	July	1926	27.17	27.47
Do	August	1926	27.59	27.95
Sound station No. 6	July	1925	27.91	28.05
Do	August	1925	28.10	28.21
Do	July	1926	27.70	27.81
Do	August	1926	28.15	28.50

The salinity is rather constant in the deeper waters of the Sound, and the variation from year to year is comparatively small, while in the inshore and harbor areas we find noticeable changes occurring according to the stage and range of tide and amount of river discharge. In several instances observations were made during a complete tidal cycle, from low water to high water and back again. In the following table the series taken at Station No. 2 on August 24, 1925, is given and shows the typical changes in water conditions that occur at various stages of the tide. This is shown graphically also in Figure 26.

TABLE 10.—*Effect of tide on physical conditions, Station No. 2, August 24, 1925*

Tide	Time	Depth (feet)	Salinity	Temperature, °C.	pH
Low water	8 a. m.	0	25.35	20.9	7.2
Do	do	10	27.66	21.8	7.4
Flood	10 a. m.	0	26.78	21.4	7.4
Do	do	11	28.04	20.0	7.8
Do	12 m.	0	27.88	21.9	7.8
Do	do	13	28.10	20.2	7.6
High water	2 p. m.	0	27.75	22.2	8.0
Do	do	15	28.10	21.0	7.4
Ebb	4 p. m.	0	27.66	23.3	7.6
Do	do	13	28.12	22.0	7.4
Last ebb	6 p. m.	0	26.18	24.2	7.5
Do	do	12	27.82	23.0	7.3
Low water	8 p. m.	0	25.50	24.0	7.3
Do	do	10	26.75	23.0	7.2

Since the range of tide on this particular date is but 0.2 foot above the mean range, the changes in water conditions can be regarded as intermediate between those that occur with extreme spring or neap tides. Changes in salinity are least at the time of neap tides and greatest with the spring tides.

The differences in salinity between top and bottom samples were generally less than 1 per mille and naturally were highest at Station No. 1, where fresh water enters the harbor from the Wepawang River, and least at Station No. 6, in the Sound. Occasionally, however, extreme differences were found following heavy

rains and with the change of tide from low water to flood. In the first instance the surface was covered with a layer of water from 6 inches to a foot deep, which was virtually fresh or of a low salinity of about 5 parts per mille, while that on the bottom was 25 or more. In the second instance the extreme difference was due to the

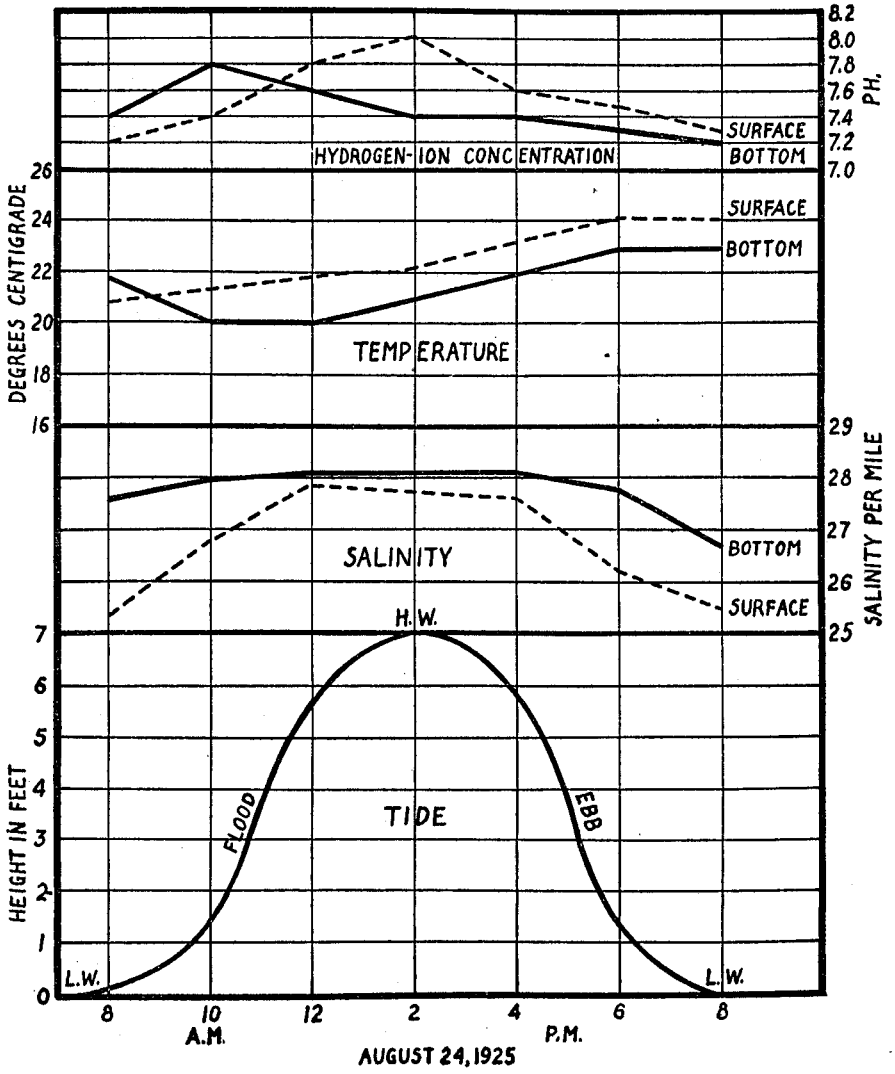

FIGURE 26.—Hourly changes in temperature, salinity, and hydrogen-ion concentration of the water during a complete tidal cycle on August 24, 1925

progression along the bottom of heavy, more saline water with the beginning of flood tide, while that at the surface was still running at ebb or at low slack water. Samples taken at such times showed a difference in salinity of from 2.5 to 3 parts per mille between the surface and bottom at a depth of 10 feet.

The range of salinity in the harbor in 1925 was from 4.5 to 28.12 per mille, while in 1926 the range was from 10.48 to 28.66 per mille. At the inshore Sound Station

No. 6 the range of salinity in 1925 was from 27.54 to 28.50 per mille and in 1926 from 27.36 to 28.74 per mille. These figures apply only to the summer months, July and August, when conditions are comparatively stable. According to Galtsoff (unpublished report), there are seasonal variations in the salinity of the Sound waters, the most noticeable of which is the freshening of the water at the time of spring floods in April and May, when the salinity is lowest; while during the cold months the salinity was found to increase gradually and reached the maximum for the year in January. He found that in these waters the seasonal fluctuation in salinity was a regular process, which repeated itself with certain constancy from year to year. At his station at the entrance to Bridgeport Harbor the annual range in salinity in 1922–23 was from 24.7 to 27.8 per mille, an average of 26.2 for the year.

HYDROGEN-ION CONCENTRATION

The hydrogen-ion concentration of the water was determined for each station by the colorimetric method and the values expressed in pH, in which no correction has been made for salt error. In this locality the water is naturally alkaline and during the summer ranges from a pH of 7.2 to 8.4. In plotting the average readings for each station, we find that the pH increases from 7.6 at Station No. 1 to 8.2 at Station No. 6 in the Sound. The lowest pH values were found in samples taken at low tide following heavy rains, and the highest in afternoon samples taken in the harbor near the time of high water. The pH was found to vary with the time of day, depth, stage of tide, and amount of river discharge. An example of the surface and bottom changes in pH during a complete tidal cycle is shown in Figure 6 for a series of observations taken on August 24, 1925. In samples taken in the morning the pH of the surface water generally was found to be a little lower than that of the bottom water. In the afternoon the reverse was true and the pH of the surface water was from 0.1 to 0.2 higher than it was on the bottom, probably as a result of increased photosynthesis in the warmer surface layer. In considering the characteristic changes in pH during both summers, we find that during July the average pH value was 7.8, while in August the readings became higher and ranged from 8 to 8.2.

RIVER DISCHARGE

The importance of river discharge in the ecology of the oyster is shown clearly by the fact that oysters are found growing naturally only in those partially inclosed bodies of water along the coast where the salinity is reduced considerably by the drainage of fresh water from the land. On its northern shore Long Island Sound receives the drainage from virtually the entire State of Connecticut and a large portion of Massachusetts, Vermont, and New Hampshire, and it is here that we find thousands of acres suitable for the growth of oysters, as shown in Figure 2. There are over 30 coastal rivers that discharge into the Sound, of which the Connecticut and Housatonic are the largest.

The Connecticut River receives the drainage from an area of approximately 11,000 square miles and the Housatonic from 1,500 miles. The lowest point for which records of river discharge are available is Sunderland, Mass., on the Connecticut River, and Falls Village, Conn., on the Housatonic River. The mean monthly discharge of the rivers at these points is shown in Figure 27 for the period from April until August in the years 1924, 1925, and 1926. The quantity of water discharged

shows a marked variation from month to month and from year to year and is representative, in a general way, of the changes in salinity that occur in Long Island Sound

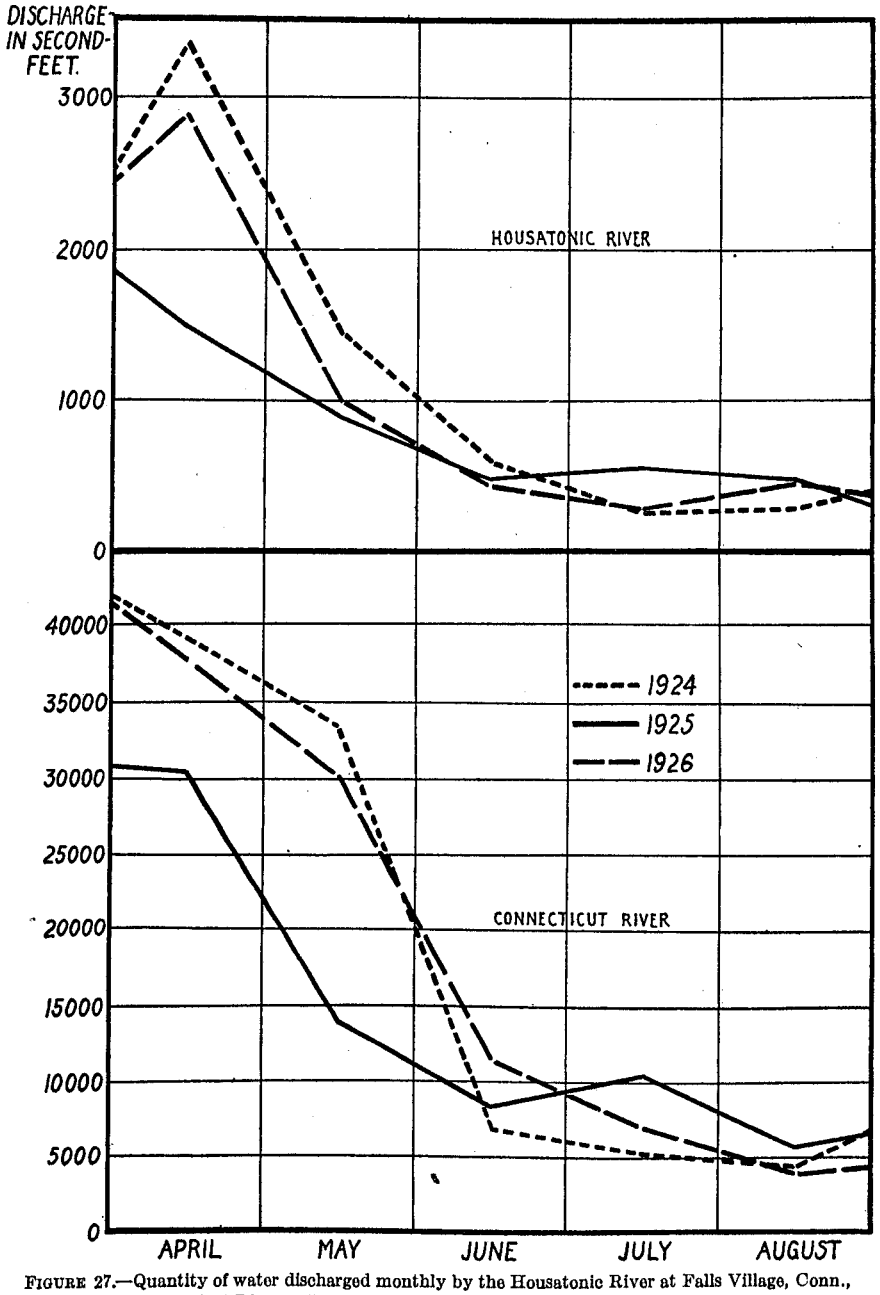

FIGURE 27.—Quantity of water discharged monthly by the Housatonic River at Falls Village, Conn., and by the Connecticut River at Sunderland, Mass., for the period April to September, 1924 to 1926

during these periods. Similarly, the effect of river discharge on the temperature of the water in the Sound varies according to the quantity and temperature of the water

emptied into it. According to Collins (1925), the mean temperature of the river water during these months is generally from 1° to 3° F. below the mean air temperature. If we use this relationship as the basis for estimating the temperature of the river water and also take into consideration the amount of river discharge, we find that in 1924 and 1926 the quantity of water emptied into Long Island Sound was much greater than in 1925, and its temperature was decidedly below normal, while the smaller discharge in 1925 had a temperature several degrees above normal. This applies especially to the months of April, May, and June, while during July and August, 1925, the river discharge was greater and its temperature approximately 71° F., which is virtually normal temperature for this period. During these summer months the river water reaches its maximum temperature for the year, which generally is greater than the mean monthly air temperature for each drainage basin. The river discharge in July, 1925, served to reduce the salinity of the water in Long Island Sound and to increase its temperature to a greater extent than did the smaller discharge in 1926. The tables of salinity and water temperatures for these two months show clearly how the amount and temperature of river discharge affected these conditions.

The prime factors influencing the amount of river discharge are quantity, intensity, and distribution of precipitation over each drainage basin. Records of precipitation along the coast must be taken into consideration, together with the discharge of these two large rivers, in order to arrive at an approximation of the quantity of fresh water that directly and indirectly, is emptied into Long Island Sound. Along the coast of Connecticut is a belt of approximately 1,300 square miles that is drained by a great many small rivers, and for this region precipitation records must be used because figures of river discharge are not available.

During the spring and summer months the drainage of fresh water from an area of over 13,000 square miles to the north of Long Island Sound is important because (1) it increases the temperature of the water over the oyster beds and (2) brings down organic matter and mineral salts, both of which increase the production of plankton

BIOLOGICAL OBSERVATIONS

CONDITION OF THE GONADS OF THE OYSTER

Oysters in Milford Harbor were found to be ripe in the period from July 1 to 15, the exact time varying in accordance with the previous water temperatures. In 1925 the gonads of the oysters were fully ripened by June 29, while in 1926 and 1927 this condition was not found until nearly the middle of July. By stripping the oysters, a small quantity of ripe eggs and sperms almost always can be found by July 1, but this can not be taken to indicate that the reproductive products are fully developed. The test employed for this purpose, which proved most reliable, was to place at least a dozen oysters in water that was pumped at high tide and warmed to a temperature of at least 25° C. Under these conditions ripe oysters invariably spawned and discharged the bulk of their products, while those that were not fully ripe generally did not spawn or, at most, spawning consisted in a few contractions of the shell and the release of but a small quantity of spawn. According to Galtsoff (unpublished report), the addition of sperm to the water will induce spawning, and, in case the oysters failed to spawn voluntarily, a small quantity of sperm from two to three oysters was added in order to accelerate the process in case the temperature was not a sufficient in-

fluence. Samples of the oysters always were examined before and after the tests so as to determine the approximate amount of spawn retained or released. In these examinations several transverse sections were cut through the body of the oyster so that the thickness of the reproductive tissue could be seen easily. In comparing these sections from year to year a very noticeable difference was found in the quantity of spawn in oysters taken from the same bed each season. In the sections cut anterior to the heart the layer of reproductive tissue surrounding the liver was found to vary

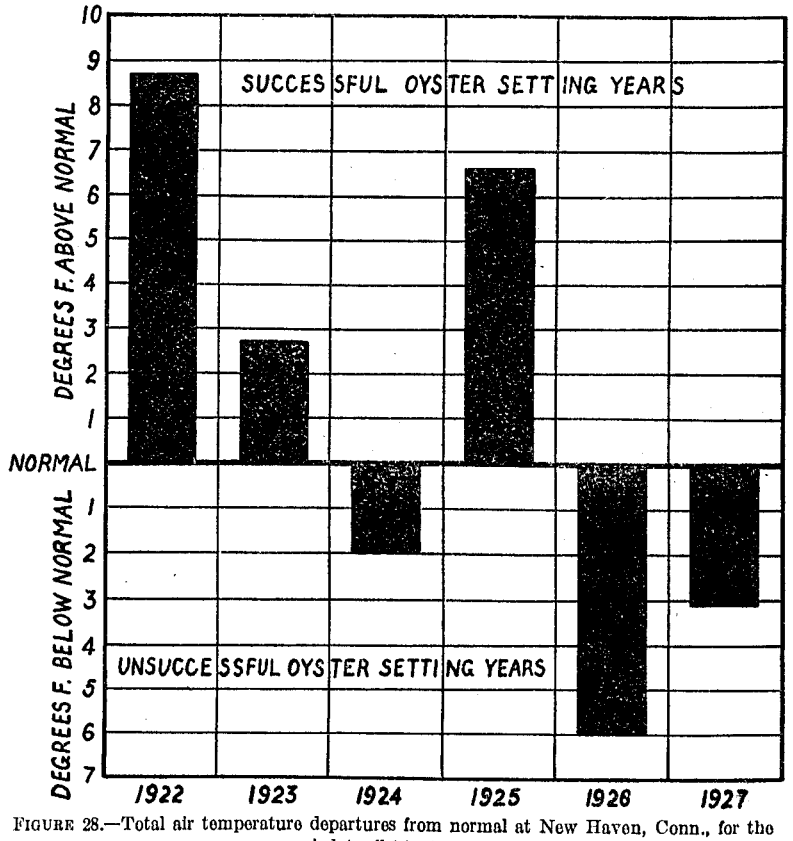

FIGURE 28.—Total air temperature departures from normal at New Haven, Conn., for the period April 1 to August 1

from over 1.5 centimeter in 1925 to 0.5 centimeter and less in 1926 and 1927. A noticeable difference was also found in the consistency of this layer, which in 1925 was extremely soft and milky, while just the opposite condition was found the other two years.

In order to determine the cause of this annual difference in the quantity and ripeness of the spawn as observed on July 1, water and air temperatures were examined during the preceding spring months. By using the departure of air temperature from normal as a basis and estimating the approximate water temperatures at 2° below the temperature of the air, we find that for the period April to July 1 the water temperature in 1925 was several degrees above normal, while in 1926 and 1927 it was decidedly below. This is illustrated by Figures 8 and 28, which show the monthly

and total departure of air temperature from normal for this period during these years and also for 1922, 1923, and 1924. In Figure 28 the total monthly departures for this 4-month period has been given because of the cumulative effect of water temperature on the development of the gonads during this interval. It can be seen clearly that in 1922, 1923, and 1925 the water temperature was *above* normal, and we know, because of the set obtained, that spawning in Long Island Sound was successful in these years. In 1924, 1926, and 1927 the water temperature was *below* normal and setting was a failure This evidently was due to unsuccessful spawning, because virtually no oyster larvæ were found in the water. The success or failure of spawning in Long Island Sound apparently depends upon the quantity of eggs and sperm developed by the oysters each year. Since fertilization of the eggs takes place outside of the oyster and is a matter of chance, it is reasonable to expect that the percentage of eggs fertilized and number of larvæ and spat produced will vary according to the amount of spawn released. A small increase or decrease in the number of eggs or spawn in a single oyster becomes of importance when we realize that it is multiplied by the number of oysters on the beds, which is from approximately 125,000 to 250,000 for each acre planted.

It is likely that the fullness of gonad development is dependent on the amount of food consumed by the oyster. We know that the process of feeding consists in filtering water through the gills, and that the amount filtered is controlled by temperature. Galtsoff has measured accurately the amount of water filtered by the oysters at various temperatures. Taking his figures (Galtsoff, 1928), we can estimate the differences in quantity of water filtered by the average oyster during cold or warm seasons. The period in which we are interested extends from the beginning of feeding (about April 15, when the water temperature reaches 7° C.) until the time of spawning (the latter part of July). During this period the approximate number of liters or quarts of water filtered by an average oyster at normal water temperatures is given in the following table:

TABLE 11.—*Approximate quantity of water filtered by an average oyster at normal water temperature*

Month	Quantity filtered		Mean temperature, ° C.
	Liters	Quarts	
April	25	26	[1] 9
May	408	431	12
June	816	862	17
July	995	1,051	20
Total	2,244	2,370	

[1] 15 days only.

As a result of the monthly and annual variations in water temperature that occurred from 1922 to 1927, the quantity of water filtered shows a corresponding variation, which is presented in the following table:

TABLE 12.—*Approximate number of liters of water filtered by an average oyster in Milford Harbor*

[S=successful setting; F=failure in setting]

Year	Liters of water per month				Total
	April	May	June	July	
Normal	25	408	816	995	2,244
1922	51	612	893	995	2,551 S
1923	46	408	918	969	2,341 S
1924	26	326	765	995	2,112 F
1925	102	408	969	969	2,448 S
1926	0	357	688	995	2,040 F
1927	10	325	765	1,005	2,105 F

In comparing the various years, we find that when spawning and setting were successful, each oyster filtered from 200 to 500 liters of water more during the 4-month

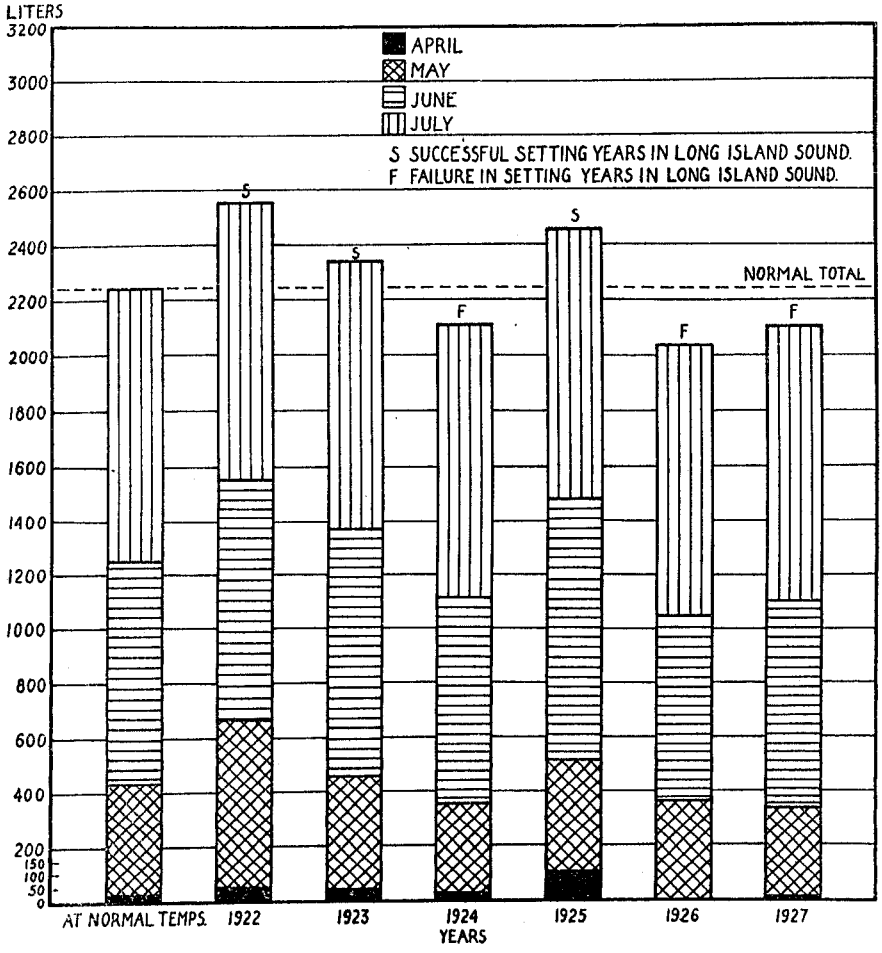

FIGURE 29.—Approximate quantity of water filtered monthly by an average oyster previous to the time of spawning. The quantity filtered during the years 1922 to 1927 is shown in comparison with the quantity that would be filtered under normal water-temperature conditions

period than it did during the years when spawning apparently was a failure. The difference in total quantity of water filtered each year is shown clearly in Figure 29.

The average of the "successful" years shows that the total quantity filtered by one oyster during this time was 203 liters more than the amount filtered at normal temperatures, while the average of the "failure" years was 159 liters *less* than the normal amount. In the following table the average liters of water filtered monthly and the total number of liters filtered during the successful and unsuccessful years are given.

TABLE 13.—*Comparison of the quantity of water filtered by an average oyster during setting and non-setting years in Long Island Sound*

Setting	Average number of liters					Departure from normal, liters
	April	May	June	July	Total	
Success	66	476	927	978	2,447	+203
Failure	12	336	739	998	2,085	−159

During the three years when air and water temperatures were above normal we should expect to find a greater quantity of spawn in the oysters because of the direct influence of higher temperatures on the development of the gonads and because of the greater feeding activity on the part of the oysters. The time when oysters are found to be ripe also varies from year to year and can be correlated with previous water temperatures. The condition of the gonads observed in 1925, 1926, and 1927 support these views and show that the development of the gonads was greater and time of ripening earlier when water temperatures were above normal, as in 1925, while the opposite was true in the other two years, when temperatures below normal occurred.

TIME OF SPAWNING

The time when the ripe oyster discharges its spawn into the water depends largely upon temperature. Studies of oyster spawning in Milford Harbor, as well as those of Galtsoff (unpublished manuscript, 1926), Churchill (1919), Nelson (1924), and Gutsell (1922), show that spawning seldom occurs when the water temperature is below 20° C. In many instances in 1925 and 1926 spawning was observed to take place in tanks and floats at temperatures ranging from 20° to 27° C. The oysters used in these experiments came from Milford Harbor and the offshore beds in Long Island Sound. It was found that those from the Sound, where the water temperature is much lower than in the harbor, spawned in about half an hour at 20° to 22° C., while the oysters from the warmer harbor waters required several hours' exposure to this temperature before spawning occurred, or, on the other hand, they could be induced to spawn in half an hour by increasing the temperature from 23° to 27° C.

The time of spawning of the oyster on the beds was determined, first, by examination of the plankton samples for the presence of larvæ 24 to 48 hours old and, second, by observations as to the quantity of spawn in the oysters. In Connecticut waters there generally occur two spawnings, the first being very light and occurring about the middle of July, while the second is heavier and occurs about the 1st of August. The time of spawning was found to vary somewhat from year to year in accordance with water temperature and tidal conditions. The dates on which spawning occurred

in 1925 and 1926 and its relation to tide and temperature are shown in Figure 30. Heavy and complete spawning of the harbor oysters occurred on July 13 in 1925, but not until August 1 in 1926. Similarly, spawning in Long Island Sound at Station No. 6 was 17 days earlier in 1925 than in 1926. In 1925 spawning occurred more than

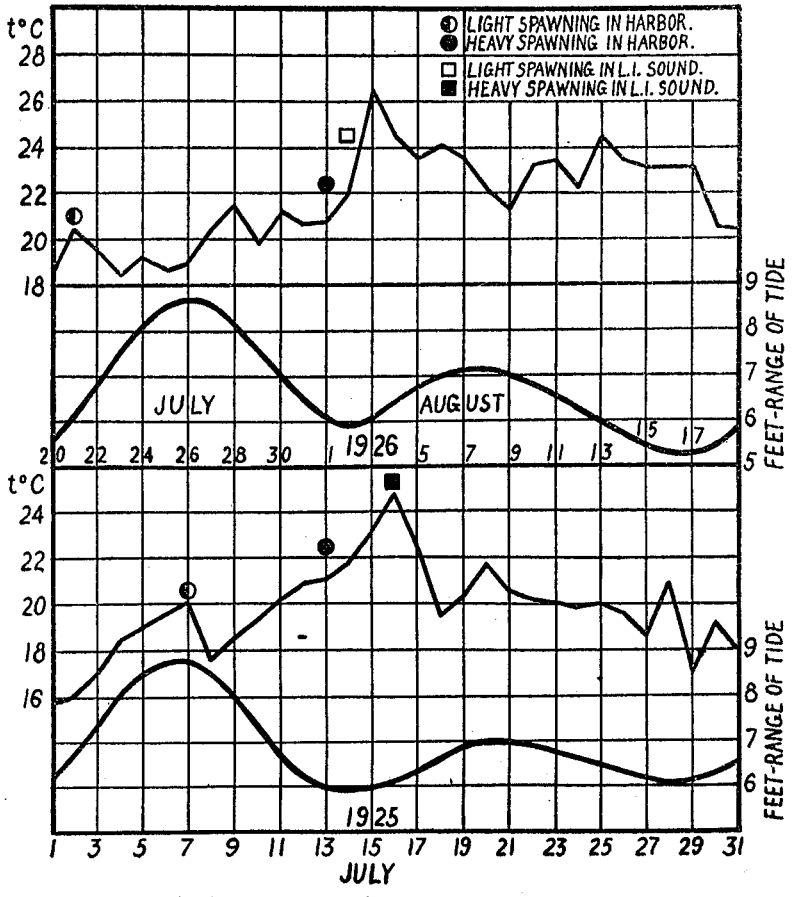

FIGURE 30.—Correlation between range of tide, temperature, and the spawning of the oysters during the summers of 1925 and 1926

two weeks earlier than has been observed during the past seven years and was due to the higher water temperature and early ripening of the oysters during July of that year. Though in 1926 the water in the harbor reached a temperature of 22.4° C. on July 10, spawning did not occur, as the oysters were unripe at this time. During both years the heaviest spawning of the oysters in the harbor was found to occur after the water had reached and maintained for a few days a temperature of from 20° to 21° C.

The part played by the tide in increasing water temperatures during July and August has been discussed previously, and its relation to the time of spawning in 1925 and 1926 is shown clearly in Figure 30. In both years, the majority of the oysters spawned at the end of the July "full-moon tidal period," when the water was brought to a favorable spawning temperature. In 1927, spawning of the oysters

in Milford Harbor was studied in relation to the moon's phases and the range of tide. The oysters were found to have spawned (as indicated by the presence and age of larvæ) on July 22, which was also at the end of the "full-moon tidal period," or eight days after the time of full moon. Fifteen days later, setting was found to occur not only in Milford Harbor but also in Southport Harbor, Conn., and several other inshore areas that were examined. The relationships between the moon's phases and time of spawning depends largely upon the range of tide occurring during any particular phase. Whether spawning will take place during or at the end of the periods of greater tidal range is determined by the water temperature at the beginning of the period and the weather conditions accompanying it. The effect of the tide on the trend of water temperatures has been discussed on page 449.

In this connection, the studies of J. H. Orton in 1925 at Falmouth, England, on the lunar periodicity in the spawning of the European oyster (*Ostrea edulis*) are very interesting. He found that spawning of the European oyster can be correlated with the moon's phases but was unable to determine the direct factors controlling spawning at such times, though he suggests tide, moonlight, food, temperature, and sunshine. Unfortunately, he did not obtain water-temperature records for the locality in which the observations were made, and consequently, the relationship between increase of water temperature and range of tide could not be determined. We know from the tide tables that the spring range of tide at Falmouth, England, is nearly 16 feet, more than twice that in Milford Harbor. Under these conditions, it is likely that the water over the Falmouth beds would show a marked increase in temperature during spring tide periods because of the warming of the water on a greater area of tidal flats at such times. It is interesting to note that he found the maximum percentage of recently spawned oysters in the week after full moon, which corresponds very closely to the spawning observations made at Milford on the American oyster. Also, the first and apparently heaviest spawning at Falmouth occurred on virtually the same date in July, 1925, as did the heavy spawning at Milford. On the basis of our observations, we can state that oyster spawning in Milford Harbor occurred at the end of the full moon tidal periods because of the increase in water temperature that is produced as a result of the greater range of tide during this period. The effect of the moon on the spawning of the American oyster is only indirect through the changes it produces in the vertical and horizontal movement of the water over the oyster beds. The effect of the tide on water temperatures and spawning in any locality depends largely upon hydrographic conditions and especially the tidal range and area of tidal flats.

Another important observation made on oyster spawning in the harbor was that the discharge of spawn occurs near or at the time of high water. From July 21 to 29, 1926, the water temperature on the last of ebb tide and at low water was often from 20° to 26° C., and yet the oysters failed to spawn. The same oysters, when placed in water pumped at high tide and warmed to the same degree, spawned in a very short time. It was observed also that oysters kept in the floats always spawned near the time of high water, at temperatures ranging from 20° to 24° C., and never at low water, though it was several degrees warmer. In analyzing the factors of temperature, salinity, and hydrogen-ion concentration at the time when spawning occurred, it was found that the hydrogen-ion concentration or pH value of the water showed the greatest difference. In all the observations but one, the

water had a pH value ranging from 7.8 to 8.2 when spawning occurred, while in the exceptional case the pH was 7.6 and the water temperature 23° C.

As shown in Figure 26, the pH value of the water in Milford Harbor is lowest at the time of low water, when the pH is approximately 7.2, and is highest near the period of high water, when the pH averages about 8.2. The failure of the oysters to spawn at low tide, when the water temperature is often above 20° C., evidently is due to the low alkalinity of the water at this stage of tide, as indicated by the pH readings. Spawning was found to occur near the times of high water at this same temperature, when the alkalinity was much higher or when the pH value was 7.8 or above. In 1925, the heaviest spawning took place on the day when the water at the times of high tide had attained a temperature of 20° and 21.5° C., and in 1926, when the temperature at the same stage of tide was 20.5° and 21° C.

In summarizing the studies of spawning in Milford Harbor, it is concluded that the most important controlling factors are the temperature of the water, the range of tide, and the hydrogen-ion concentration.

OCCURRENCE AND DISTRIBUTION OF THE LARVÆ

For several years, studies of the oyster larvæ in Connecticut waters have been carried on by various investigators of the bureau (Churchill and Gutsell, unpublished reports), and extensive plankton collections were made in the region between Bridgeport and New Haven. In these collections the abundance and distribution of the larvæ were extremely irregular, and in the majority of the samples no larvæ could be found. In locating stations over this comparatively large area such a variety of changes in the physical conditions is encountered that the results at each station are hardly comparable and there are insufficient data for the study of any one locality.

The plan that was put into operation in 1925 consisted (1) in the rehabilitation of a natural oyster-growing body of water, such as Milford Harbor, by the establishment of spawning beds and (2) in an intensive study of the occurrence and distribution of the oyster larvæ in this restricted area in relation to the physical conditions existing there. Both quantitative and qualitative plankton samples were collected, together with data as to temperature, salinity, and stage of tide. The oyster larvæ were found in two rather distinct groups, the first of which was rather small in number and appeared on July 8 and 9 in the straight-hinge stage, which indicates that light spawning occurred on July 7; while the second or larger group of larvæ was found in the water on July 14 following a heavy spawning of oysters on July 13. The duration of the larval period in the first group was approximately 13 days, with a mean daily water temperature of 20.8° C., while in the second group the period from spawning to setting was 16 days at a mean water temperature of 20.6° C. The completion of the larval period, with setting of the larvæ on the 20th and 29th of July in 1925, occurred approximately two weeks earlier than had been observed at any time previous and can be attributed to the higher water temperatures of that year.

In 1925, 130 plankton samples were collected at the various stations from both the surface and bottom. The results obtained from these collections were much different than had been expected, and the oyster larvæ not only were scarce but occurred very irregularly. The majority of the larvæ found were either a day or two old or nearly fully developed and ready to set. The number of larvæ at any station,

in proportion to the intensity of setting, was extremely small, as, for example, at Station 3, where the total number collected in a period of several weeks scarcely reached 100, while in the same spot many thousands of them were found later attached to the shells and brush. In studying the occurrence of the larvæ in relation to the stage of tide when the sample was taken, a rather definite relationship was found to exist; namely, that the larvæ were most abundant near and at the period of low water and generally absent at the time of high water. In 1926 the methods of collection were changed and planned so as to permit study in greater detail of the occurrence of the larvæ in relation to stage of tide. For this purpose two quantitative methods of plankton collection were employed, one of which was to take 3 samples of 50 gallons each from the top, bottom, and middle zone at each stage of the tide, and the other was to pump the water continuously from a point 1 foot below low-water mark (which corresponded to the level of the spawning bed) and determine the number of larvæ present at each hour of the day and height of the tide. In 1926 the larvæ were found in the samples at a much later date and again occurred in two rather distinct "schools" or groups following light spawning on July 22 and heavy spawning on August 1. The larval period of the first group was approximately 16 days at a mean temperature of 21.3° C., and of the second group was 14 days at 23.2° C. During this summer, more than 185 plankton samples were collected, the majority of which were taken in Milford Harbor within a short distance of the spawning bed and especially over the area of heaviest setting.

DISTRIBUTION

The abundance of the larvæ from the surface of the water to the bottom was found to vary according to the stage of tide, which for convenience was divided into three arbitrary periods—namely, low water, intermediate, and high water—each of which covers an interval of four hours. The low-water period covers the last two hours of ebb tide, slack water, and the first two hours of flood tide. The intermediate period included the two hours of flood tide and two hours of ebb tide when the tide was approximately halfway between high and low water marks. The high-water period consisted of the last two hours of flood tide, slack high water, and the first two hours of ebb tide. At mean range of tide the vertical movement of the water during the low-water period is approximately 1½ feet; during the intermediate period, 3½ feet; and during the high-water period, 1½ feet.

In 140 samples made with reference to the tide the larvæ were found to be most abundant during the low-water period, virtually absent during the intermediate period, and present only in small numbers during the high-water period. In the following table the average number of larvæ per 50 gallons that were collected during three complete tidal cycles from August 11 to 13, 1926, is given as an example. In this table the counts of the larvæ include only those that have passed the straight-hinge stage, or, in other words, "umbo" larvæ that were from 3 days old to setting size; and, of these, the majority in nearly every case were found to be in late stages of development and within a few days of setting. The only time when umbo larvæ of different ages were found swimming in the water was at the time of low slack water and even then the older forms predominated.

TABLE 14.—*Vertical distribution of oyster larvæ in Milford Harbor in relation to the stage of tide, August 11 to 13, 1926* [1]

Period of tide	Average number of larvæ per 50 gallons			
	Surface	Mid-zone	Bottom	Total
Low water:				
Last ebb	2	7	12	21
Slack water	15	18	19	52
First flood	22	13	6	41
Intermediate:				
Flood	1	1	3	5
Ebb	0	0	1	1
High water:				
Last flood	0	2	2	4
Slack water	3	3	7	13
First ebb	1	0	3	4

[1] Figures refer only to number of "umbo" larvæ collected during three tidal cycles.

One thing the table clearly shows is the general scarcity of swimming oyster larvæ in this small harbor, where later many hundred thousands were found attached as spat. It can be seen that the vertical distribution of the larvæ during the low-water period as a whole was comparatively uniform, and approximately the same number was found in each sample taken from the surface to the bottom. However, upon further examination of each stage of this period, a noticeable variation in the distribution according to tidal movement was found at the time the sample was taken. On the last of ebb tide the larvæ were found to be most abundant in the bottom and mid-zone samples; at low slack water there was practically no difference in the numbers of larvæ at each depth; while in the first of flood stage the larvæ were most abundant in the surface samples. During the intermediate period only a few larvæ were found, and these were chiefly small larvæ that occurred most frequently in the bottom samples. In the samples taken during the high-water period the larvæ were also much less abundant than at low water and occurred mostly in the bottom and middle zone. The results obtained from this series of plankton collections are presented graphically in Figure 31, which shows the distribution and abundance of the oyster larvæ in relation to the height and stage of the tide.

If we classify all the plankton collections made in the harbor in 1925 and 1926 according to the stage of tide, and include also the straight-hinge larvæ, we find that the distribution of the larvæ is similar to that shown in the previous table. In the collections as a whole the straight-hinge larvæ were the most abundant, and, though a certain number were collected at nearly all stages of the tide and at all depths, they also were found to be most numerous during the low-water period, and their abundance in any zone was much the same as that of the older or "umbo" larvæ. One thing in Figure 31 that deserves notice is that the oyster larvæ are extremely scarce during the intermediate period or at the times when the vertical movement of the water is greatest.

By means of the second quantitative method employed the concentration of the larvæ at the level of the oyster bed—that is, 1 foot below low-water mark—was determined hourly according to the stage and height of the tide. In the following record for August 11, 12, and 13, 1926, the number of larvæ collected in each hourly sample of 200 gallons is given, together with the tidal data.

TABLE 15.—*Concentration of umbo larvæ in 200-gallon hourly samples taken at the level of the oyster bed*

Sample No.	Stage of tide	Height of tide (feet)	Number of larvæ per sample			
			Aug. 11	Aug. 12	Aug. 13	Total
1	Low water	0	65	74	81	220
2	First flood	1.0	120	91	106	317
3	Flood	2.2	8	5	11	24
4	do	3.8	0	0	0	0
5	do	5.0	0	1	1	2
6	Last flood	6.0	1	0	3	4
7	High water	6.2	4	2	5	11
8	First ebb	5.4	2	3	1	6
9	Ebb	4.0	0	0	1	1
10	do	2.8	0	2	0	2
11	do	1.6	2	3	4	9
12	Last ebb	.8	15	11	23	49
13	Low water	.4	54	45	67	166

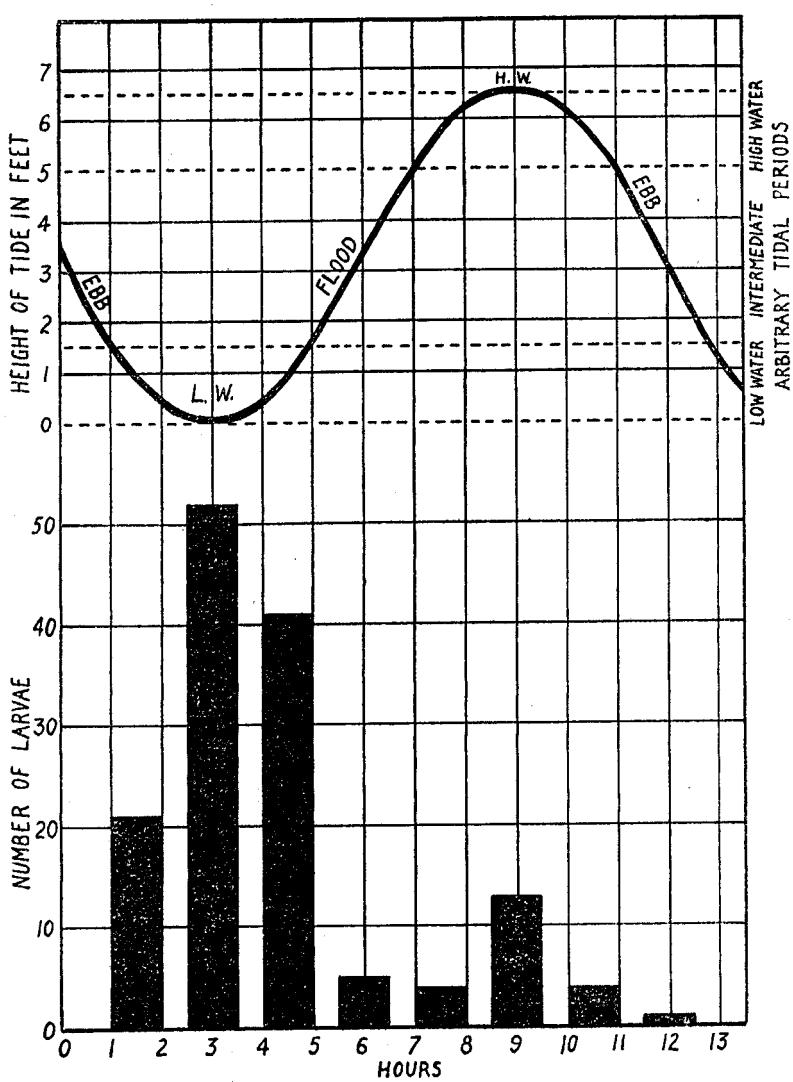

FIGURE 31.—Distribution and abundance of the oyster larvæ in relation to the stage of the tide

These collections were made a few days before heaviest setting occurred in 1926, and consequently the majority of the larvæ were full grown and were retained by the 80 and 100 mesh screens. The greatest concentration of larvæ in the hourly samples was found at the time the tide changed from low slack water to flood, when an average of 106 larvæ per 200 gallons of water were collected. This finding is quite significant in view of the fact that this is also the particular level or zone in which the heaviest setting was observed to occur. In comparing the results of both quantitative methods for the same days, we find that they are very similar and show that the largest numbers of oyster larvæ are swimming in the water in Milford Harbor during the "low-water period." In making the plankton collections from August 11 to 13, 1926, there were no unusual meteorological conditions and the range of tide was approximately 6½ feet, which is about equal to the mean daily range for this locality.

Since a general scarcity of swimming larvæ was found in the plankton collections, the question naturally arises as to where the large numbers of larvæ come from or remain that later are found attached as spat in the same areas. Two possible explanations of this phenomenon could be advanced: First, that the oyster larvæ were carried into the harbor by the flood tide from the sound, and second, that the larvæ were lying on the bottom during the greater part of the time. To investigate the first possibility, it was necessary to determine (1) the horizontal distribution of the oyster larvæ during the low-water period and (2) the occurrence and abundance of the larvæ during the flood-tide interval at Stations Nos. 4, 5, and 6, which are located outside of the harbor.

In the following table, the horizontal distribution of the larvæ during the period of low water is shown for Milford Harbor and vicinity. In this series, made on July 25, 1925, the majority of the larvæ were fully developed and were retained by the 80 and 100 screens.

TABLE 16.—*Horizontal distribution of larvæ at low water on July 25, 1925, for Milford Harbor and vicinity*

Station No.	Hour (a.m.)	Number of larvæ per 50 gallons		
		Top	Bottom	Total
6	8	16	23	39
5	8.30	2	0	2
4	8.50	18	11	29
3	9.20	35	26	61
2	9.45	27	13	40
1	10.10	8	5	13

At Station No. 6, which is located in Long Island Sound 1 mile distant from Milford Harbor, there is a large spawning bed, and here we find the larvæ fairly abundant at low water. At Station No. 5, which lies halfway between the harbor spawning bed and that at Station No. 6, the oyster larvæ were found to be virtually absent not only in the series taken at low water, but also in the samples taken at all stages of the tide during both summers. The larvæ were found in greatest abundance at Stations 2, 3, and 4 located close to the harbor spawning bed, which is the area where later the heaviest setting occurred. In their horizontal distribution we find

the oyster larvæ present in greatest numbers at stations near the spawning beds and which are heavy setting areas.

The plankton collections of 1925 and 1926, which were made during flood tide at Stations 4, 5, and 6 contained, on the average, less than 2 larvæ per 50 gallons. From studies of the distribution of the larvæ at various stages of the tide in both the harbor and the Sound, it is evident that since the larvæ are absent during flood tide they could not be carried into the harbor from Long Island Sound.

The second possibility (that the larvæ were lying on the bottom the greater part of the time) was studied next by collecting thin layers of bottom at Station No. 3, near the spawning bed. The area of bottom covered by each sample was approximately 4 square feet, and the thickness of the layer that was removed was about one-fourth inch. The samples were taken during half-flood and half-ebb stages of the tide, when no larvæ could be found swimming in the water. In all, 12 bottom samples were collected, 4 of which were made in 1925 and the remainder in 1926. The bottom samples were placed in wood tanks filled with sea water and allowed to settle, after which a small stream of filtered sea water was maintained in the tank and the overflow strained through a No. 20 bolting-silk net. Oyster larvæ were obtained from all of the samples, the number per sample ranging from 15 to 147. The total number of larvæ collected in the 12 samples was 662, the average being 55 larvæ per 4 square feet of bottom. This number of larvæ on a given area of bottom is small as compared to the number of spat that were found near by on the shells and other collectors, and may be due to the fact that the samples were taken from clean and smooth areas that contained no shells or other objects that could obstruct the currents. The finding of oyster larvæ on the bottom at certain stages of the tide shows that they are not passive planktonic forms, and therefore are not subject to wide dispersal by the tides and currents. By remaining on the bottom during the greater part of the larval period, and by limiting their swimming activities to the tidal periods, when horizontal movement of the water is least, the oyster larvæ are able to remain and set on and near to the spawning bed that produced them.

One of the important questions that has presented itself in the study of the oyster is, Where does the spawn or larvæ from a bed of oysters finally attach or set? The greater production of oyster larvæ and spat in Milford Harbor following its rehabilitation has shown definitely, during the past three years, that oyster larvæ are not distributed far from the spawning bed by the currents, the predominating drift of which is out of the harbor. The final distribution of the larvæ can be determined easily by studying the relationship of setting areas to spawning bed. It has been found that the majority of the larvæ set within a radius of 300 yards from the center of the spawning bed and that the greatest number of spat per square inch or per shell is to be found on the bed within a radius of 100 yards. As indicated by setting, the larvæ are distributed both above and below the spawning bed and attach in greater numbers on the areas that are below or in the direction of the Sound. Though the intensity of setting varies from year to year, the distribution of the larvæ was found always to have this same relation each year to the spawning bed.

The occurrence and distribution of the oyster larvæ in Milford Harbor was entirely different from that found in Great South Bay, Long Island, by Churchill and Gutsell (1920 and 1921; unpublished reports) and by Nelson (1922) in Barnegat

Bay, N. J. In these bodies of water, which are quite similar, they found that oyster larvæ are abundant and actively swimming at all stages of the tide and are about evenly distributed from the surface to the bottom during the entire larval period. In order to determine the possible cause for this difference, a comparison was made of the physical conditions in each locality. Various factors, such as temperature, salinity, and hydrogen-ion concentration, were found to vary slightly but gave no indications of being controlling factors. The chief difference appeared in the tidal range and the velocity of the tidal currents in each body of water. In both Great South and Barnegat Bays the mean range of tide is approximately 1 foot and the tidal currents are very weak, while at Milford the mean range is 6.6 feet and the tidal currents attain considerable velocity, as shown previously. Since the oyster larvæ were found to be most abundant in the harbor during slack-water periods, it is probable that the current velocity is an important controlling factor. To test this, a few experiments were made during the past summer, in which the swimming movements of the larvæ were observed in relation to the current. For this purpose, an elliptical wood tank of 1,000 gallons capacity, in which larvæ were being reared, was employed, and tests were made as to the presence of the larvæ when the water stood or was in circulation. The velocity of the current created in the tank was 0.5 foot per second at the surface and 0.3 foot on the bottom. The average results obtained in four experiments are given in the following table:

TABLE 17.—*Abundance of oyster larvæ in a tank when the water is standing or in circulation*

Test	Condition of water	Number of larvæ per 200 gallons	
		Surface	2 inches above bottom
1	Standing	114	320
2	Circulating	2	3
3	Standing	154	268
4	Circulating	0	2

Additional tests were made at various points in the tank during circulation to see if the larvæ had collected in eddies or in the center, but none could be found at any place except on the bottom of the tank. The results of these experiments indicate that oyster larvæ cease swimming and settle to the bottom in currents having a velocity of approximately 0.5 foot per second. In comparing this with conditions in the harbor, we find that the larvæ were most abundant in the slack-water periods, especially at low water, when the current velocity ranged from 0 to 0.6 foot per second. When the velocity of the current exceeded this figure, the larvæ were absent from the water and were found on the bottom. The correlation between the distribution and abundance of the larvæ and the current velocity enables us to understand how the natural development and growth of the oyster beds has been possible in many harbors and estuaries where the tidal movement and river drainage would soon carry away free-swimming organisms.

In many coastal regions we find prolific oyster beds in swift running rivers that empty directly into the ocean and have currents that are many times stronger than

those in Milford Harbor. The drift of the water in these streams is decidedly seaward, and the fact that under such conditions the oyster larvæ remain and set there strongly indicates that they are not actively swimming at all times. The experiments with drift bottles and the current measurements in Milford Harbor (mentioned on pp. 452 to 455) have shown that the horizontal movement of the water during ebb was much greater than during the flood, and that floating objects carried out of the harbor by the ebb current never were returned by the flood. A similar excess of ebb over flood in tidal movement can be found in nearly all of the bays and rivers emptying into Long Island Sound, and these are the very places where in the past the most prolific natural beds were found to exist.

One of the theories advanced by the oystermen to explain the continued failure of setting in Long Island Sound is that the inshore and harbor areas supply larvæ and spat for the deep-water beds in the Sound; and since the depletion of these inshore areas, oyster setting in the Sound has been a failure. Such a theory is contradicted by (1) the location of the natural beds, as shown in Figure 2; (2) the general set of 1925, when there were very few oysters on the inshore areas; and (3) the distribution of the oyster larvæ and setting in Milford Harbor in relation to the spawning bed.

In recent years, when oysters were plentiful on the natural beds, setting oftentimes failed on the leased bottoms lying outside of them in the Sound. The fact that during the past centuries the natural beds were not extended into the deeper waters of the Sound strongly indicates that oyster larvæ were not distributed freely by the currents over these areas. In 1925, oysters in sufficient quantity to produce the set that was obtained could be found only on the planted beds in the Sound, and the production of a greater number of larvæ by these oysters is the only logical explanation that can be given for successful setting during that year.

In many cases the failure of setting has been attributed to a mortality of larvæ as a result of sudden changes in temperature or salinity and to heavy rainstorms. In the studies of physical conditions in Milford Harbor during the larval period it has been found that many changes in temperature of 5 to 11.5 degrees in 24 hours and in salinity from 5 to 25 per mille produced no noticeable decrease in the numbers of larvæ present in the water. During the larval period in 1925 and in 1927 the precipitation was several inches above normal, and a tremendous amount of fresh water was discharged into Milford Harbor. The changes in salinity and the increased velocity of the ebb current following these storms apparently did not kill the larvæ or carry them out of the harbor. These studies show that oyster larvæ can withstand extreme changes in temperature, salinity, and hydrogen-ion concentration of the water and are not widely distributed by the tides and currents.

SETTING

A most important and significant period in the life history of the oyster is that during which the larva sets or attaches itself to some clean, firm surface, such as shells or stones. The act of setting was observed many times by the author, and it was possible to view this interesting process from several angles by causing the larvæ to attach themselves to glass slides. To accomplish this, the fully developed larva releases a fine, threadlike byssus, or anchor, which adheres to the first suitable

surface with which it is brought in contact. The larva then ceases swimming and crawls over the surface by means of its long muscular foot, at the same time laying down the byssus behind it. After crawling about for a short time, the larva comes to a standstill, ejects a quantity of cement on its left side, and quickly brings the lower or left valve into contact with the cement-covered surface. The foot is used in bringing the shell in contact with the substratum and holds it in position for about one minute. This short interval of time is all that is necessary for complete hardening of the cement and setting of the oyster larva. Immediately following fixation, a metamorphosis occurs, and the larva develops into a spat with organs similar in structure to those of the adult oyster. At this time the newly formed spat is of the same size as the fully developed larva and measures 0.33 of a millimeter, or approximately one seventy-fifth of an inch through its greatest diameter. In shape it closely resembles a hard clam and has an amber-colored, irridescent shell, near the center of which can be seen a small, deeply pigmented spot. The spat grows rapidly and in one week is over five times its original length and in two weeks over twenty times, when it reaches a length of about 7 millimeters, or one-fourth inch. Spat of this size can easily be seen on the shells and other collectors and were the smallest to be counted in the field observations with regard to the number attached on a given area of surface.

In the studies of the distribution of setting, various types of spat collectors were used, such as tiles, brush, tar paper, and containers filled with oyster, clam, scallop, and mussel shells. The collectors were arranged so as to cover the entire zone from the bottom of the channel to high-water mark, a vertical distance of approximately 17 feet, of which the upper 5 to 9 feet are exposed by the tides. In addition, four ropes, to which tiles were attached, were suspended from an oyster float anchored near the beds.

Setting in Milford Harbor has been observed to occur from July 20 to September 1, but is generally most intensive during August, the peak occurring about the middle of the month. It was found that setting was not a continuous process, as there occurred definite periods of setting that followed spawning by about two weeks. The first set that occurs is early and extremely light and is followed by a heavy and final set about 8 or 10 days later. For example, in 1925 there were 10 to 15 spat per shell at Station 3 in the light set and from 150 to 250 spat per shell in the heavy set. An examination of the shell samples taken up daily showed that the majority of the larvæ from a single spawning became attached within a day or two of each other. In 1926 the heavy set occurred on August 16, which is representative of the average time of setting for this region. In 1925 spawning and setting occurred two weeks earlier than usual, and the heavy set was observed on July 29.

The number of spat produced in the harbor each year varied considerably, though the size of the spawning bed was virtually the same in each instance. It was found that the intensity of setting could be clearly correlated with the quantity of spawn in the oysters and the early water temperatures. In 1925, when the temperature was above normal and the oysters contained a large amount of spawn, setting was heaviest, and an average of 15,000 spat per bushel of shells was collected. In 1926 and 1927 we had the other extreme—that is, water temperatures below normal and a small amount of spawn in each oyster, with the result that the average

number of spat collected per bushel was only 2,000 and 2,500, respectively. Such annual variations in the production of seed on both natural and cultivated oyster beds have long been observed and are largely the result of the annual and monthly fluctuations in the physical conditions that have been discussed previously.

DISTRIBUTION OF SET

On a given area of bottom the setting was found to be distributed unevenly and varied in intensity according to the distance from the spawning bed and the depth of water. In the harbor the set was found to occur on such areas as are covered with water when the tide is 2 feet above mean low water mark, with the exception of a small portion above Station 1, where setting occurs rarely because of the discharge of fresh water. In 1925 a set of commercial value was found principally within a radius of 300 yards from the spawning bed, the number of spat ranging from 5 or 6 spat per shell on the outside edge to 200 and 300 per shell in the central portion. The spat were most abundant on shells planted over the spawning bed and within approximately 100 yards of its center. The concentration of spat at the 100-yard circle averaged 50 per shell. Though setting occurred at virtually the same distance upstream, or above the bed, as it did below, it was found to be of slightly greater intensity in the areas lying below or toward Long Island Sound. The horizontal distribution of the set in relation to the spawning bed clearly shows how close the oyster larvæ remain and attach to the place where they were produced. No noticeable difference in the distribution of set from the spawning bed could be found in the last three years. These facts make possible the development of special methods of oyster-seed collection on the same areas where the heaviest setting is found to occur.

The variations in intensity of setting according to depth, or, in other words, the vertical distribution of spat, has been found to be quite peculiar in Connecticut waters. Setting occurs in a zone extending from the bottom of the channel to a point 2 feet above mean low-water mark, while from above this level to high-water mark, a distance of about 5 feet, no setting takes place. The vertical range of setting found in other bodies of water is quite different, as shown in Figure 32. In Great South Bay, Long Island, setting occurs from the bottom to nearly high-water mark, while in South Carolina and Georgia the set is found chiefly between low and high water marks and not below low-water mark. Since the velocity of the tidal current was found to be an important controlling factor in the distribution and occurrence of the oyster larvæ, it appeared likely that it might also exert considerable influence on the distribution of setting. In the studies of the relationship between current velocity and setting it was found that in Milford Harbor the larvæ began to attach at low slack water and continued to do so during the first two hours' run of flood tide until the current had developed a velocity of one-third foot per second, or 20 feet per minute. This was determined not only by plankton collections of fully developed larvæ but especially by observations as to the position of the larvæ on the collectors in respect to the stage of tide and the velocity and direction of currents. The portion of the collectors covered at low water, when there was no current, was found to be covered equally with spat on all sides, while above this level spat occurred chiefly on the lee side or that which was protected from the force of the flood current. Shells

that were put out at low water and taken up after two hours' run of flood tide were the only ones on which newly attached spat had collected.

In Great South Bay, Long Island, the zone of setting can be correlated with the vertical distribution of the oyster larvæ and the current. Here there is virtually no current, and the spat are found attached from the surface to the bottom, which corresponds to the distribution of the larvæ. Tidal conditions similar to South Bay were found in Holly Pond on the Connecticut shore, where the water was impounded for hydraulic power by means of a dam. There are insignificant tidal currents in the pond, as it receives water from Long Island Sound only on the very last of flood tide before high water. An examination of the pond showed that seed oysters were attached in a zone extending from the bottom of the pond to within 1 foot of high-water mark, while just outside and below the dam the vertical distribution of spat was entirely different and the same as found at Milford. In this instance the chief difference in the physical conditions above and below the dam was the velocity of the tidal current, which undoubtedly is an important factor in controlling the zone of setting in both places.

In South Carolina and Georgia waters, where setting occurs between the tide marks, it may also be interpreted on the basis of current velocity, though no actual measurements in this region have yet been made. According to Marmer (1926), the tidal current in the mouths of most bays and rivers is different than in Long Island Sound, and slack water occurs when the tide is about halfway between low and high water marks. This means that in these coastal rivers the current will have zero velocity at about half tide level in the lower portions of the streams. In examining the piling and tidal flats at many points in South Carolina it was found that oyster setting was heaviest about halfway between tide marks and gradually decreased in intensity in the zones a few feet above or below this level in accordance with the increase in velocity of the currents. An interesting observation in this connection was made near Beaufort, S. C., where a bridge was being constructed and cofferdams had been used in laying the piers. An examination was made of several of the steel plates used in mid-channel in the Beaufort River operations and which had been taken up and placed on the wharf. On the outer surface of the plates, the spat were found attached between high and low water marks, a distance of about 6 feet, the distribution being the same as is found on the piling along the shore. However, on the inner surface, the attachment of the spat was quite different and was found to extend from the mud line, or bottom of the channel, nearly to high-water mark, a difference of approximately 16 feet. The extreme difference in the vertical distribution of setting on the outside and inside of the cofferdam apparently was due to the fact that there were no currents within the dam and consequently the larvæ were able to attach there from virtually the surface to the bottom.

Although the vertical range of setting in Milford Harbor is several feet, the intensity or number of spat per square inch at all points or levels is not the same. The relative intensity of setting throughout the zone of attachment is shown in three different localities in Figure 32. In Milford Harbor the actual number of spat attached per square inch at all levels was determined for the set of 1925. The setting was found to be most intensive in a narrow strip extending approximately from a

point 1 foot above the level of low-water mark to 1 foot below it. Here the concentration of spat averaged 25 per square inch of surface. Above this strip, setting gradually decreased in intensity until at a level 2 feet above low-water mark scarcely one spat was found per square inch. From a point 1 foot below low-water mark to the bottom of the channel setting was comparatively light, averaging about one spat per square inch. Directly on the bottom setting was slightly heavier, and an

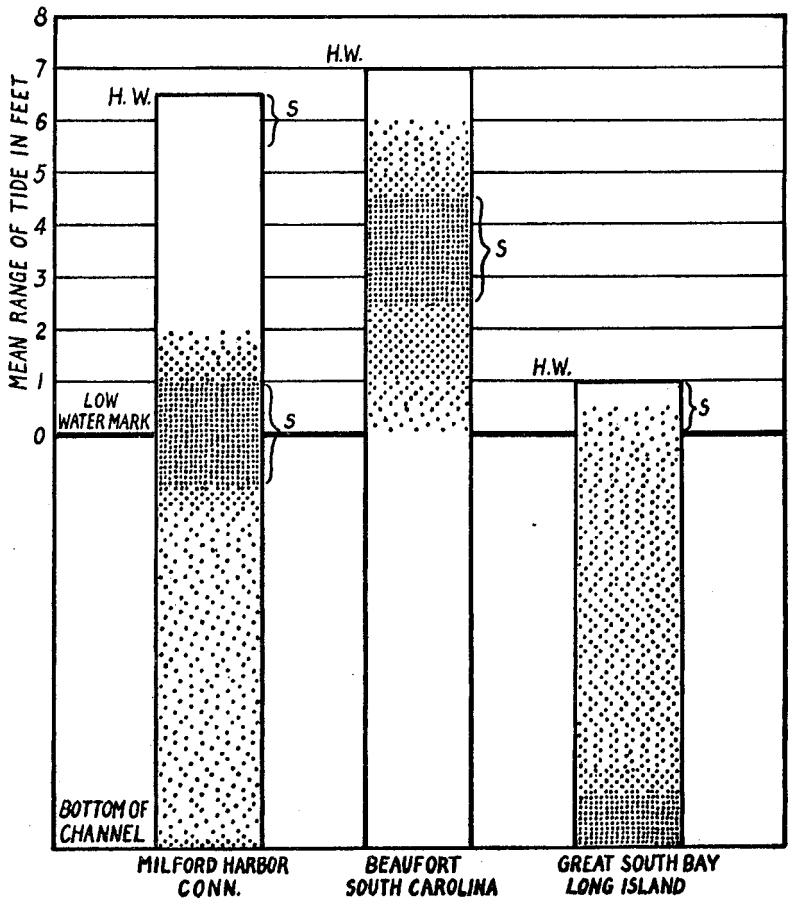

FIGURE 32.—Vertical distribution and intensity of setting of oyster spat in relation to range of tide. H. W.=high-water mark. S.=height of tide when slack water occurs

average concentration of 3 spat per square inch was found. The variations in intensity of setting at different levels can be correlated closely with the distribution and occurrence of the larvæ and the velocity of the tidal currents. During low slack water the zone in which the larvæ are most abundant and where the heaviest setting of spat takes place is that in which the velocity of the current is least, or practically zero. The reason that setting is not of equal intensity from low-water mark to the bottom of the channel can be accounted for by the fact that at low slack water, when setting occurs, the zone of least velocity is at the surface only and does not extend to

the bottom. This is due to the underrun of flood tide along the bottom while the surface strata of less saline water is still on the ebb or at a standstill.

It was found that at low water in Milford Harbor the current velocity increases from zero at the surface to 24 feet per minute on the bottom, where the tide has already been running flood for some time. Under such conditions it is apparent that at any point from the surface layer to the bottom the current will be slack or of low velocity for a very short interval. Consequently, the oyster larvæ in this zone have a limited time in which to attach, and setting here is of a much lower concentration on a given area than is found at low-water mark when the slack-water interval is much longer. With the change of tide from ebb to flood, it was observed that as the water level rose from low-water mark to approximately 1 foot above it, there was virtually no current at the surface, while during the next rise of 1 foot the current increased rapidly to one-third foot per second. This sudden increase in the horizontal movement of the water as it rises from 1 to 2 feet above low-water mark is due to the water leaving the channel and spreading rapidly over the tidal flats. In the zone from low water to 1 foot above, setting is heavy; while at from 1 to 2 feet above, the number of spat per square inch decreases gradually until, at the 2-foot level, very few are found. The upper limit of setting in Milford Harbor is determined by the height of the tide when the surface current has attained a velocity of one-third foot per second after the period of low slack water.

Since the current velocity at any level varies from day to day with the changes in the range of tide, it is to be expected that sets occurring at different times would have a different upper limit. This actually was found to be the case with the two sets of 1925 and was the first clue that led to the studies of the relationship between current and setting. For the light set on July 20, 1925, the upper limit of setting on the glazed-tile collectors was 1 foot above mean low-water mark, while with the heavy set on July 29 it was 2 feet above. The range of tide in the first instance was 7 feet, while at the time of heavy set it was 6 feet. We know that current velocity increases with range of tide, and consequently the current on July 20 was stronger at the 1 or 2 foot level than it was on July 29. Under these conditions the limit of setting naturally would be lower for the light set, when the currents were noticeably stronger, and would prevent attachment of the larvæ above the 1-foot level. The tile collectors, under the same conditions, also show clearly the relative intensity of the two sets in 1925. The surface of the tiles was approximately 1,000 square inches, and the average number of spat collected per tile was 1,500 from the first set and 4,000 from the second or heaviest set. The setting on the tiles was not uniform, of course, but decreased in intensity from the bottom to the upper setting limit.

Observations were made, also, in regard to the distribution of the spat on the collectors in relation to the direction of the tidal currents when setting took place. At low water and on the first of flood tide the horizontal current movement is very weak, so that the current meter was useless for determining its direction or velocity. For this purpose a simple device was used, which consisted of a hollow brass rod ¼ inch in diameter, to which pieces of fine white thread 1 foot long were tied at intervals of 3 inches. By setting up the rod near the collectors the direction of the current could be seen easily at depths up to 3 or 4 feet. The distribution of setting

on the collectors was found to depend largely on their shape and the position in which they were placed on the tidal flats in relation to the direction of the flood current. The heaviest setting was found near the bottom and on the lee side of the collectors, presumably because of the eddies created by them. The setting on the brush that was planted on the tidal flats is a good example of the effect of the current on attachment of the larvæ. For a distance of about 3 inches above the bottom the spat were found on all sides of the main branches and were most numerous on the lee side. From above the 3-inch level to about the 1-foot level the majority of spat were distributed only on the lee side and decreased gradually in numbers from the bottom upward. Branches having the greatest diameter caught the most spat, while small twigs at the same level caught virtually none. Further indication that current velocity is an important factor controlling setting was found from a comparison of the distribution of spat in wire baskets filled with oyster shells with that on the brush. The baskets were set out next to the brush and were found to have received a much heavier set. The spat were found attached in the baskets up to 2 feet above the bottom, whereas on the brush setting stopped 1 foot above the bottom. The intensity of setting in the baskets varied from 150 to 200 spat per shell in the bottom layer to an average of 25 per shell at the top of the basket. The differences in the intensity and upper limit of setting in the baskets as compared with the brush undoubtedly is due to the type or shape of each collector. The baskets were a greater obstruction to the current, and by decreasing its velocity they facilitated the setting of a larger number of larvæ.

In summarizing the studies of the time and distribution of oyster setting in Milford Harbor, it has been found that—

1. Heaviest setting occurs in the surface layer during the period of low slack water, which is the zone in which the oyster larvæ were found to be most abundant.

2. Setting continues as the tide begins to run flood, gradually becoming less intense as the velocity of the current increases, and finally ceasing altogether when the current attains a velocity of 10 centimeters, or one-third foot, per second.

3. The intensity and vertical distribution of setting varies according to the current velocity at the times when oyster larvæ that are ready to set are found swimming in the water.

4. The distribution of spat on various types of collectors depends upon their shape and especially on the position in which they are placed in relation to low-water mark and the direction of the flood current.

5. The upper limit of setting varies according to tidal conditions when each set occurs. The range of tide, level of low slack water, and rate of increase in current velocity can be correlated with the intensity of setting and changes in the upper setting limit.

By comparing the tidal conditions in various oyster regions it has been found that the zones in which the oysters are attached and the distribution of the natural beds can be correlated with the velocity of the currents and the distribution of the oyster larvæ, the heaviest setting occurring at the levels where the larvæ are abundant when the current reaches its minimum velocity.

PREDICTING THE INTENSITY AND TIME OF OYSTER SETTING [2]

The production of seed oysters on both the natural and cultivated beds in Connecticut has fluctuated tremendously from year to year; for example, from over 1,000,000 bushels in 1925 to virtually none in 1926 and 1927.

The present investigation has shown that the physical conditions in 1925 were decidedly different than in 1926 and could be correlated with the quantity and ripeness of the spawn in the oysters, the time of spawning and setting, and the intensity of setting or quantity of seed oysters that were produced each year.

The data on the various factors have been presented, analyzed, and discussed as to their effect on the oyster and oyster larvæ and the environmental conditions over the oyster beds. Of the many factors involved, water temperature has been found to be the most important in controlling the development and ripening of the gonads and in determining the time of spawning and setting. The studies have shown that the success or failure of setting and its intensity depend largely upon the departures of temperature from normal. As is shown in Figure 28, during the past six years setting in Long Island Sound has been successful when the temperature was above normal and has failed when it was below, for the period April to August. Another important factor is the relationship between the range of tide and the increase in water temperature to 20° C. and above, which is necessary to induce spawning of the oyster.

The present investigation would not be complete without a discussion of the economic and practical value of the results that have been obtained. The most important application that can be made is in predicting the intensity and time of oyster setting in Connecticut waters. A method or plan of procedure has been developed for the purpose of determining or predicting, one month in advance, (1) the relative intensity of setting that will occur and (2) the time when spawning and setting will take place. The fundamental principle of the method is a comparison of the records of the present season with those of the preceding years for which the time of spawning and yield of seed oysters is known. The predictions can be made from about the 1st to the 10th of July of each year after careful consideration has been given to the following conditions:

1. The quantity of adult oysters on the beds.
2. Water temperature from April to July.
3. Quantity and degree of ripeness of the spawn.
4. The range of tide for July and August, as shown in the tide tables.

The first condition obviously is important and can be determined without difficulty from the planting records of the oyster-growing concerns or by examination of the oyster bottoms. This factor is of great significance because it is multiplied by the quantity of spawn per oyster and gives the approximate total quantity of spawn that can be discharged into the water.

The second condition, water temperature, preferably should be determined by a thermograph, although an approximate estimation can be made as to its departure

[2] Predictions in regard to oyster spawning and setting in Connecticut waters were made on July 1, 1928, using as a basis the conditions herein described. The light general set that was predicted to occur on Aug. 11 did take place at that time and in the quantity anticipated. On the beds off Stratford Point and Bridgeport the set on Aug. 11 averaged 10 spat per shell, while off New Haven an average of 12 spat per shell was found on Aug. 15.

from normal by reference to the air temperatures at near-by stations. If water temperatures for this period are found to be above normal, the outlook for setting is favorable; when below, it is unfavorable. The mean daily water temperature on the bottom or the temperature at the times of high and low water must be determined for a few days around the 1st of July, as it has direct bearing on the attainment of a spawning temperature later.

The third condition, quantity of spawn per oyster and its degree of ripeness, can be determined by the methods discussed previously on page 474. These factors not only reflect water temperatures that occurred previously, but will show how great a quantity of spawn can be discharged by each oyster when water temperatures are suitable. Successful spawning can be expected only at a temperature of 20° C. or above, when the gonads are ripe and when a sufficient amount of spawn is released to insure fertilization.

The final analysis of the first three conditions mentioned will indicate whether the total amount of spawn available is large or small and whether it is ripe enough to be released by the oysters. It will indicate also whether a light, medium, or heavy set can be expected, as this has been found to depend largely upon the combination of the first three conditions.

The fourth condition, range of tide, should be considered for the purpose of determining the time of spawning and setting. The relation of this factor to water temperature and spawning, as discussed previously on page 480, shows us that during the full-moon tidal period, in July or the first part of August, we may expect a rise in water temperature of approximately 10° C. as a result of the warming of the water on a greater area of tidal flats. The time of full-moon tides and the daily range can be found in the tide tables issued by the United States Coast and Geodetic Survey. During this period the date on which the water will reach 20° C. or more certainly depends upon weather conditions and the temperature of the water at the beginning of the period. The records for 1925 and 1926 show that when the temperature at the beginning of the full-moon tidal period was 16° to 18° C., spawning occurred about 10 days later in the harbor and inshore areas and about 15 days later, or at the end of this period, in Long Island Sound. In calculating the time of spawning, the ripeness of the oysters and early July water temperatures must be taken into consideration. The time of setting depends, of course, on spawning and will follow it by an interval of approximately two weeks.

In the following table a comparison is given of the four conditions as they were observed in Milford Harbor on July 1 in 1925, 1926, and 1927, together with the results obtained each year in regard to time of spawning and setting and intensity of setting.

TABLE 18.—*Comparison of conditions in Milford Harbor on July 1 with intensity and time of setting in 1925, 1926, and 1927*

Conditions observed	1925	1926	1927
Water temperature variations (Apr. 1 to July 1)	+3.5° C. above normal	−3.3° C. below normal	−1.7° C. below normal.
Water temperature on July 1 (at Station 2)	15.8° C	13.5° C	14° C.
Quantity of spawn per oyster	Large	Small	Small.
Condition of gonads	Ripe	Unripe	Unripe.
Quantity of adult oysters	700 bushels	1,000 bushels	1,000 bushels.
Greatest range of tide	July 7	July 26	July 17.
Time of spawning	July 13	Aug. 1	July 14.
Time of setting	July 29	Aug. 16	Aug. 8.
Intensity of setting (spat per bushel of shells)	15,000	2,000	2,450.

Milford Harbor is a natural oyster region, and virtually every year there is a set of oysters that varies in intensity in accordance with the conditions shown in the table. In Long Island Sound, oyster setting is less regular, and here there was a similar fluctuation from a good set in 1925 to virtually none in 1926 and 1927.

Though the method is new and far from being a statistical computation as to the probability of the time of spawning and intensity of setting, it has proved to be reliable after a trial of three years, and the results obtained strongly indicate that it is based on the predominating factors that control oyster propagation. By accumulating a greater number of data of this sort the method can be placed on a statistical basis, definite values can be given to each variable, and more accurate predictions can be made as to the yield of seed oysters per year.

PRACTICAL APPLICATION OF THE METHOD

Advance knowledge of the time and intensity of setting of oysters is of value from a practical standpoint, because it can be utilized in controlling shell-planting operations so as to obtain the maximum yield of seed oysters per year. On the results obtained on July 1, deductions can be made as to (1) the quantity of shells or cultch to be planted so as to take full advantage of the years of good set; (2) how rapidly shell-planting operations must be carried on in order that they may be completed before setting occurs; and (3) the areas or beds that are most favorable for obtaining a set under the existing conditions.

There is no better way to increase the yield of seed oysters during favorable years than by increasing the amount of cultch, especially on the best setting areas. An acre of bottom that produces 500 to 1,000 bushels of set, averaging 25, 50, or more spat per shell, has been poorly utilized, because its production could easily have been increased many times by additional shell plantings. By obtaining the maximum yield during the best setting years the industry is benefited not only by having seed to grow for the market but by having, in the coming summers, a good supply of oysters for the production of spawn and future sets.

This method of predicting the intensity of oyster setting can be used in the future in conjunction with the improved methods of seed collection that have been developed by the bureau and will be described in a later report.

SUMMARY

1. The physical conditions in Milford Harbor and vicinity during the summers of 1925 and 1926 have been discussed with special reference to the more important factors—temperature, salinity, hydrogen-ion concentration, tides, and currents.

2. The most important factor, water temperature, varies according to climatological conditions and is affected most by them when the daily range of tide is greatest.

3. The water temperatures from April to July were found to have a pronounced effect upon the quantity and ripeness of spawn in the oysters, while the temperatures in July and August were found to be important in affecting the time of spawning.

4. Annual fluctuations in the intensity of setting and the production of seed oysters in Milford Harbor and Long Island Sound can be correlated with water temperatures during the spring and early summer months.

5. During the past six years oyster setting in Long Island Sound has been successful when air and water temperatures were above normal and has failed when they were below normal.

6. Though some setting occurs each year in Milford Harbor, it was found that over seven times as many spat per bushel were produced in 1925, when early water temperatures were 3.5° C. above normal, than in 1926, when they were 3.3° below normal.

7. Oyster spawning occurred on different dates during each summer and was found to be dependent upon an increase in water temperature to 20° C. and above.

8. The time of spawning and the greatest increase in water temperature were found to take place during the "full-moon tidal period" in July or the first part of August. As a result of greater range of tide during this period, the water was brought to a spawning temperature by heating on a larger area of tidal flats.

9. In studying the occurrence and distribution of the oyster larvæ, over 315 plankton collections were made, which showed that the larvæ were relatively scarce in the water in proportion to the number of spat found later in the same areas.

10. The oyster larvæ were found to be most abundant at the time of low slack water and gradually disappeared as the tide began to run flood.

11. When the flood current had developed a velocity of 0.6 foot per second, virtually no larvæ could be found swimming in the water; while samples of bottom taken at the same time contained an average of 14 larvæ per square foot of surface.

12. Experiments with oyster larvæ in a tank showed that they swam while the water was at a standstill but dropped to the bottom when it was put in circulation with a current velocity of 0.3 to 0.5 foot per second.

13. The majority of oyster larvæ produced by the spawning bed in Milford Harbor were found to remain and set within 300 yards of its center. This is accomplished by the oyster larvæ remaining on the bottom during the greater part of the larval period and limiting their swimming activities to the tidal periods, when horizontal movement of the water is least.

14. The duration of the larval period was found to vary from 13 to 16 days. The average of the four periods observed during 1925 and 1926 was 15 days at a mean water temperature of 21.5° C.

15. Setting of oysters occurs at from 2 feet above low-water mark to the bottom of the channel and is of greatest intensity in a zone lying at from 1 foot above mean low-water mark to 1 foot below it.

16. Setting or attachment of the larvæ was found to take place during low slack water and continued until the flood tide had developed a velocity of 0.33 foot per second or 20 feet per minute.

17. It was found that the vertical distribution of spat and the intensity of setting in any zone could be correlated with velocity of currents and distribution of oyster larvæ.

18. As a result of the investigation of the physical conditions and the biological studies of the oyster, a method has been developed for determining or predicting, one month in advance, (1) the relative intensity of setting that will occur each year and (2) the time when spawning and setting will take place.

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