

THE LIFE HISTORY OF THE GIZZARD SHAD,
DOROSOMA CEPEDIANUM (LESUEUR),
IN WESTERN LAKE ERIE

DISSERTATION

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By

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THE LIFE HISTORY OF THE GIZZARD SHAD,
DOROSOMA CEPEDIANUM (LESUEUR), IN WESTERN LAKE ERIE

INTRODUCTION

Probably no other fish has been so highly praised and at the same time so heartily disdained as the gizzard shad. Its value as a direct link between plankton and food fish has long been extolled, but at the same time the health and economic problems resulting from 'winter kills' have brought it into much public disrepute.

Economic and Biological Problems Created.

Increasing reports in recent years--particularly during late fall and winter--of gizzard shad problems such as: vast windrows of dead shad thrown ashore by waves after a sudden cold spell; the stench and the health problems arising from these dead shad; tons of shad being removed from municipal waterfronts; innumerable shad milling about dazedly in basins receiving warm waters from electric plants, and in stream mouths and imposing damages at various power plants; tons of shad filling the gill, trap, and pound nets and drag seines of commercial fishermen, adding hours of profitless work in separating and disposing of them have made it desirable that this fish be studied thoroughly. From such studies its relative value can be better understood, and its control and utilization better attacked.

Taxonomic Position.

The gizzard shad is a clupeid fish of the genus Dorosoma of the order Isospondyli. That occurring in Lake Erie, Dorosoma cepedianum LeSueur, has the northernmost distribution of the gizzard shads, some species of which are found as far South as the Great Lakes of Nicaragua (Miller, 1950).

Throughout the literature, mention of this fish by the following names has been found:

Megalops cepediana (cepedina) LeSueur (1818)
Clupea heterura (heterurus) Rafinesque (1818)
Dorosoma notata Rafinesque (1820)
Chatoëssus ellipicus Kirtland (1839)
Dorosoma insociabilis Abbott (1860)
Dorosoma cepedianum Gill (1861)
Chatoëssus cepedianus Gunther (1868)
Dorysoma heterura (L.S.)--Gill (1876)
Dorosoma cepedianum Uhr and Lugger (1876)
Dorosoma cepediana heterura Jordan (1877)
Dorysoma cepediana Jordan (1878)
Dorosoma cepedianum notatum (1879)
Dorosoma cepedianum Jordan and Gilbert

The common names of this fish are even more abundant and usually refer to some anatomical or behavior character. Note the more common names:

Gizzard Shad and Hickory Shad--(possession and appearance of gizzard).

Sawbelly--(presence of abdominal scutes which give it a serrated appearance).

Threadfin and Hairy-back--(prolonged dorsal filament).

Mud Shad--(presence of mud in the gut).

Stink Shad--(odor associated with its decay).

Distribution.

The gizzard shad (Dorosoma cepedianum LeSueur), which occurs most abundantly in the southern portion of the North Temperate zone, is a fresh-water fish--often living in brackish water, tolerating salt water, but spawning in fresh water. Its distribution is limited to the Atlantic drainage of North America--more specifically to the Great Lakes-St. Lawrence drainage; to the eastern U. S. Coast drainage; and to the Gulf of Mexico drainage.

Judging from the present distribution of Dorosoma cepedianum and of its three nearest relatives--D. anale; D. chavesi; and D. smithi--the common ancestor probably arose along the southwestern shores of the Gulf of Mexico. See Figure 1. The D. cepedianum evolutant probably migrated by way of brackish marshes and bays along the western and northern shores of the Gulf and entered its tributary streams. It is found in practically every stream emptying into the Gulf from the Río Pánuco Basin of eastern Mexico, northward and eastward to the southwestern third of Florida. It migrated most extensively in the Mississippi River drainage, having been found as far west as Pueblo, Colorado (Ellis, 1914); as far north as the 45° N. Latitude in Wisconsin (Greene, 1935); and eastward to the swifter, colder tributaries draining the Appalachians.

Although I could not find a record of it for the southern tip of Florida, it is conceivable that it tra-

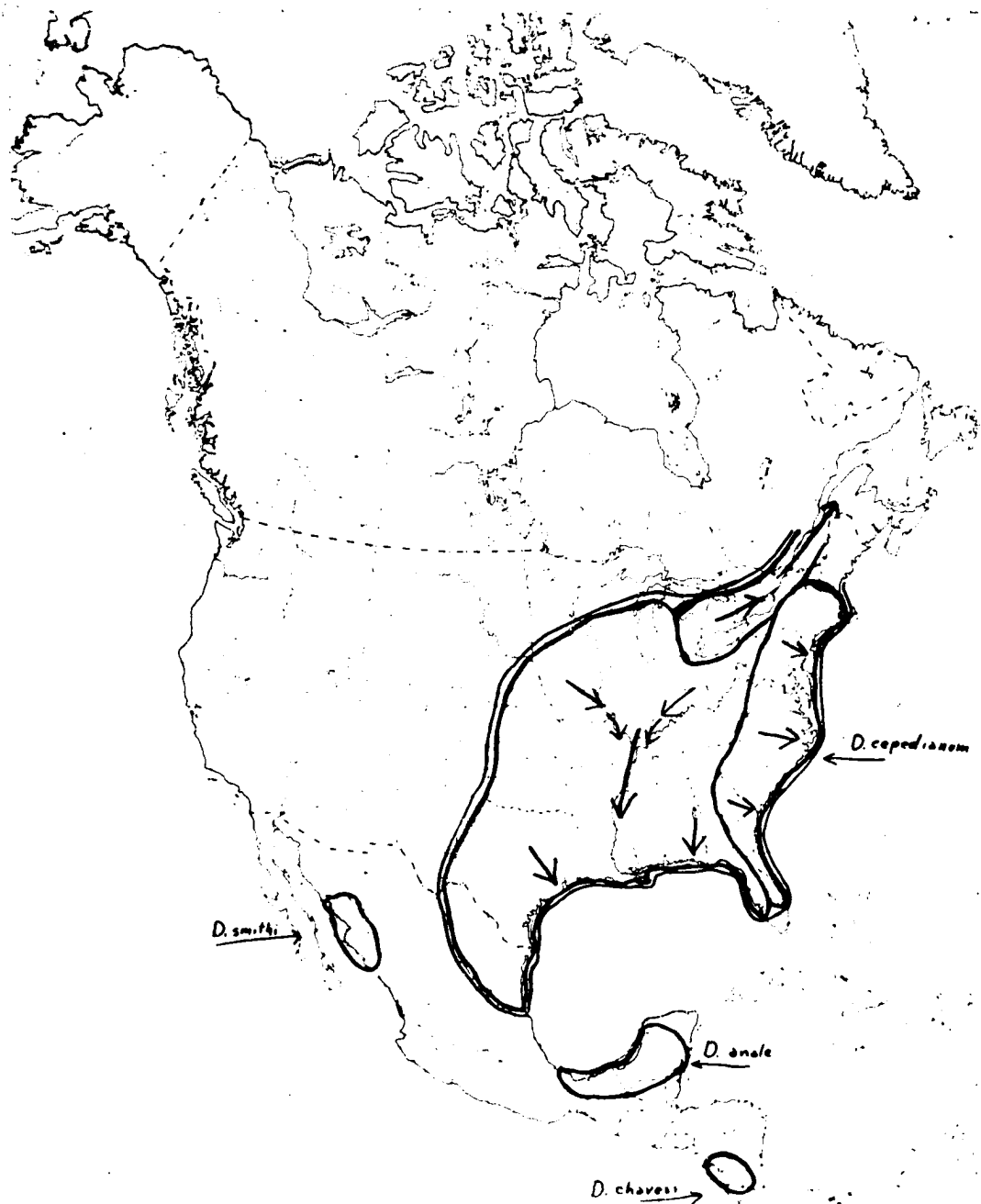


Figure 1. Distribution of *Dorosoma cepedianum*, *D. anale*, *D. chavesi*, and *D. smithi* in North America, and the Drainages in Which *D. cepedianum* is found.

versed this region long before fish collections were being made or it may have migrated through the passage across Northern Florida, which, according to paleogeographic evidence, existed from the interglacial periods of the Pleistocene to relatively recent times (Rivas, 1954), and migrated northward along the Atlantic Coast, invading the streams emptying along the coast until now practically every stream and bay from the northeastern coast of Florida northward along the Atlantic seaboard to 40° N. latitude has had gizzard shad recorded from it. There their western limits are bounded by the swifter, colder waters draining the Appalachians.

The presence of gizzard shad in the Great Lakes-St. Lawrence drainage could have come about by migrations up the Atlantic Coast into the St. Lawrence River and thence into the Great Lakes (Vladykov, 1945); or from the Mississippi drainage into the Glacial Great Lakes during the Lake Maumee outlet stage (Gerking, 1945); or quite recently by way of various Ohio canal connections (Kirtland, 1850). Of these, the latter suggestion appears to be the most plausible; because the presence of gizzard shad in the Great Lakes was unknown before the canal connections, their establishment in Lake Erie in numbers appears to have taken place fairly recently, and their presence in Lakes Huron and Ontario became known subsequent to collections of them along the south shore of Lake Erie. The report of their

presence in the St. Lawrence River at Quebec is of even more recent date. It must be noted, however, that freshwater fishery investigations--especially of rough fish--were very meager prior to 1850 and the presence of these fish could easily have been overlooked. Then, too, establishment need not be too closely related to invasion. In the Great Lakes-St. Lawrence drainage the gizzard shad has been reported from Lake Huron in the West to Quebec in the East, having become best established along the western and southern shores of Lake Erie and in the streams entering therein.

In addition to the natural invasion of this fish, they have been planted and became established in reservoirs and impoundments.

In Western Lake Erie the very small shad, measuring an inch or so in total length, are found mostly in the shallower waters close to the lake shores--especially where the waters are quiet. They are also abundant in protected bays and in ponds and marshes connected with the lake or its tributaries. They are not usually found along precipitous shores which are more or less constantly buffeted by waves. Their habitat often possesses a sloping sand bottom without submergent vegetation. More often, however, the bottom is mucky and covered with an abundance of submergent vegetation.

The reference for these small shad appears to be some sight barrier rather than type of bottom or distance of bottom.

When wave action becomes violent they are swept or swim into deeper water further from shore. This I assume, because repeatedly I have been unable to get shad along the shores during, and for some time after, heavy wave action, where previously they were continually present.

Gizzard shad upwards of 4 inches (total length) were seldom caught close to shore. During the summer and fall they were more abundant in waters less than 10 feet deep. This is especially true for the smaller of these shad. The bigger (and older) shad come into waters often less than 5 feet deep during the spawning season, after which they re-enter deeper water. Before and after the spawning season I have been able to net only a very few large and old fish in these shallow waters.

How much of their time is spent on the bottom has not been ascertained but the presence of sand particles in the gut suggests that they visit the bottom at times.

During the winter most of these fish must be in deeper waters. I assume this because from under-ice gill net settings I got one shad in comparison to perhaps a hundred during the summer gill net setting of similar yardage. Reduced activity accounts for some decrease in catch but by no means all since the carp/shad ratio is much greater in

favor of the carp in winter than it is in the summer. Of course, the carp may be more active than the shad at the near freezing temperatures.

Migrations

As the spawning season approaches, the shad are caught (by commercial fishermen) in greater and greater abundance in the trap nets set closest to shore in shallow waters. In Fishery Bay, on a gravel bar between Oak Point and Gibraltar Island, during spawning season, I have gotten more and more shad as the height of the season approached, the catch dropping rapidly thereafter. Before and after the spawning season no shad were caught there. This bar is covered by 2 - 4 feet of water. When gill nets were set transversely across this bar so that either end of the net lay in 5 - 7 feet of water, shad were invariably caught in greater abundance where the net crossed the bar while carp predominated in either end of the net. Thus, there appears to be a spawning migration of shad toward shallower water. The presence of water current, vegetation, and/or rock bottom seems to be desired. This combination is fortunate--the eggs stick to the rocks and are oxygenated by the moving water. There also appears to be a migration into deeper water when the temperature drops during late fall.

Whether there are migrations with reference to currents within the lake has not been determined--if there

are, the temperature of the moving water mass is probably of greater import than is the mere motion of the water. It is well known that shad follow warm waters to their source when the lake temperature has fallen. For example, they accumulate in vast numbers in the collecting basins for discharge waters from electric plants, and migration up streams have been noted during the winter when the lake is colder than the stream.

Abundance.

The layman's conception of the great abundance of shad in Lake Erie is somewhat exaggerated. The millions of young-of-the-year shad which are in evidence on still, warm, moonlight nights especially in August are misleading--these masses are not continuous throughout the lake, but rather they are congregated in sheltered areas close to shore. Furthermore, by the time they reach maturity their numbers will have been tremendously decimated by piscivorous fishes and birds and by the elements.

The milling masses seen during the winter in the collecting basins of warm industrial waters also are misleading. They are not at all indicative of the numbers in the lake. The shad have come from far and near, attracted by the warmer water discharged into these basins. This is also true of the masses migrating up streams during the winter.

Nor is the winter kill, due to sudden 'cold snaps', an accurate measure of abundance. These 'cold snaps' follow warm spells or warm rains--the shad follow the warmer water shoreward where the 'cold snap' quickly lowers the temperature of the shallower waters. The masses are accumulations of fish there--then too, many of the dead fish which were cast ashore have been dead for some time but have not decayed in the cold water.

Historically, it has been well established that the shad has been slowly growing in numbers in Lake Erie. Commercial fishermen tell me that three decades ago the 'sawbelly' was something of a rarity--an occasional one being picked up now and then. The species has been slowly increasing in numbers, having attained (according to the commercial fishermen) greatest abundance during the last two or three years. Whether this be due to evolutionary adaptations to this environment, to changes in the character of the lake, to high reproductive rates or to increasing surpluses of shad beyond environmental and predatory inroads has not been determined.

The shad seem to be most abundant in the shallower waters around the periphery of Western Lake Erie, around the islands, and especially in protected bays and tributary mouths. Their abundance here varies according to the season, being greatest in the late summer and early fall when their numbers are greatly increased by the presence of

new young-of-the-year, and next most abundant prior to and during spawning in late spring. Then, too, in winter they congregate in places whence warm streams emanate.

At other times there are relatively few of them--frequently days go by without shad being caught by the commercial fishermen.

Physical Characteristics of Western Lake Erie.

This portion of Lake Erie receives about 90% of the water entering the lake, yet it contains only about 5% of the total volume of the lake. Its mean depth lies usually between 7.5 and 8.0 meters, depending upon the season. Besides the seasonal high and low waters related to lake rainfall and evaporation and to inflow and outflow, there are short time variations due mostly to wind action--these seiches generally vary from a few inches to about 5.5 feet.

Turbidities vary with suspended matter from about 5 ppm to over 100 ppm with 1% of surface light penetrating about two meters at greater turbidities and about eight meters when the waters are clearest. Turbidity is usually highest in March, April, and November; lowest in February, July, and August. The yearly mean lies somewhere between 20 and 30 ppm. Western Lake Erie is not uniformly turbid--being clearest along the northern and most turbid along the southern shore. Besides the influx of sediment, mostly by the southern tributaries, turbidity is readily brought about by

a relatively small wind action stirring up the bottom in this shallow region. So constant is this stirring that top and bottom temperatures seldom vary more than 2° C.

During the ice cover period, which usually begins about the middle of January and lasts to about the middle of March, the water temperature remains about 0.5° C. or lower. During the last half of July and the first half of August it rises to a high of around 26° C. Only rarely, during a period of warm calm days, is there to be found a thermocline.

A plankton pulse usually occurs during the latter half of the February and during the July-August periods of low turbidities. The plankton involved are diatoms, and green and blue-green algae. The diatoms predominate in both pulses--specifically, *Asterionella* in the former and *Melosira* in the latter. The algal group present in the smallest percentage is the Cyanophyceae in the former and the Chlorophyceae in the latter.

Collections--Places.

Small gizzard shad were captured in the Sandusky River at Fremont, in the Huron River at Norwalk, in the Portage River above Oak Harbor; in the following bays: Sandusky Bay, Portage River Bay, Maumee Bay, Hatchery Bay (Fishery Bay); in Terwilligar's Pond, in Squaw Harbor, in East Harbor, and in Marshes off Green Creek which empties

into the Sandusky River; along the sandy or shallow shores of Mouse Island, South Bass Island, North Bass Island, Kelley's Island, Pelee Island; and along the shores of Lake Erie west of Colchester, Canada, at Point Pelee, Canada, and at Long Point, Michigan. See Figures 2, 3, and 4.

Large shad were collected continuously throughout the year from Fishery Bay of South Bass Island. During spawning season they were captured in greatest abundance on a bar extending from Oak Point to Gibraltar Island. In addition to these local catches, shad were brought in by commercial fishermen (April to December) mostly from within a radius of five miles from South Bass Island. During late spring in 1953 several catches were acquired from commercial fishermen operating in Sandusky Bay. District I, of the Ohio Department of Conservation brought in samples from Vermilion, Ohio during a winter kill early in 1953. I had taken a number at Avon Lake, Ohio in February 1954 and some at Erie, Pa. later that year.

• Collections--Dates.

Small gizzard shad, mostly less than three inches in total length, were taken during the summer months of 1952, 1953, and 1954. Occasionally, stragglers from late hatches and runts from sub-marginal habitats were taken in the fall and even in winter. The very smallest gizzard shad (less than one inch TL) were first taken during the latter

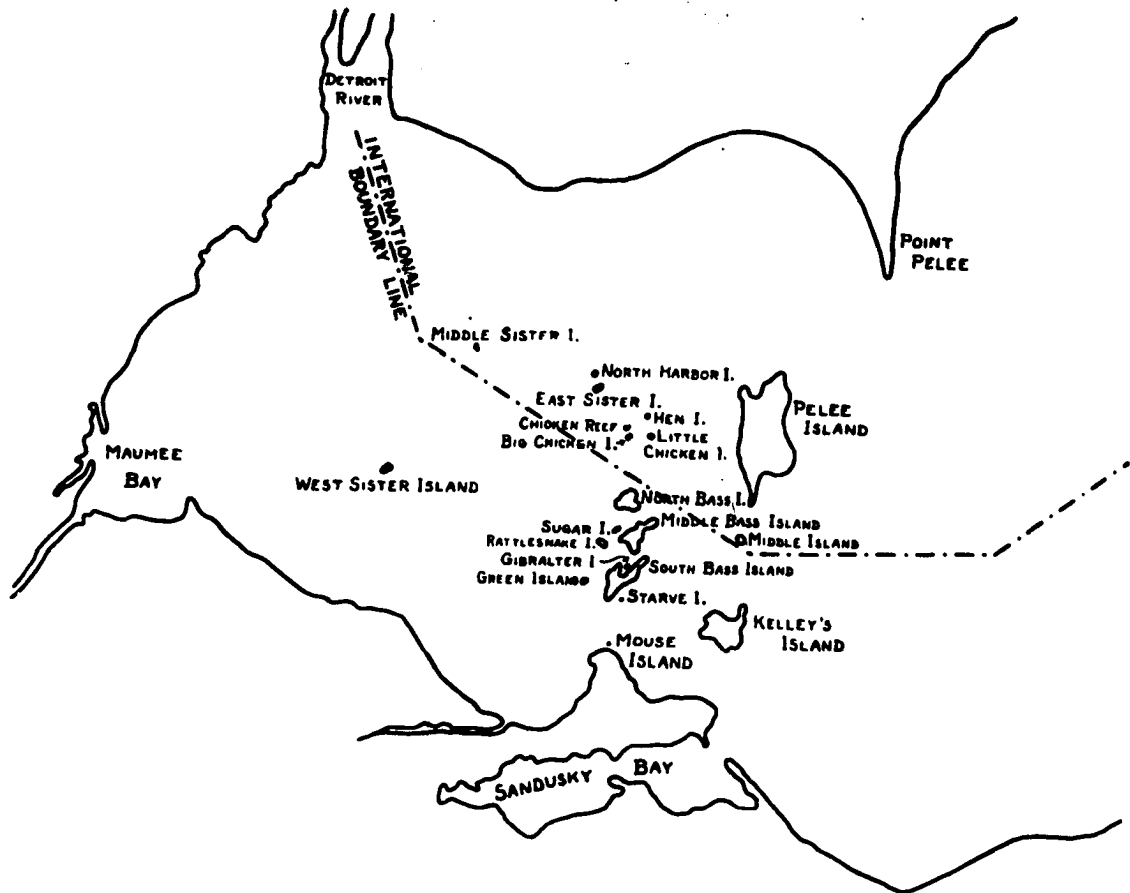


Figure 2. Western Lake Erie (Core)

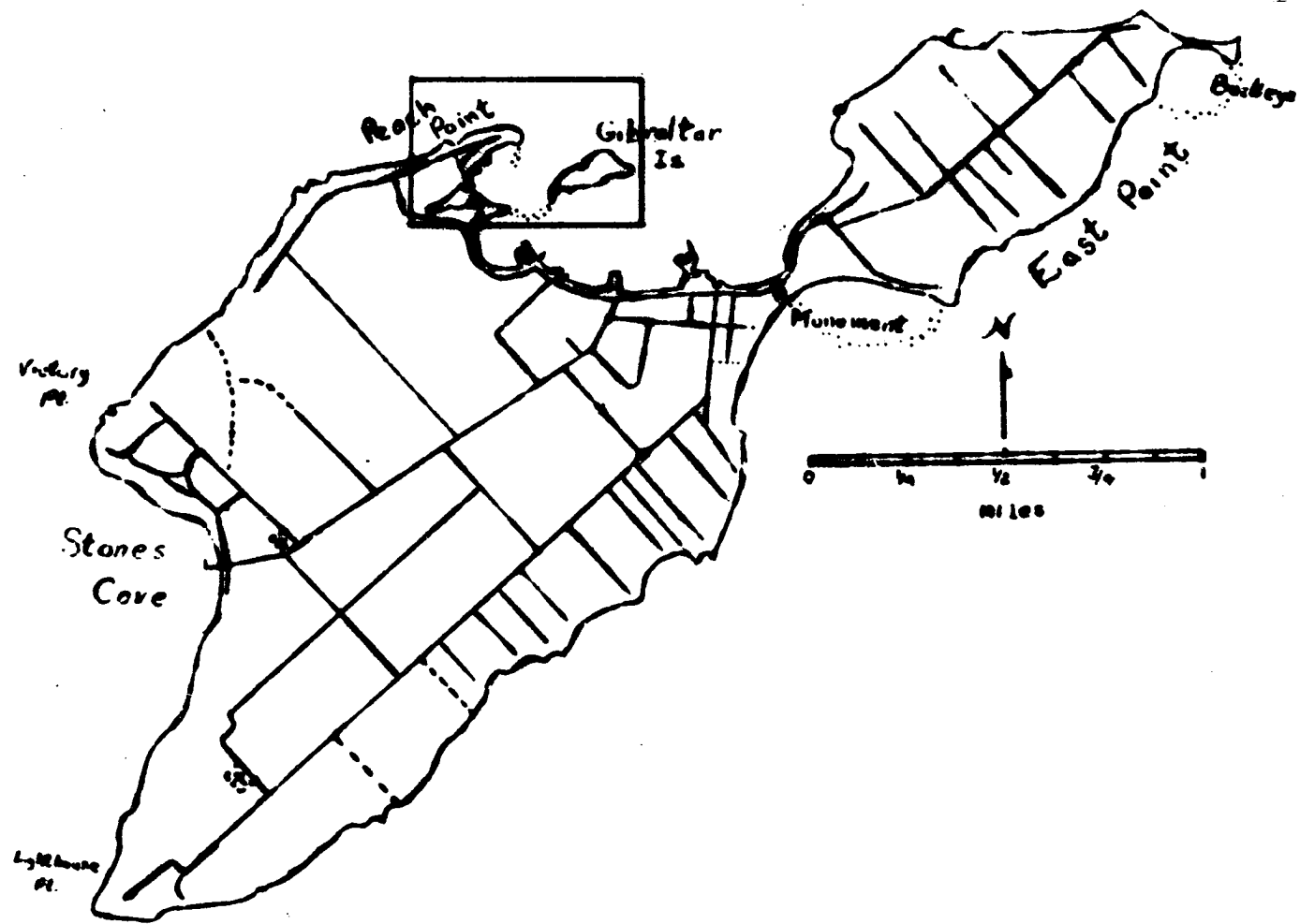


Figure 3. South Bass Island (Stansbery)

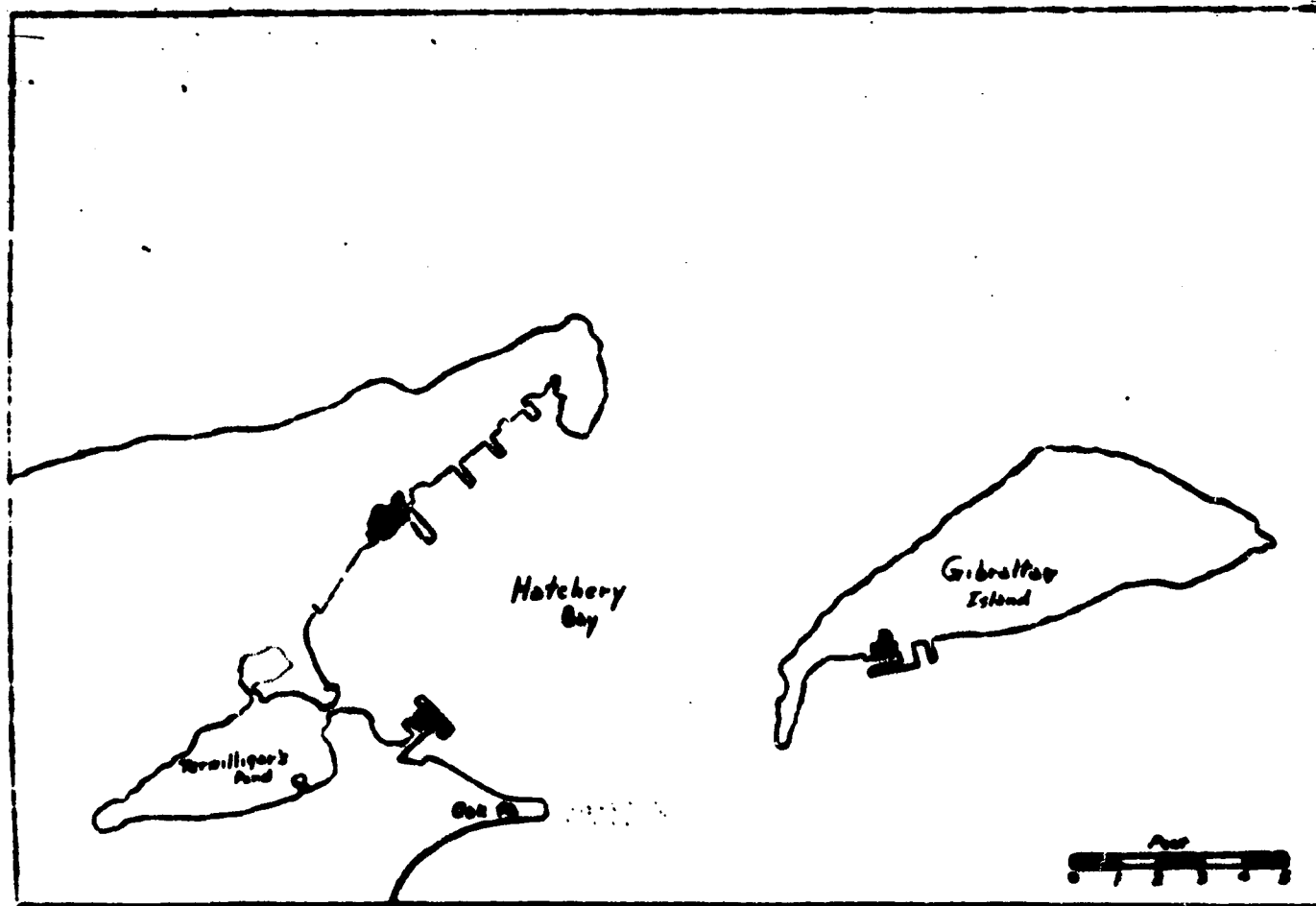


Figure 4. Fishery Bay (Hatchery Bay)--South Bass Island (Stansbery)

half of June and were intermittently present in the collections until about the first half of August. The upper limits of this group were first taken in the last week of July in streams emptying into this end of the lake, and early in the first week of August in Fishery Bay. They persisted in collections until about the first of October--a few were occasionally taken later. In Sandusky Bay they appeared quite abundant even in December.

The large shad, mostly over four inches in total length were taken more or less constantly throughout the year from the fall of 1952 to the early summer of 1955. The larger and older shad were gotten mostly prior to and during the spawning season. Fewer shad were taken during the winter than during any other season due to fewer samplings and probably to the presence of fewer shad and to their decreased activity.

Distinguishing Young Shad from Young Alewives.

During the summer of 1953, many young-of-the-year alewives (Pomolobus pseudo-harengus, Wilson) were found schooling with similar young gizzard shad. The mixed schools were found mostly in Fishery Bay but also at Cedar Point (in Sandusky Bay), in the Canadian waters at Pelee Island, and along the Canadian shore west of Colchester. Alewives having a total length of about 50 mm or more could be readily distinguished from the gizzard shad by their

possession of a dusky silvery lateral band, a terminal mouth, and not being as deep as the gizzard shad. The gizzard shad at this length does not yet possess the prolonged dorsal filament. A microscope was needed for the recognition of smaller alewives. The most evident character of the smaller alewife was the larger maxillary bones which protruded below the lower jaw when the mouth was forced open--this did not occur in the case of the shad. In addition, the anal ray count of the alewife was around 20 as compared with around 30 for the shad. By these means alewives of 20 mm could be distinguished from similar sized shad.

Composite of Collections.

| Mo. | Yr. | O | I | II | III | IV | V | VI |
|-------|------|-------|-----|-------|-----|----|---|----|
| July | 1952 | 125 | | | | | | |
| Aug. | 1952 | 269 | 5 | | | | | |
| Sept. | 1952 | 20 | 7 | | | | | |
| Oct. | 1952 | 1 | | | | | | |
| Nov. | 1952 | 259 | | | | | | |
| Dec. | 1952 | 482 | | | | | | |
| Jan. | 1953 | | 30 | 1 | | | | |
| Feb. | 1953 | | 24 | 2 | | 1 | | |
| Mar. | 1953 | | 1 | 1 | | | | |
| April | 1953 | | 183 | 137 | 2 | 5 | 1 | |
| May | 1953 | | 216 | 30 | 1 | 1 | 1 | |
| June | 1953 | 76 | 151 | 28 | 2 | | | |
| July | 1953 | 2,247 | 9 | 6 | | | | |
| Aug. | 1953 | 1,384 | 92 | | | | | |
| Sept. | 1953 | 942 | 270 | 7 | 1 | 1 | | |
| Oct. | 1953 | 684 | 192 | 11 | 1 | | | |
| Nov. | 1953 | 1,609 | 164 | 2 | | | | |
| Dec. | 1953 | 322 | 97 | 5 | | | | |
| Jan. | 1954 | | 65 | 43 | 1 | | | |
| Feb. | 1954 | | 2 | 232 | 6 | | | |
| Mar. | 1954 | | 2 | 15 | 2 | | | |
| April | 1954 | | 22 | 43 | 6 | | | |
| May | 1954 | | 20 | 59 | 2 | | | |
| June | 1954 | 268 | 29 | 1,048 | 50 | 9 | 2 | 2 |
| July | 1954 | 787 | 287 | 488 | 29 | 4 | 1 | 1 |
| Aug. | 1954 | 8,456 | 159 | 27 | 1 | | | |
| Sept. | 1954 | 876 | | | | | | |
| Oct. | 1954 | 98 | 30 | 4 | | | | |

Table 1. Monthly Composite Collections of Gizzard Shad
 Showing Numbers in the Various Age Groups
 (Using January 1 as the Beginning of each
 Age Group).

METHODS AND MEANS

Means of Capture.

The very smallest gizzard shad acquired were timed samples taken from eggs which were hatched in the Ohio State Hatchery at Put-in-Bay. The smallest shad taken in the field were gotten with dip nets. The following means for getting them were used with varying degrees of success: common seine, bag seine, push seine, electric shocking, rotenoning, and dynamiting. Of the seines, the bag seine was the most effective. Electric shocking was ineffective for small fish. Rotenoning was undesirable because one had to wait for calm water when the drug would not be quickly dissipated. When poisoning a small portion of the bay this method was selective in favor of the small fish which were not able to swim through the poisoned water unharmed. Dynamiting was the least selective since it surfaced fish of all sizes within the radius of its effectiveness. Of course, there is a spatial selectivity--the smaller fish being in shallower water and larger fish in deeper water--which no small-scale collecting method can bridge.

In Fishery Bay I used gill nets almost wholly for netting the larger shad. The mesh sizes ranged from one inch, bar measure, to two and one-half inches. These gill nets were set in all seasons except during the formation and the breaking up of the ice cover in winter.

In the lake the commercial fishermen used both gill nets and trap nets. In Sandusky Bay they used drag seines. At Avon Lake I used the fish screens at the water intake of the Electric Plant in addition to a gill net for getting samples. After some of the winter kills I got dead shad from the shore and chopped some out of the ice.

Length and Weight Determinations.

The standard length (SL) in millimeters is the basis of all fish length relationships expressed herein. For small fish, a pair of dividers was used to obtain this length. Larger fish were laid on a fish board and the measurement obtained directly from it. The contour of the body was not considered. These methods apply also to total length and depth. The fish were measured soon after being caught. Sometimes too many fish were acquired and some had to be preserved in ten per cent formalin for a day or two. (Formalin preservation for a week resulted in no change in length and a loss in weight of approximately one per cent.)

The fish weights are expressed in terms of grams. The largest fish were measured to the nearest gram; fishes between 100 mm and 200 mm SL to the nearest one-half gram, those between 50 mm and 100 mm SL to the nearest tenth of a gram. In catches of large numbers of shad, smaller than 50 mm SL, equal length fishes were weighed en masse and the average weight assigned to each member.

Formalin preserved fish were sometimes used. Some fish were not weighed when collection pressure was too great.

Gonads were weighed to the nearest hundredth of a gram. Gonad weights were taken from fresh shad only.

Scale Selection.

Since the gizzard shad loses its scales readily and as a consequence, regenerated scales are common, it was decided to use scales from a key area rather than to use key scales for determining scale/body length ratios. This minimized the chance of a fish having no scale or of having a regenerated one as the key scale. This key area is located just dorsal to a midline drawn from snout to tail fork and is midway between the operculum and the origin of the dorsal fin--on the left side of the fish. Usually a dozen or so scales were removed from this area and were placed in a scale envelope on which was recorded the information pertinent to the fish. From these scales three non-regenerated ones were picked at random for determining the average values of the dimensions employed. Scale samples were taken of some 5,000 shad.

Aging by Scales.

The fish's age was determined by counting the number of annuli on the scales with the aid of a dissecting scope. The first annulus is often not as obvious as are later ones. The circuli within the first scale zone are

set closer together than they are in succeeding scale zones and they arch but little laterally, not being as semi-circular as are the later ones. There is a narrow line of demarkation between this zone and that immediately following. Circuli of the latter zone cut abruptly across the course of the circuli of the first zone in the lateral fields. Often this line is difficult to see and may require use of the medium power of the scope for detection. See Figure 5.

Succeeding annuli are characterized by possessing some width in which there may be fragmentary circuli. The earlier circuli of the new growth zone 'cut over' the older circuli of the previous zone, particularly in the antero-lateral fields. See Figure 6. These annuli form a semi-circle around the focus, sometimes interrupted briefly or ending in a different plane, circuli-wise, and are sometimes not evident on all the scales of a fish.

Frequently, an accessory annulus appears--usually between the first and second annuli. This lacks the width and the completeness of a true annulus, often extending only in the lateral halves of the scale. Often it has a closer resemblance to the first annulus than to succeeding ones. In a few cases the second annulus has this appearance, but it can be recognized by being in the 'usual' position. See below and see Figure 7. Compare with a 'normal' scale (Figure 8).

It appears that the first annulus is that of an

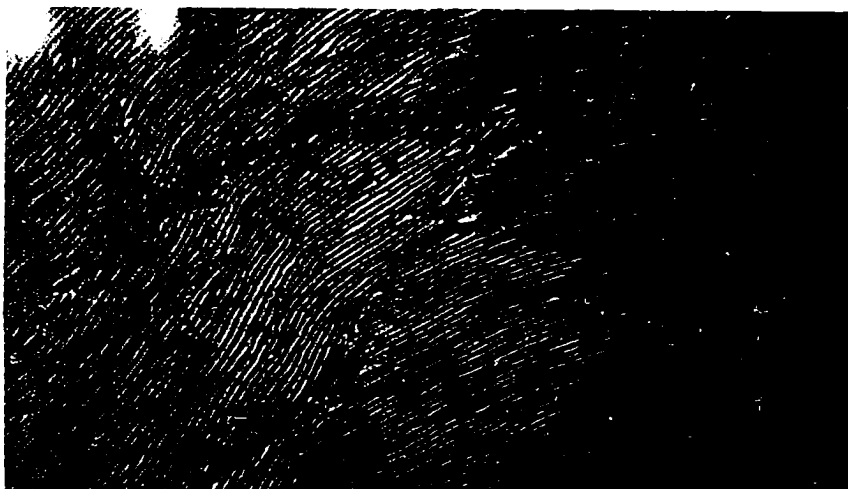


Figure 5. Enlargement of the 1st Annulus.

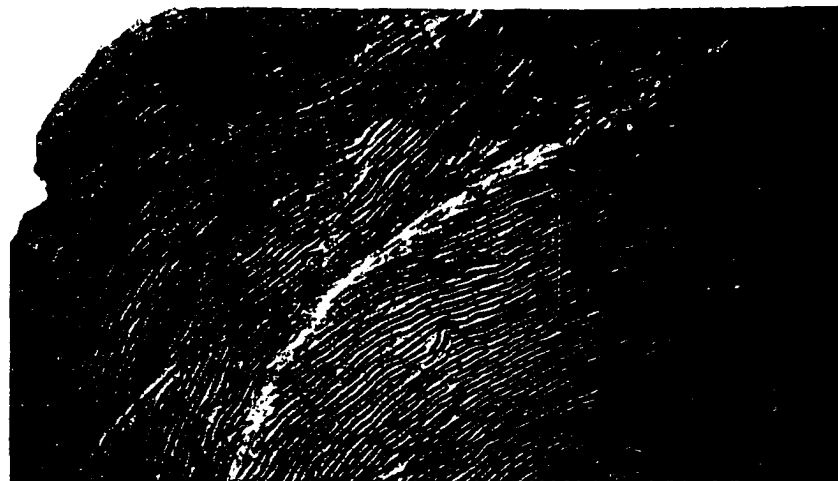


Figure 6. Enlargement of the 2nd Annulus.



Figure 7. VI-yr. Shad Scale Showing an Accessory Annulus.

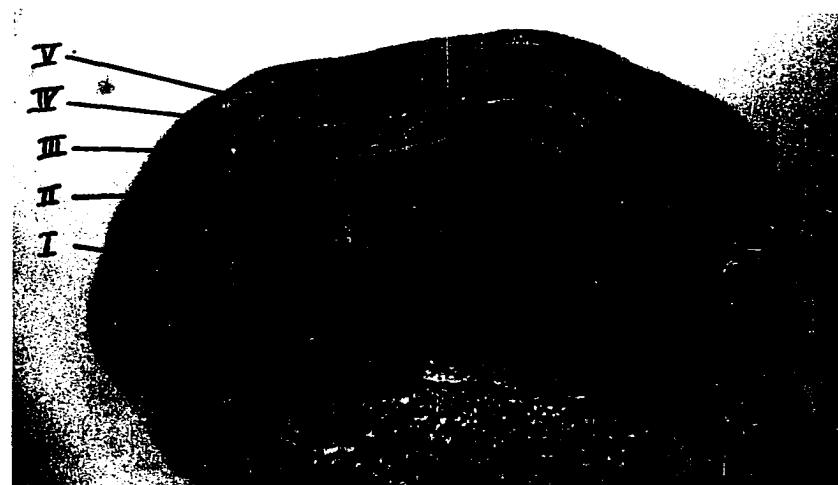


Figure 8. Normal Scale from Same VI-yr. Shad.

immature shad. This annulus is formed earlier in the season than are the others. (See under Annulus Formation.) Although I don't have concrete evidence, I am of the opinion that if the fish should spawn in its second year of life (and several have been observed to be mature at this time) a spawning mark would be formed which would not coincide with its first annulus (these fish spawn perhaps two months after their 1st annulus was formed), hence an accessory annulus would appear. That this is not a second annulus altered by an extended starvation period is evident from the position of the second 'true' annulus at the 'usual' distance from the first.

Should an individual not mature during its third year of life (this condition has been observed) the 2nd annulus formed would be somewhat like the first one--that is, narrow and lacking continuity. However, it would be in the usual position. Maturation of the fish, or its preparation for spawning, however, influences the appearance of the annulus so that the second annulus is more rugged and more obvious than is the first. It is a combination annulus and spawning mark.

Lagler and Applegate (1943) and Lagler and Van Meter (1951) demonstrated that the annulus is a true year mark in Indiana and Illinois gizzard shad. Lake Erie gizzard shad scale data add support to the belief that annuli

are valid indicators of age.

The use of the scale method for determining the age of gizzard shad in this region is justified by the following observations:

1. Fish known to be the young-of-the-year had no annuli on their scales.
2. The length frequency groupings of captured fish agreed with the number of annuli present on the scales.
3. The distance between the last annulus and the anterior edge of the scale increased throughout the growing season.
4. The calculated length was similar for fish of identical age groups (by scales) in the same and different year's collections.
5. Scales of fish taken in the fall and winter and early spring showed no annulus at the scale edge, while those taken in May, June, and July showed one near the anterior edge.
6. The calculated lengths for an age group, as determined by scales, showed a closer agreement than did those between different age groups.

The convention of giving fish a birthday on January 1 (Hile, 1948) has been followed. The relationships between age terminology and calendar periods follow:

THE SPECIAL TERMS PERTAINING TO AGE INCLUDE:

Year of life. From the time the fish is hatched until the end of that calendar year it is in its first year of life. During the next calendar year, it is in its second year of life, etc. By using this convention, the first year of a fish's life is only about six months long.

Age. A fish is 0-yr. old until it has terminated the first calendar year of its life, then it becomes 1-yr. old. It remains 1-yr. old until it has reached the end of its 2nd

calendar year of life, etc.

Number of annuli. The number of annuli always corresponds with the age of the fish during the last part of the year only. During the first part it is one less--at mid-year, both are represented in that year group.

Fry. Larva-like shad from hatching to the beginning of deepening when the fish begins to assume the adult shape.

Young-of-the-year. Juveniles to the end of the first December.

Juveniles. Shad from assumption of adult shape to acquisition of 1st annulus.

Adults. Shad from 1st annulus on.

Immature. Fry to the end of their second year of life (specifically to their first spawning).

Mature. Adults from the beginning of their third year of life on (specifically after their first spawning).

Seniles. Those adults whose gonads show signs of marked absorption and within whose ovaries is found a large percentage of connective tissue.

Fish/Scale Length Determinations.

For the fish/scale length ratios and for the back calculating of fish lengths at various ages, three non-regenerated scales were selected at random from the scale envelope. These scales were impressed on strips of plastic by the cold roller press of Smith(1954). The borrowed press was returned to the U. S. Fish and Wildlife Service in the fall of 1954 and the scales thereafter were prepared by temporarily mounting them on glass slides. The scales had dried while they were pressed flat in the scale envelope. They remained flat on the slide long enough for

measurements to be taken.

Using the scale-study apparatus described by Van Oosten, Deason, and Jobes (1934) a metric scale was projected and marked out on a strip of heavy paper. This strip was used to measure the fish scale projections. The magnitude of the magnification did not matter since the metric scale and the fish scales were magnified equally. Scale measurements were recorded to the nearest hundredth of a millimeter.

For convenience, the various dimensions of the three scales were marked on a numbered strip of paper. The strip was held on the fish scale image with one end at the focus while the other end cut through the mid-anterior field. The annuli and scale edge were indicated on the card by numbered pencil marks. These distances were then measured with the "enlarged" metric scale.

The 706 scale lengths (focus to anterior edge) plotted against the corresponding fish lengths (S.L.'s ranged from 43 mm to 390 mm) gave the appearance of a straight line relationship. By the method of least squares the following regression line was obtained:

$$SL = 22.1 + 44.25 (\text{Scale})$$

All months of capture, all ages, and both sexes are represented. Body/scale length ratios were investigated for each month, for each sex, and each age group.

In my opinion the slight variations found were insignificant.

For the back calculation of fish lengths at the different ages used in comparing lengths of different year classes and in the compensatory growth study a graph was prepared. Along the ordinate the units were in millimeters of fish length (SL). Along the abscissa, the scale lengths were in units of hundredths of a millimeter, to facilitate handling the small dimensions of the scale parts. A stop in the form of a pin was inserted at the intercept between fish and 0 scale length. This is 22.1 mm ordinate on the 0 abscissa. One end of a straight edge was pivoted from this point.

To illustrate, consider a fish having the following characteristics: SL = 254 mm, scale length (focus to anterior edge) = 5.02 mm, 1st annulus length (focus to first annulus in anterior field) = 2.92 mm. To estimate the length of the fish at the time the 1st annulus was produced, we find the intercept of 254 (ordinate) and 5.02 (abscissa). We pivot the straight edge to this point and obtain the value SL = 157 from its intercept with 2.92 on the abscissa. See Figure 9.

Very rarely will the fish/scale juncture meet on the regression line for the average fish. So we must assume that, however much it is off, it has been off that

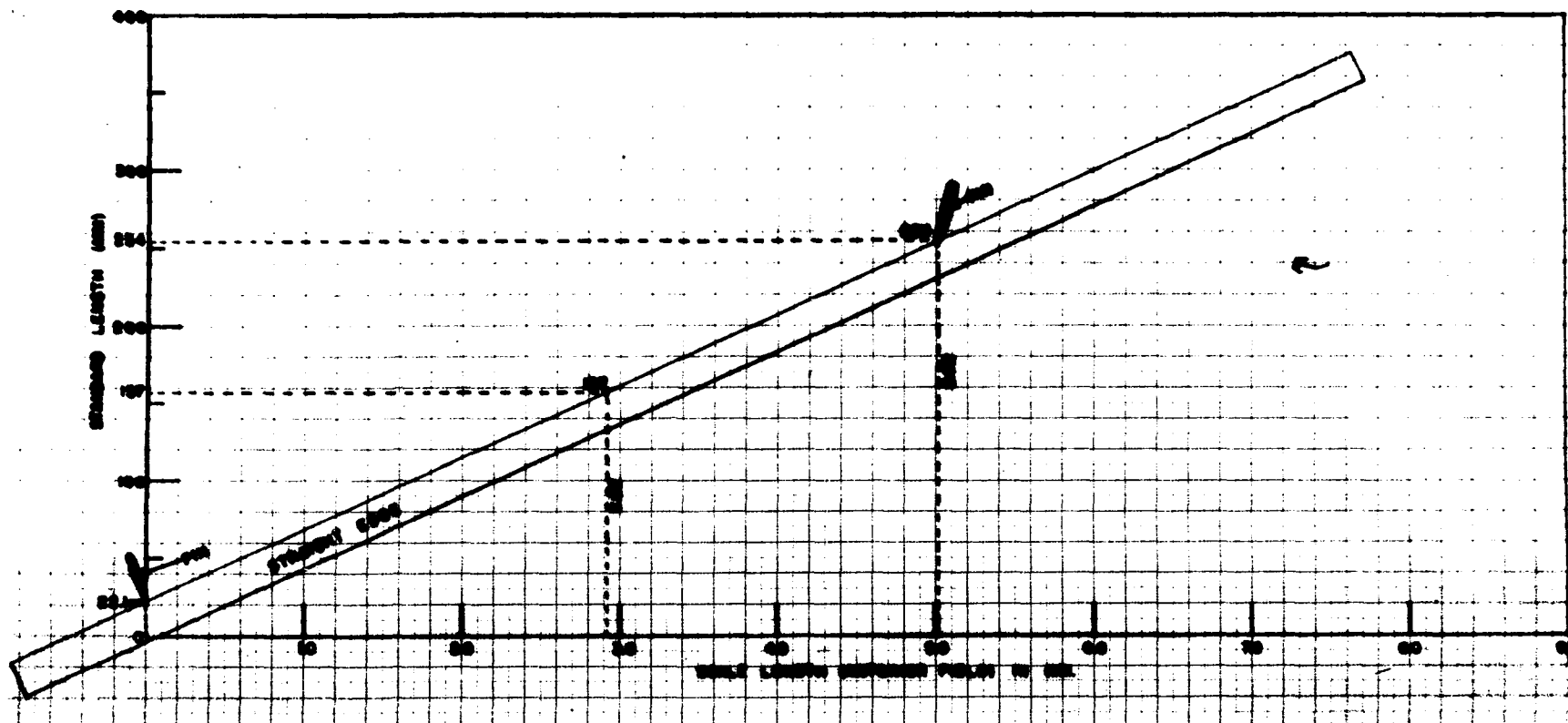


Figure 9. Illustration of Fish Length Calculation from Graph.

much, percentage-wise during the previous history of that fish. We must also assume that the intercept is fairly uniform for all the fish.

Sex Determinations.

Sex was always determined by dissection except for those fish from which eggs or milt were flowing during the spawning season. In the case of large fish sex was easily determined--the testis being white and homogeneous while the ovary was mostly a light yellow or pink and always had a semi-translucent appearance. In the case of small shad, after much practice and much study of histological preparations of their gonads, the sexes could be distinguished macroscopically frequently when the gonad was one millimeter in diameter, and readily when it attained a diameter of two millimeters. The minimum size (SL) fish which could be sexed with certainty was about 120 mm although an occasional larger sized shad could not be sexed. All fish larger than 120 mm (SL) were sexed when possible.

Vladykov (1945) states that males have darker fins, but I found this characteristic unreliable for distinguishing sexes. I was not able to find any external character which indicated with reasonable consistency the sex of the fish. Generally, however, one might suspect a shad which is relatively deep for its length, of being a

female.

Determination of Sexual Maturity.

Although a fish whose milt or spawn flows is sexually mature, the absence of this feature, even during the spawning season, does not indicate immaturity. Histological studies of ovaries obtained throughout the year have enabled me to recognize a potential spawner several months in advance of the spawning season, and spent females a month after having spawned, by gross observation of the ovaries. Fair sized eggs are clearly discernible through the ovarian wall several months prior to their being spawned. Minute, scarcely visible, eggs are also present. Completely spent females have only the minute eggs--as do those shad which will not spawn during that year. The ovaries of the spent female, however, are more flaccid, the minute eggs are some little distance apart, and the inter-ovule spaces are neither pinkish nor white but have a semi-translucent, watery appearance. For greater detail see Growth and Maturation of Eggs. In the case of males, maturity could not be determined in the absence of flowing milt. The presence of motile sperm obtained by lancing the testis does not assure maturity. Males examined in January had motile sperm--even the new 1-yr. males which would not fertilize eggs this spring! Maturity in males is undoubtedly associated with structural development which would

permit release of these sperms, and this release mechanism does not usually become functional in I-yr. males.

Determination of Fecundity.

Ovaries from May and June captures of potential spawners were used for egg counts. Since mature I-yr. shad were captured only in July, their ovaries are included.

For the egg counts the ovaries were weighed, a small transverse section (1 - 2 grams) of one ovary was weighed on an analytical balance, this season's eggs counted, and the number of eggs for the fish determined.

Stripping ripe fish does not yield accurate egg counts. Examination of ovaries after the most thorough stripping revealed the presence of a great many eggs, ready for expulsion but unable to be forced through the ovarian substance.

ANNULUS FORMATION

In 1953 no collections were made from May 22 to June 4; in 1954--none from May 20 to June 3. Up to the last collecting period prior to June 3 a new annulus had not been observed for any age group. Table 2, a composite of 1953 and 1954 collections, gives the percentages of the different age groups by sex which had formed the new annulus in each of the four time periods of June and July. It is noted that by the first period of June all the I-yr. shad had formed their new annulus. The II-yr. shad had almost all formed their new annulus by the end of the fourth period of June. The older shad appear to have formed theirs a week later--data for these ages are meager. This is in general agreement with Figure 15 which shows growth in length of the I-yr. shad beginning some time in May while that of older shad begins later.

Except when all have it present, the percent of females having the new annulus is generally in excess of that of the males in each period. Although the data are meager, I believe the female shad form their new annulus earlier than do the males--perhaps by as much as a week.

There is considerable variation in weight among female shad at this time due to differences in stages of spawning. The weight variation among males is less. Consequently, only males were employed in determining the effect of length and weight on earliness of annulus formation.

JUNE 1953-54

JULY 1953-54

| Latest Annulus | | June 1 June 8 | June 9 June 15 | June 16 June 23 | June 24 June 30 | July 1 July 8 | July 9 July 15 | July 16 July 23 | July 24 July 31 |
|-------------------|---|------------------|-------------------|--------------------|--------------------|------------------|-------------------|--------------------|--------------------|
| 1st | M | 100% | -- | 100% | 100% | 100% | 100%*** | 100% | 100% |
| | F | 100% | -- | 100% | 100% | 100% | 100%* | 100% | 100% |
| 2nd | M | 7.7%* | 1.2%*** | 24.1% | 93.3% | 100% | 87.5% | 100% | 100% |
| | F | 27.7% | 18.9% | 34.8% | 94.7% | 100% | 100% | 100% | 100% |
| 3rd | M | 0%*** | 0% | 0% | 50%*** | 75%* | 100%* | -- | -- |
| | F | 0%*** | 0%* | 0% | 76% | 100% | 100%* | -- | -- |
| 4th | M | -- | -- | 0%* | 0%*** | -- | -- | -- | -- |
| | F | 0%*** | -- | 0%* | 50%* | 100%* | 0%*** | -- | -- |
| 5th | M | -- | -- | -- | -- | -- | -- | -- | -- |
| | F | -- | -- | -- | 50%*** | 100%*** | -- | -- | -- |
| 6th | M | -- | -- | -- | 100%*** | -- | -- | 0%*** | -- |
| | F | -- | -- | 0%*** | -- | -- | -- | -- | -- |

Table 2. Percent of Shad Having the New Annulus in June and July.

*** = One Individual in Sample.

* = Five or Less Individuals.

Investigations of II-yr. male gizzard shad, having and not having formed the new annulus, show that neither length nor weight are determining factors in earliness of annulus formation.

To determine the effect of spawning on earliness of annulus formation, II-yr. 'not spawned' and 'spent' female shad were compared. Spawning did not appear to either hasten or to retard the time of annulus formation.

LENGTH RELATIONSHIPS

TL/SL and Depth/SL.

The plotting of total lengths of gizzard shad against their corresponding standard lengths indicated a straight line relationship. By means of the least squares method, the regression line $TL = 4.9 + 1.23(SL)$ was obtained. For this relationship 611 fish varying from 20 mm to 380 mm (SL) were employed.

The regression line obtained for depth/standard length is $D = 0.998 + 0.349(SL)$.

Lengths of Age Groups at Capture.

Table 3 shows the lengths of captured fish by age groups (determined from scales). The sexes have been combined.

In Table 4 are summarized the average standard lengths of the age groups by sex. The lengths were taken of fish captured in January, February, March, April, and May for all ages. For the II-yr. group, June captures were included, and for the III-yr. and older groups, July captures were included. During these periods the lengths of the fish are rather stable--active growing has not yet begun. Since these lengths will be compared with calculated lengths, and calculated lengths are based on the presence of annuli, only fish not having the new annulus during the last month mentioned were included. Since annulus form-

| STANDARD LENGTH (MM) | I-YEAR | | II-YEAR | | III-YEAR | | IV-YEAR | | V-YEAR | | VI-YEAR | |
|-----------------------|----------|------------|----------|------------|----------|------------|----------|------------|----------|------------|----------|------------|
| | CAPTURED | CALCULATED | CAPTURED | CALCULATED | CAPTURED | CALCULATED | CAPTURED | CALCULATED | CAPTURED | CALCULATED | CAPTURED | CALCULATED |
| 390 | -- | -- | -- | -- | -- | -- | -- | -- | 1 | 1 | -- | -- |
| 380 | -- | -- | -- | -- | -- | -- | 1 | 3 | 3 | 1 | 2 | -- |
| 370 | -- | -- | -- | -- | -- | -- | 5 | 2 | -- | -- | -- | -- |
| 360 | -- | -- | -- | -- | 5 | -- | 7 | 3 | -- | -- | -- | -- |
| 350 | -- | -- | -- | -- | 9 | 3 | 3 | 1 | 1 | 2 | -- | -- |
| 340 | -- | -- | -- | -- | 31 | 8 | 1 | 2 | -- | -- | -- | -- |
| 330 | -- | -- | 1 | -- | 32 | 7 | 5 | 2 | -- | -- | -- | -- |
| 320 | -- | -- | 3 | 8 | 21 | 2 | 3 | -- | -- | 1 | 1 | 1 |
| 310 | -- | -- | 26 | 15 | 19 | 6 | -- | 1 | -- | -- | -- | -- |
| 300 | -- | -- | 77 | 27 | 13 | 5 | -- | -- | -- | -- | -- | -- |
| 290 | -- | -- | 206 | 68 | 3 | 2 | -- | -- | -- | -- | -- | -- |
| 280 | -- | -- | 286 | 57 | 1 | 2 | -- | -- | -- | -- | -- | -- |
| 270 | -- | -- | 243 | 49 | 1 | -- | -- | -- | -- | -- | -- | -- |
| 260 | -- | -- | 115 | 28 | -- | -- | -- | -- | -- | -- | -- | -- |
| 250 | -- | -- | 36 | 17 | -- | -- | -- | -- | -- | -- | -- | -- |
| 240 | -- | -- | 19 | 4 | -- | -- | -- | -- | -- | -- | -- | -- |
| 230 | -- | -- | 5 | 5 | -- | -- | -- | -- | -- | -- | -- | -- |
| 220 | -- | -- | 1 | 3 | -- | -- | -- | -- | -- | -- | -- | -- |
| 210 | -- | 1 | 1 | 1 | -- | -- | -- | -- | -- | -- | -- | -- |
| 200 | 9 | 10 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 190 | 37 | 22 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 180 | 85 | 46 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 170 | 121 | 52 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 160 | 126 | 65 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 150 | 67 | 80 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 140 | 50 | 91 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 130 | 34 | 104 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 120 | 36 | 79 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 110 | 25 | 75 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 100 | 5 | 49 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 90 | 3 | 33 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 80 | 1 | 6 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 70 | -- | 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| AVERAGE | 157.3 | 137.7 | 277.6 | 279.2 | 325.8 | 320.6 | 350.0 | 354.3 | 376.0 | 358.0 | 360.0 | 320.0 |
| NUMBER OF INDIVIDUALS | | | | | | | | | | | | |

Table 3. Comparison of the Lengths of Captured Fish and the Calculated Lengths at Each Age (Sexes Combined).

| | Average Standard Length of Captured Shad (mm) | | Average Calculated Standard Length of Shad (mm) | |
|---------|---|-------|---|-------|
| | M | F | M | F |
| I-yr. | 164.8 | 162.1 | 138.5 | 139.9 |
| II-yr. | 272.7 | 283.0 | 274.8 | 288.2 |
| III-yr. | 313.0 | 334.6 | 312.5 | 334.9 |
| IV-yr. | 327.5 | 360.6 | 335.0 | 362.0 |
| V-yr. | 350.0 | 382.5 | 335.0 | 370.1 |
| VI-yr. | 340.0 | 360.0 | | |

Table 4. Average Lengths by Sex of All Age Groups
--Lengths of Captured Shad Compared with
Calculated Lengths.

| Age Group | MM Female is longer than Male | |
|--------------|-------------------------------|------------|
| | Captured | Calculated |
| I-yr. | -2.7 | 1.4 |
| II-yr. | 10.3 | 13.4 |
| III-yr. | 21.6 | 22.4 |
| IV-yr. | 33.1 | 27.0 |
| V-yr. | 32.5 | 35.1 |
| VI-yr. | 20.0 | |

Table 5. Comparison of the Sex Differences
between Lengths of Captured Fish
and Calculated Lengths at Different
Ages.

ation varies with age the last month for I-yr. group is May, for the II-yr. group, June, and for the older groups, July. Collections are those for 1953, 1954, and for 1955 to May 16.

It will be noted that the females in all age groups except the I-yr. group have a greater average length than have the males. For the different ages the average sex differences in lengths are given in Table 5.

Calculated Lengths.

The calculated lengths (sexes combined) of the various age groups of shad are given in Table 3. The average calculated standard lengths of the age groups by sex are summarized in Table 4. It will be noted that in every age group the females attained a greater average length than did the males. Except for the I-yr. group this is in general agreement with the length differences noted among captured fish in Table 4. The average calculated sex differences are given in Table 5.

The data for the captured fish extend over the collecting periods (1952, 1953, and 1954), while those for the calculated lengths extend over the years during which the shad had at least one annulus (1948, 1949, 1950, 1951, 1952, 1953, and 1954). The period covered by the data of captured fish and the calculated data overlap but are not of identical year classes. Nevertheless, there is a fairly good degree of correlation for all age groups.

WEIGHT RELATIONS

Length/Weight Relations.

The length/weight relationship of Western Lake Erie gizzard shad is given in Figure 10. Empirical data are included for comparison with the curve which was constructed using the general length/weight formula.

For the empirical data the shad whose lengths ranged between two successive centimeters were averaged--both lengths and weights. Samples were selected at random from each month's collections. These samples, covering 26 months, were pooled for the general length/weight relationship data. The general length/weight formula is:

$\text{Log } W = -4.71241 + 3.02313 (\log SL)$. Considering that seven age groups and every season of the year are represented, the agreement between empirical and calculated weights is good.

Seasonal Fluctuations.

During the course of collecting and recording data, it was noticed that shad of a given length differed in weight from month to month. To minimize the differences individual fish or certain lengths may appear to bring about, length/weight relationship formulae were determined for each month's collections. The formulae for the monthly pooled length/weight relationships are given in Table 6. It will be noted that variations occur from

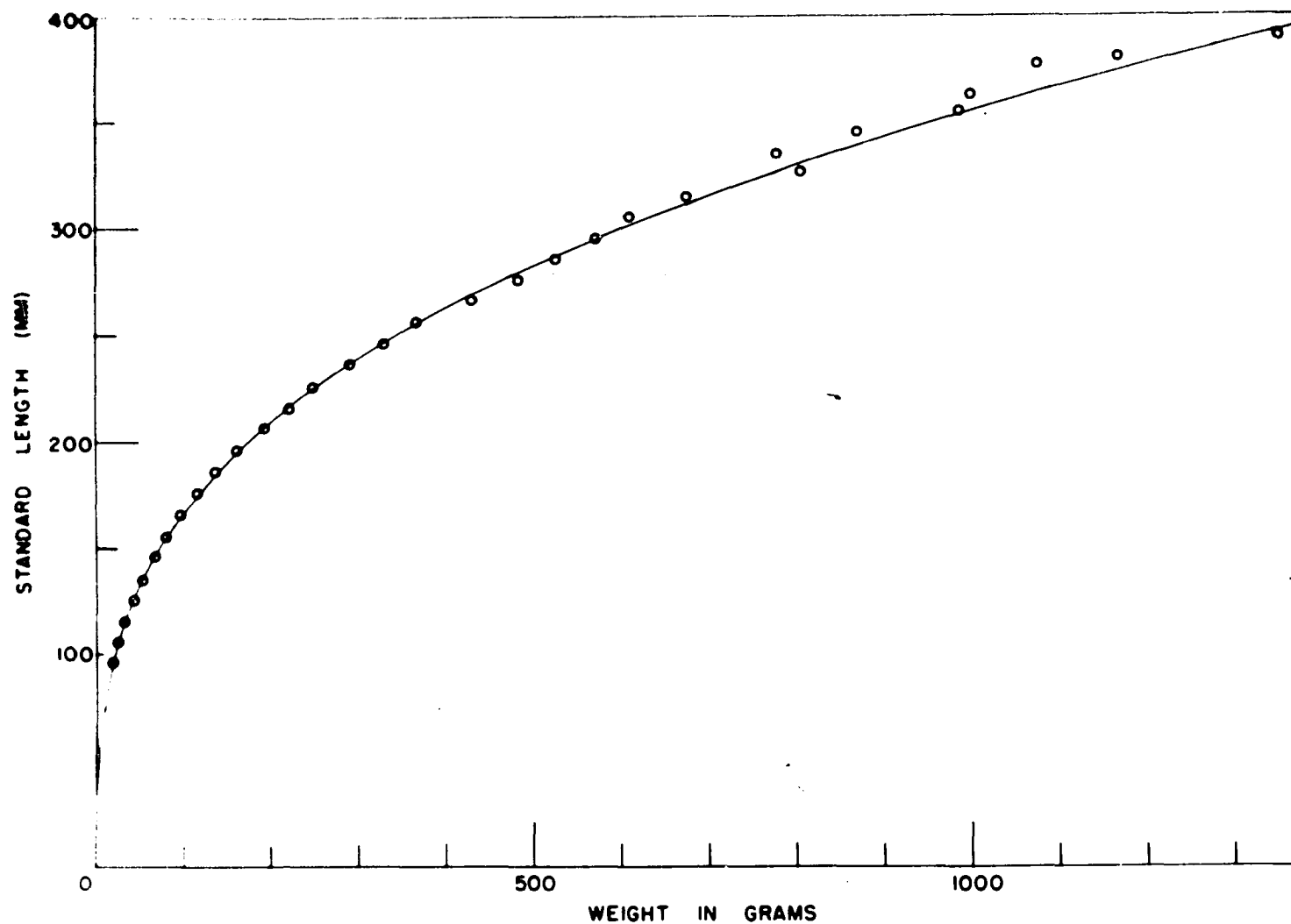


Figure 10. Length/ Weight Curve for Western Lake Erie Gizzard Shad Compared with the Empirical Data.

month to month. To make these formulae more meaningful, a theoretical fish, 200 mm long, was selected for each month and its weight calculated using each month's length-weight formula. The result is given in Figure 11.

| Date | Formulae | | | | Number of Months Included |
|-------|----------|----------|---|------------------|------------------------------------|
| Jan. | Log W= | -5.05176 | + | 3.17062 (log SL) | 2 |
| Feb. | Log W= | -4.93132 | + | 3.11525 (log SL) | 3 |
| Mar. | Log W= | -4.82163 | + | 3.07333 (log SL) | 1 |
| Apr. | Log W= | -5.46595 | + | 3.34044 (log SL) | 2 |
| May | Log W= | -5.08826 | + | 3.15994 (log SL) | 2 |
| June | Log W= | -4.59729 | + | 2.96419 (log SL) | 2 |
| July | Log W= | -4.29293 | + | 2.85248 (log SL) | 2 |
| Aug. | Log W= | -4.54217 | + | 2.96920 (log SL) | 3 |
| Sept. | Log W= | -4.47117 | + | 2.92328 (log SL) | 1 |
| Oct. | Log W= | -4.97008 | + | 3.14735 (log SL) | 2 |
| Nov. | Log W= | -4.55154 | + | 2.95952 (log SL) | 2 |
| Dec. | Log W= | -4.78471 | + | 3.05737 (log SL) | 2 |

Table 6. Monthly Composite Length/Weight Formulae.

Beginning with January, it will be noted that the theoretical 200 mm shad weighs progressively less until it reaches a low value of 152.4 grams in May. Then it becomes increasingly heavy until it reaches a peak of 195.0 grams in August after which it steadily declines in weight. It appears to make its greatest gain in weight between June and July and drops most rapidly between April and May.

This is, of course, theoretical for there are very few 200 mm shad before June (the fastest growing 1-yr. fish) and very few after July (the more retarded ones).

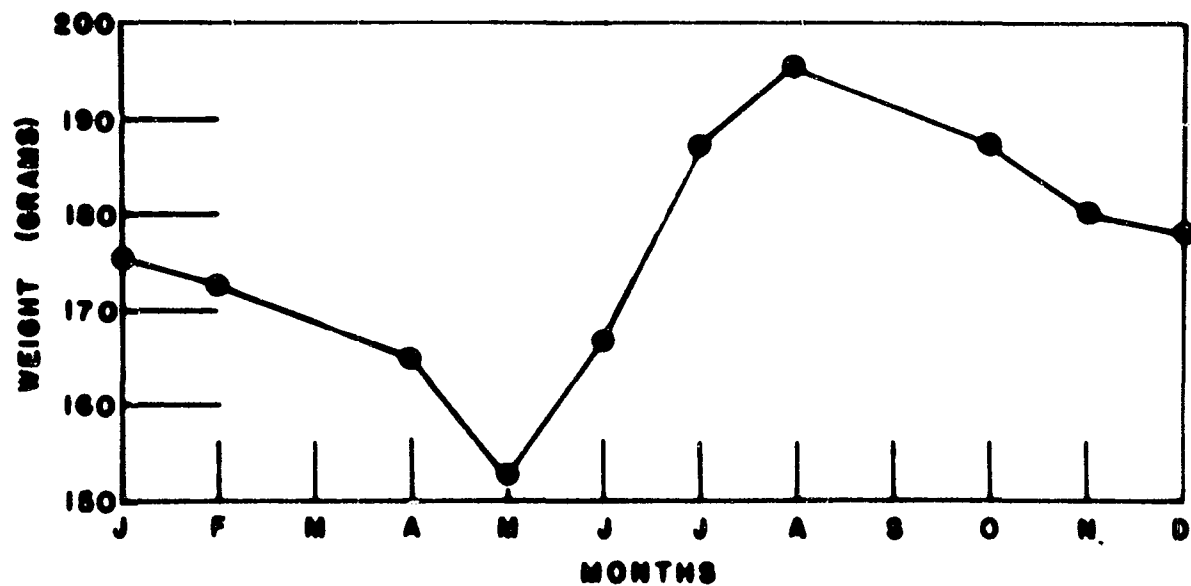


Figure 11. Monthly Weights of Theoretical 200 mm Shad (Averages for 1953 and 1954--March and September excluded as there was Only One Collection in Each Large Enough for Inclusion).

Nevertheless, it was interesting to speculate on how great a weight fluctuation a fish of this size would undergo during the course of the year.

Annual Fluctuations.

In the course of collecting it was noted that seasonal fluctuations of one year followed closely that of other years. However, they were not identical. Many variables are present from one year to another--the most obvious are differences in year class composition, and yearly environmental differences (temperature, food etc.).

To learn whether it is year class composition differences or environmental differences which effect the greatest change in the length/weight relationship from one year to another, the length/weight relationships for 1952, 1953, and 1954 were compared. Since I am interested here in the end results due to one or the other of the factors involved, I chose August as the month for comparison. This is the only month for which I have adequate data for all three years. By this time the yearly growth in weight has attained its peak and the older fish are free from the disturbing effects of spawning. The hatch of 1952 was compared with these. The hatch of 1952 consisted of the 0-yr. fish of August 1952, the I-yr. fish of August 1953, and the II-yr. fish of August 1954. See Figure 12. Empirical data are given for each curve.

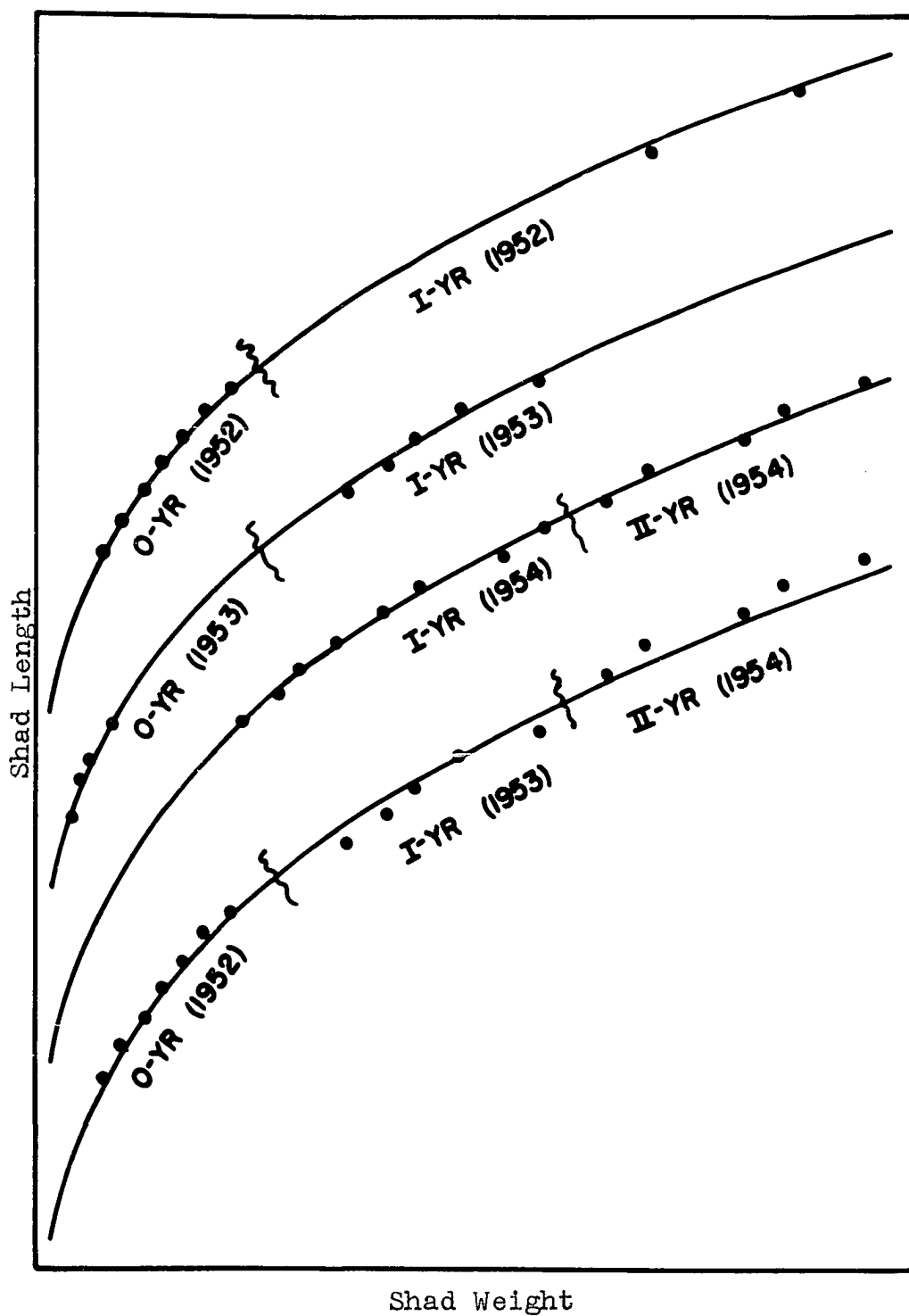


Figure 12. Length/Weight Curves for Growth Years 1952, 1953, and 1954 Compared with That for Hatch of 1952 (Empirical Data Shown by Dots).

It will be noted that length/weight curves for the August collections of 1952, 1953, and 1954, in each instance, come into close relationship with the empirical length/weight data, while the length/weight curve for the 1952 hatch as taken through the Augusts of 1952, 1953, and 1954 widely misses many of the empirical length/weight data. It would appear that a different curve would best fit each yearly segment of the empirical data for the 1952 hatch.

It would seem that the environmental conditions obtaining during the year affect all ages rather similarly so that a smooth curve adequately penetrates empirical length/weight data of all ages. It would also seem that fish having a low 'coefficient of condition'--low weight per unit length--during one year, will have a higher one next year if environmental conditions are more favorable. Thus, a year hatch, if followed through several years, will show different degrees of 'plumpness' during these years.

The length/weight relationships of shad, here, then, are not expressions of differences in hatches, but rather they are expressions of environmental conditions present as portrayed by the shad growth.

Coefficient of Condition.

I did not use 'coefficient of condition' as derived from the formula $K = \frac{100,000 W}{L^3}$ in comparing sea-

sonal and annual variations in length/weight relationships among shad. Since the coefficient of condition ratio varies with fish length it was thought simpler to use one fish length and by means of the appropriate length/weight formulae get the weights for that length during the seasons in question. However, should one want the 'coefficient of condition' he can arrive at it by substituting the weight equivalent of the length/weight formula for the W in the formula $K = \frac{100,000 W}{L^3}$. This gives him $K = \frac{100,000 CL^n}{L^3}$ and using logarithms he gets: $\text{Log } K = \frac{5.0 + \log C + n \log L}{3 \log L}$. Using the length/weight formula gets away from individual fish variations.

Western Lake Erie Gizzard Shad Compared with Those from Other Regions.

Patriarche and Lowry (1953) found that the shad in the Black River Basin of Missouri had a length/weight relationship of $\text{Log } W = -2.2071 + 2.9812 (\text{Log } L)$, while Lagler and Van Meter (1950), working on this fish in Illinois, report the relationship as being $\text{Log } W = -2.2789 + 3.034 (\text{Log } L)$. In both cases weight is in terms of ounces and length is total length in inches. Converting them into terms of grams for weight and millimeters for length (as standard length) I get:

$$\begin{aligned}\text{Missouri--Log } W &= -4.53455 + 2.93163 (\text{Log } SL) \\ \text{Illinois--Log } W &= -4.66813 + 2.98135 (\text{Log } SL)\end{aligned}$$

Figure 13 gives a comparison of the length/weight curves

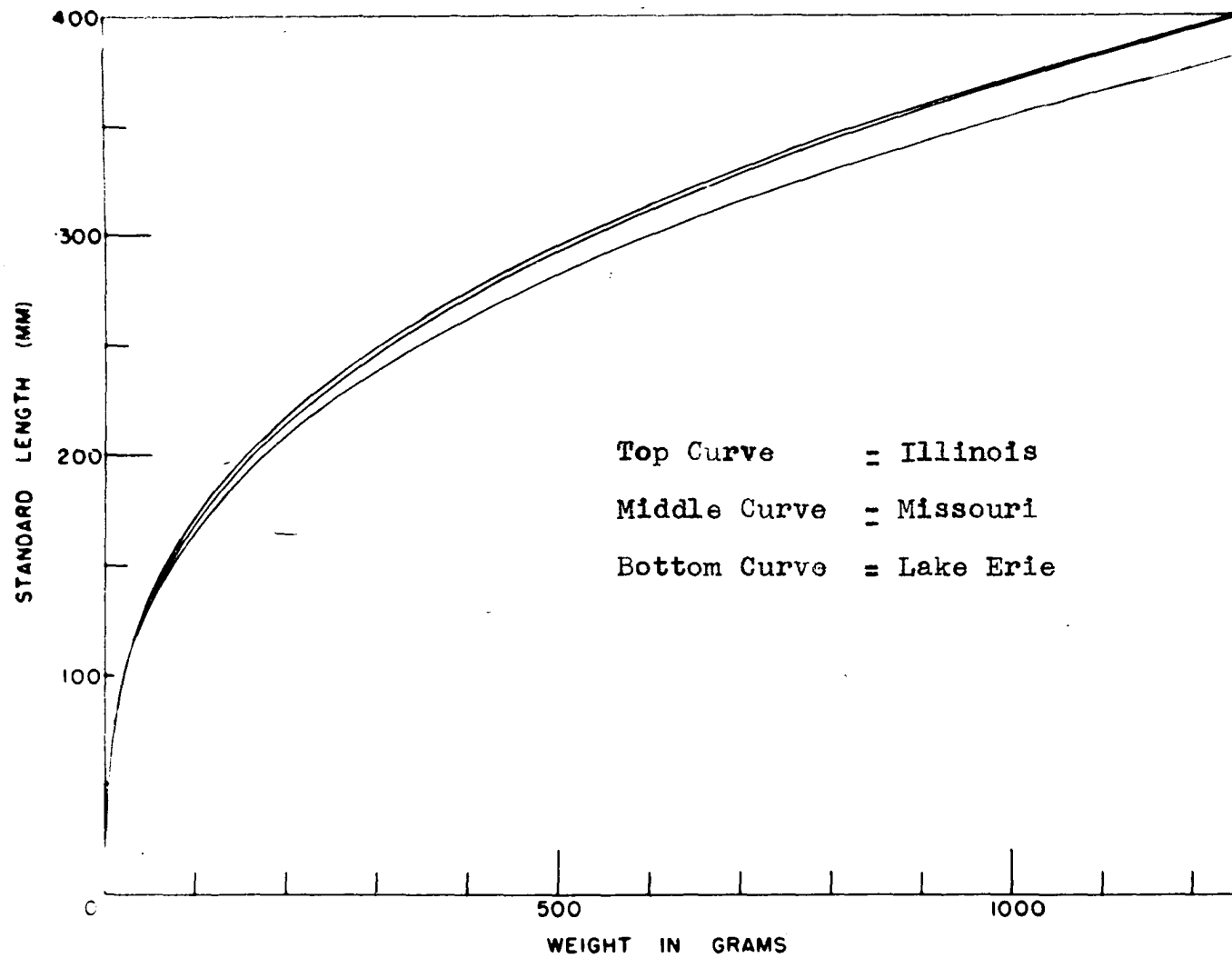


Figure 13. Comparison of Length/Weight Curves for Gizzard Shad from Three Regions.

for Missouri, Illinois, and Western Lake Erie gizzard shad. The shad here are heavier, length for length, than are those studied in Missouri and Illinois.

GROWTH

Seasonal Growth in Length.

Attempts at following seasonal growth of gizzard shad by periodic recaptures of tagged individuals were unsuccessful. To date, no recaptures resulted from tagging 600 shad during the winter of 1952.

However, the monthly captures give us some idea of their seasonal growth. See Figures 14 and 15. From the latter figure it is noted that growth in length begins earlier in the year (May) for the I-yr. fish than for those older; proceeds rapidly during the summer months; comes to a close in November; and does not resume again until the following June. All age groups appear to follow this pattern, although the amount of growth for the year becomes less with increasing age. The most rapid growth in length for all ages occurs between May and October. The amount and percentage of growth during the best three months is given for each age group in Table 7. The data are obtained from Figure 15.

| Age | Yearly Growth (MM) | Growth During 3 Months (MM) | %Growth During 3 Months | 3 Best Growing Months |
|-----|--------------------|-----------------------------|-------------------------|-----------------------|
| 0 | 143.0 | 105.0 | 73.4 | July Aug. Sept. |
| I | 132.0 | 87.0 | 65.9 | May June July |
| II | 45.0 | 28.0 | 62.2 | July Aug. Sept. |
| III | 22.2 | 19.8 | 89.2 | May June July |
| IV | 19.4 | 15.8 | 81.4 | May June July |
| V | 17.8 | 14.3 | 80.3 | May June July |

Table 7. Growth in Length of Shad for the Year and for the Three Best Growing Months.

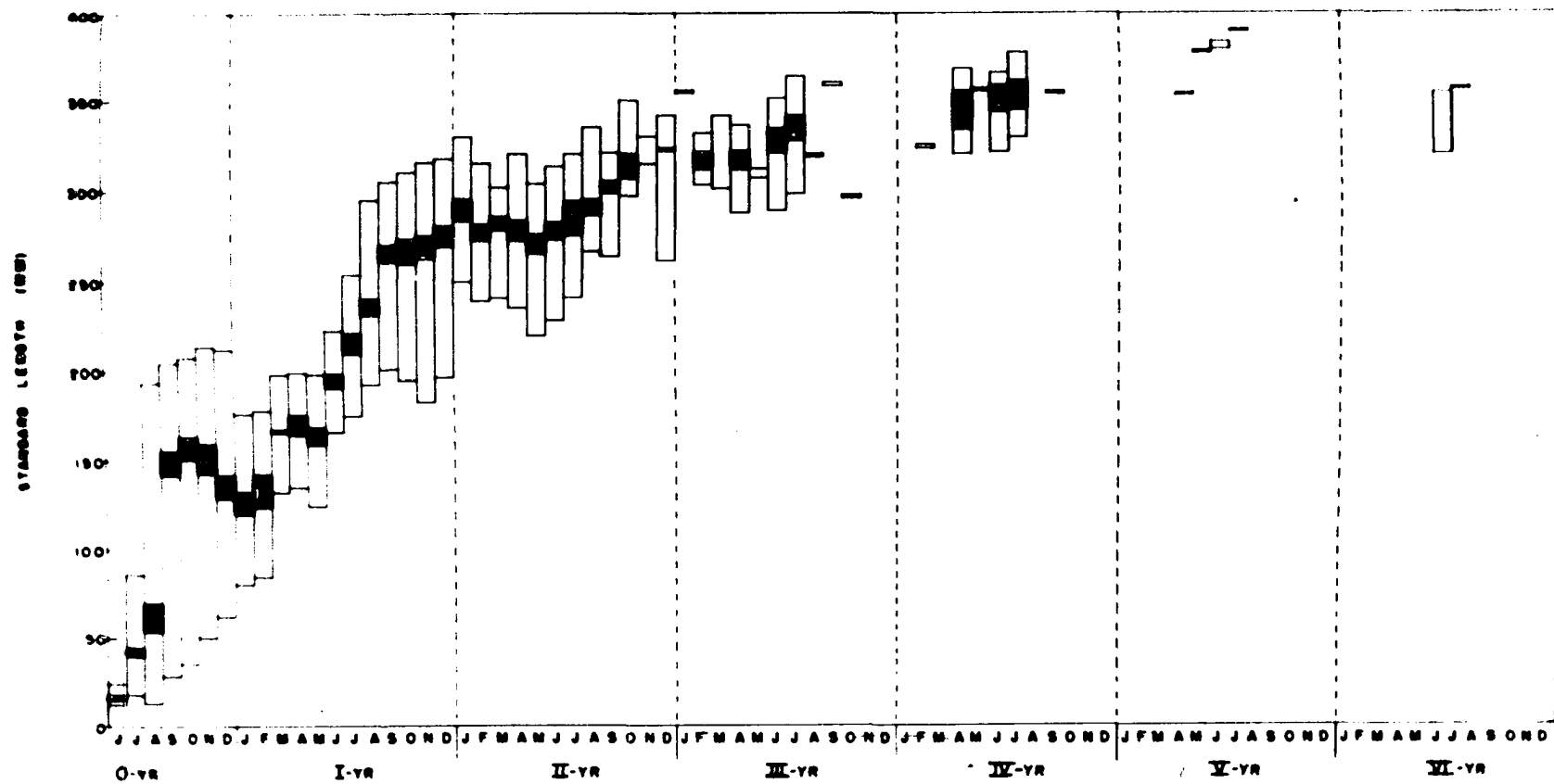


Figure 14. Frequency Distribution of Shad (Data of 1952-53-54 Pooled).
(The Range and Middle $\frac{1}{4}$ Population of Each Age Is Indicated by Months).

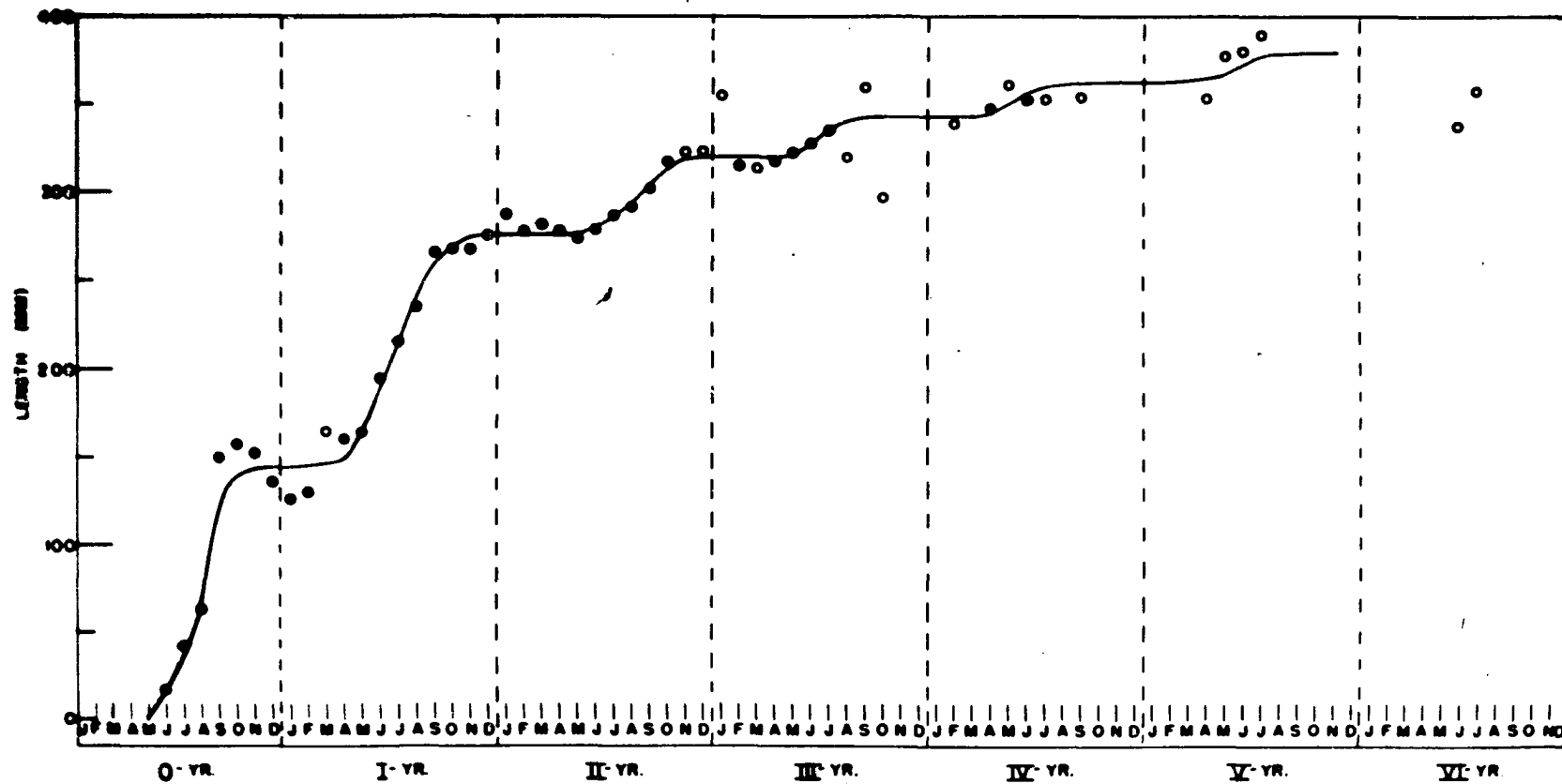


Figure 15. Shad Length Growth by Months. Circles and Dots are Empirical Averages (Sexes Combined). Circles Indicate 5 or Less Individuals. Curve is Drawn by Inspection.

Since the gizzard shad in Western Lake Erie spawns mostly from mid-May to mid-July, every collection, except a very early one, will usually contain members of different hatches which differ in ages from a few seconds to several days or weeks. These raw collections will usually yield low length averages due to the greater percentage of the newer, smaller members present. I have concluded that the way to handle the early growth problem of a changing population, whose membership is continually supplemented by recent hatches, is to try to follow the several hatches present in an early collection through a succession of days by frequent sampling.

In each subsequent collection, those groups were discarded which fell short of the lowest group of the preceding collection.

By this means, assuming June 1st as the hatching date, I arrived at the early growth pattern (Figure 16) of newly hatched shad in Fishery Bay in 1954.

During the first day or two after hatching the shad does not eat--subsisting only on its yolk.

Increase in length during this time is due mostly to the straightening of the cephalic flexures. See Figure 17. During the interim between the 20 mm and the 30 mm lengths it slowly transforms its shape from a long filiform larva into the slab-sided deep bodied form of the adult.

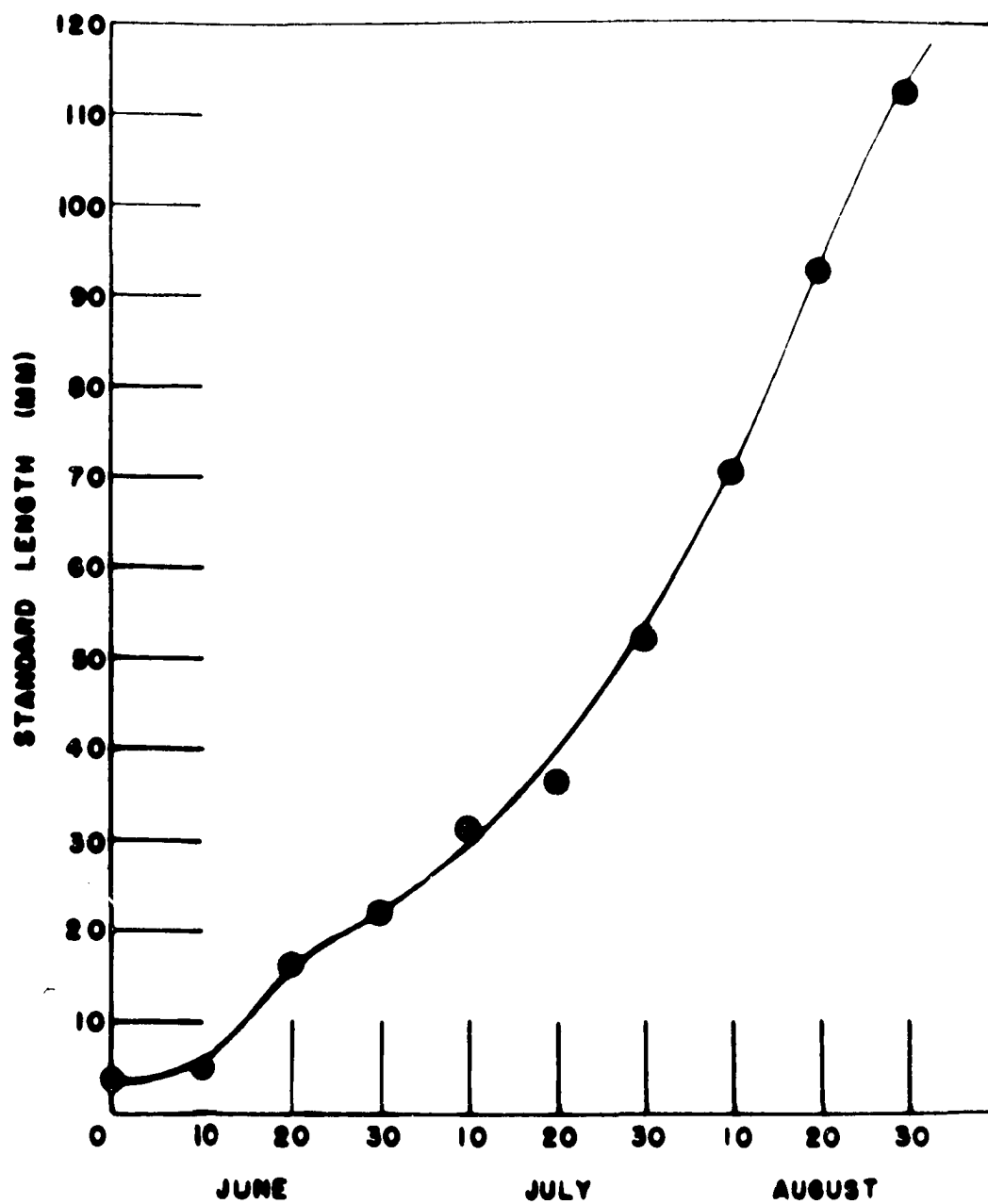
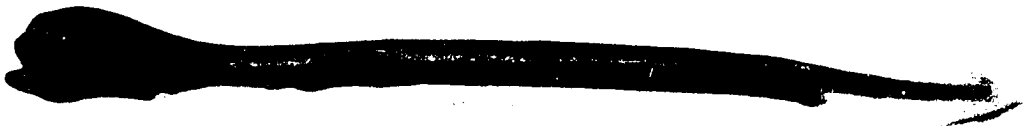


Figure 16. Growth in Length of Very Young Shad.



Newly Hatched--3.5 mm (SL).



4 Days Old--5.2 mm (SL).



10 Days Old--6.2 mm (SL)

Figure 17. Early Growth Stages of the Gizzard Shad Fry.

During this transformation, increase in length has slowed down--note Figure 16.

Seasonal Growth in Weight.

To get a picture of the seasonal growth in weight see Figure 18. Since weight is roughly a cubical function of length, the average of the weights of an age group during a given month would exceed the actual weight of the average length fish, hence, the average weights of these fish were arrived at by using the appropriate monthly length/weight formulae given on page 43.

It will be noted that seasonal growth in weight follows the pattern of that in length--except that between the peak weight attained by an age group during one year and the resumption of growth during the following year, there is a decrease in weight. This decrease is most pronounced during early May. For this phenomenon I offer the following explanation: Studies of the gut contents indicate that shad consume little food during the winter and early spring. During this period they subsist largely on the energy stored in the body tissues. Low metabolic rates during the winter decrease the original body weight slightly. As the water temperature rises during early spring, the metabolic rate of the fish increases and the body weight decreases more rapidly. This process gains momentum with the progression of spring until apparently the

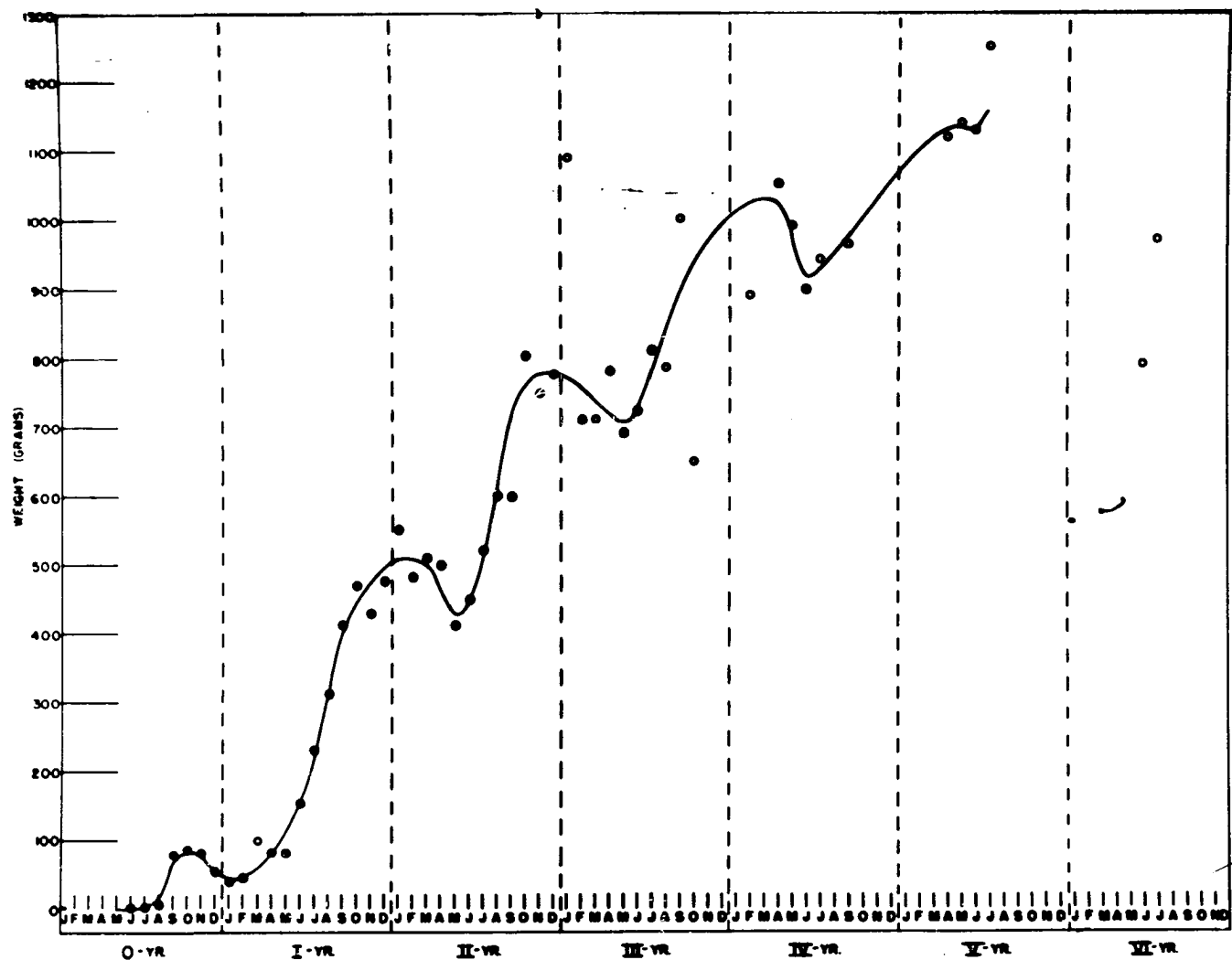


Figure 18. Shad Weight Growth by Months. Circles and Dots are Calculated Weights of Av. Length Fish. Circles Indicate 5 or Less Individuals. Curve is Drawn by Inspection.

lowest body weight is attained just before renewed feeding begins to meet the energy requirements of the fish.

Annual Growth--Length and Weight.

Annual growth in length of Western Lake Erie gizzard shad has been given in Table 4. Although there are slight variations from year to year, I believe they warrant only a few words of explanation. When the annual growth of the hatches of 1948 to 1954 were compared there were no obvious fast-growing hatches. However, when they were compared on the basis of 'growth years' there appeared the tendency for some years to produce greater shad lengths for all ages.

Differential length growth of the sexes was given in Table 5.

Annual growth in weight can best be obtained from Figure 18.

Compensatory Growth in Length.

In following the progress of growth in length of the gizzard shad by seasons two things become obvious regarding future growth. One is that the larger shad of a year group maintain a length advantage over the smaller shad during subsequent growth. The other is that the smaller shad of a year group grow more rapidly in subsequent years than do the larger ones; consequently, the length difference becomes progressively smaller.

Aside from rearing marked fish and measuring them periodically (which I was unable to do), the best way to note this is to compare the fish length at capture with the calculated size at the last annulus on its scales.

The figures used to illustrate amount of growth, maintenance of length advantage, and compensatory growth follow the pattern of Figure 19.

It should be made clear that the growth in length made each year of a fish's life (as calculated from scales) is represented by the interim between annuli and that the growth made subsequent to the time when the last annulus was formed is represented by the distance between that annulus and the scale edge. Since I am discussing compensatory growth in terms of inter-annular distances on the shad's scales these distances are, in reality, measurements of fish length as calculated from the scale data and not the actual measurements of scale parts.

In Figure 19 the ordinate represents gizzard shad length at the time of first annulus formation. The abscissa represents gizzard shad length at all ages. Line A represents the first annulus on both the ordinate and the abscissa. Lines B, C, and D are possible regression lines (in terms of the 1st annulus) of a subsequent annulus or of the scale edge. On the abscissa the distance between 0 and line A, denotes the amount of shad growth to the time of

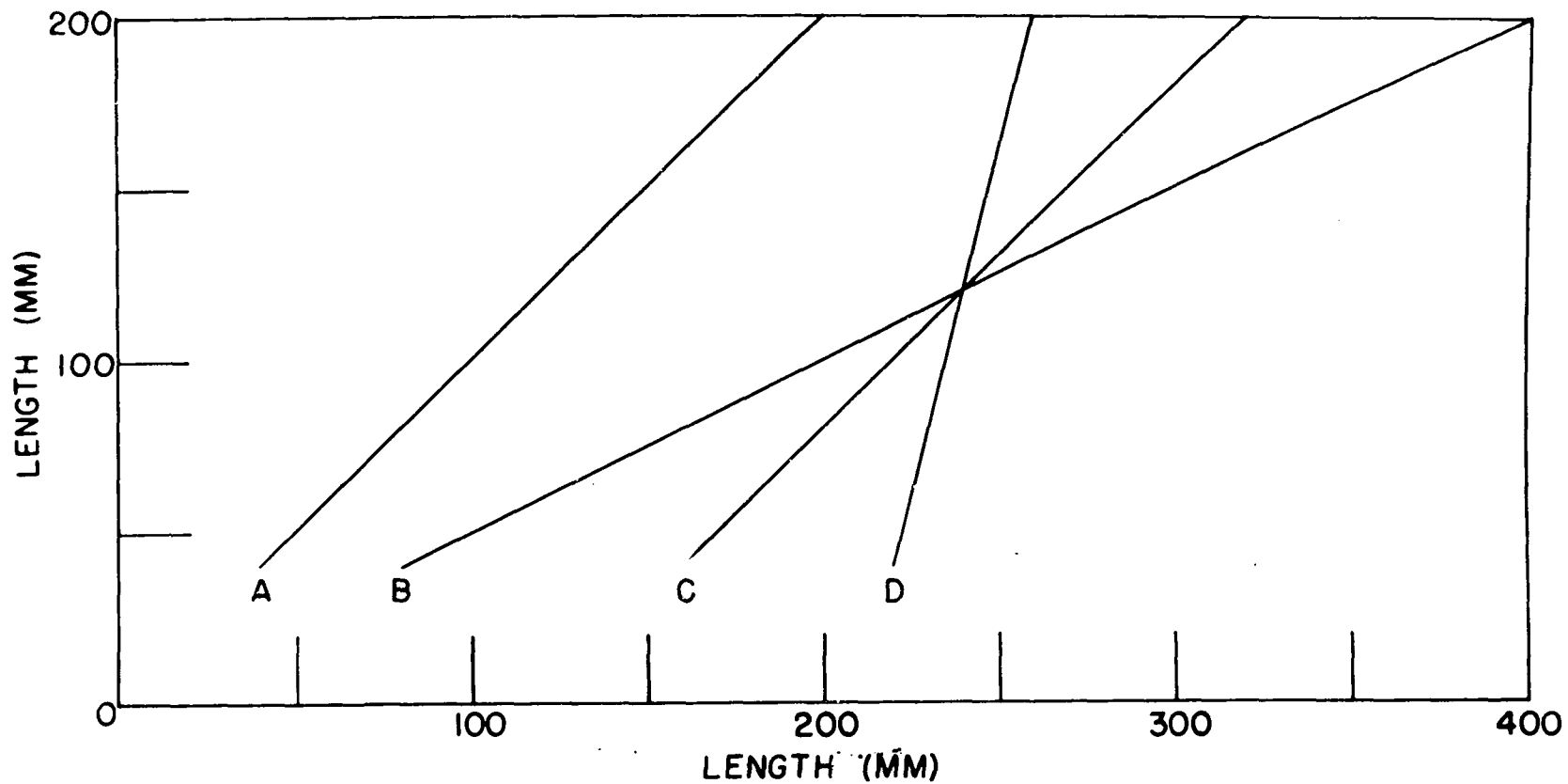


Figure 19. Pattern: Shad Length at 1st Annulus vs. Length at Subsequent Annuli or Scale Edge.

first annulus formation. The distance between O and lines B, C, or D represents shad growth to that landmark, while the distance from line A to one of these lines represents shad growth from the time of first annulus formation to the landmark selected. Assuming line B, C, or D to be the second annulus, if the rate of the first year's growth is maintained during the second year, the regression line of the second annulus will assume position B. That is, the longer shad of the first year will augment its length advantage over the smaller shad during the second year. If, however, the growth of large and small one year shad are similar during the second year, the regression line of the second annulus will assume position C--the longer first year shad merely maintains its length advantage. But if the smaller one year shad grow faster during the second year than do the larger shad, then the regression line of the second annulus will assume position D. This is compensatory growth as shown by scales.

Seasonal compensatory growth becomes evident shortly after the first annulus is produced, and its progress can be followed by a study of the scales of shad captured at regular intervals thereafter. For illustration, the compensatory growth of II-yr. shad is given, month by month for the year in Figure 20.

The formulae for the regression line of the scale edge (length at capture) in terms of the length at the first

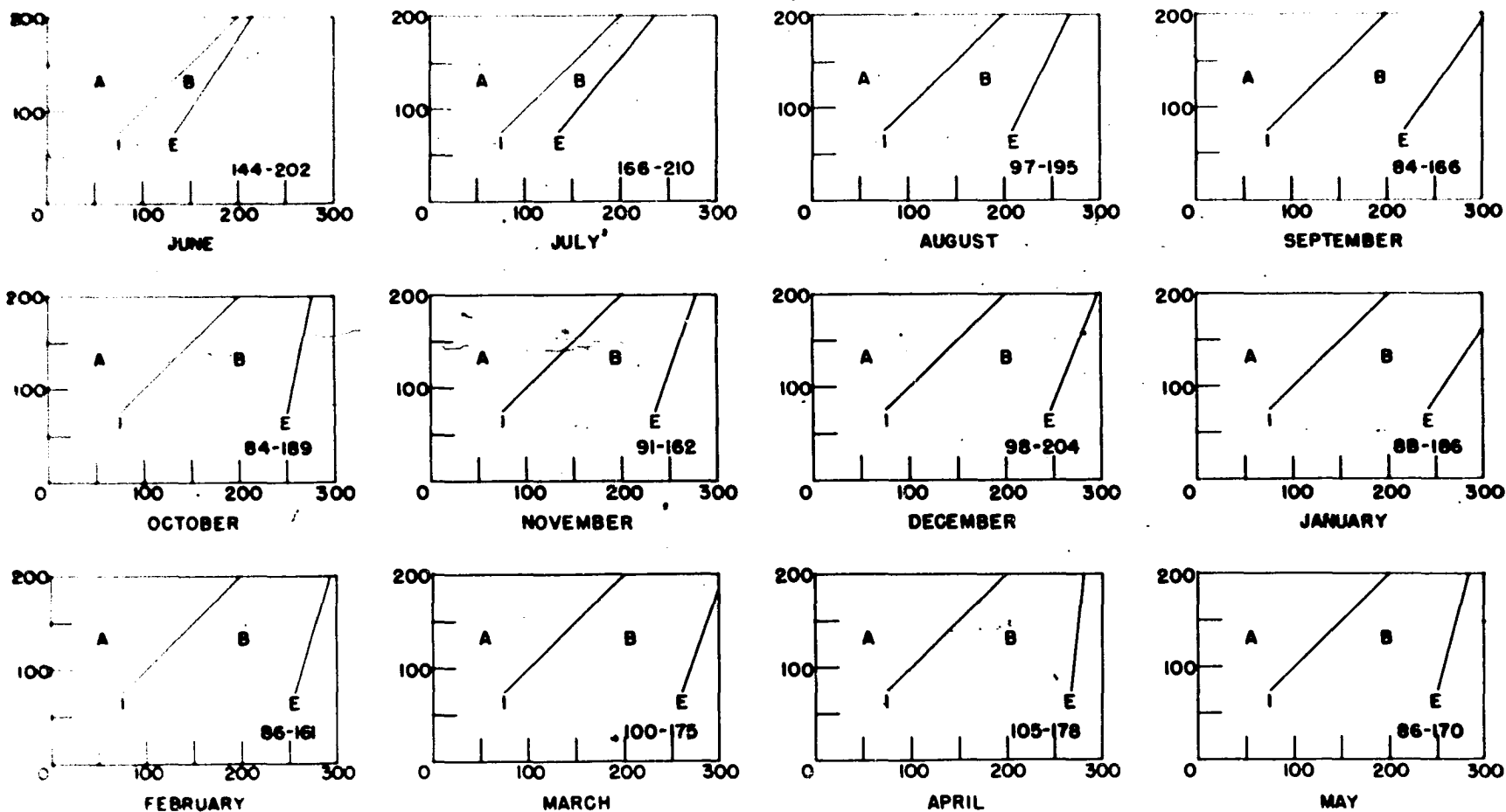


Figure 20. Seasonal Regression Lines (Formulae of Table 8) Showing Compensatory Growth in Length of II-yr. Shad (1 = 1st Annulus E = Scale Edge).

annulus on which Figure 20 is based are given in Table 8.

| | | | | | | | | |
|-------|--------|----|---------|---|--------|---|-------|-----------|
| June | Length | at | Capture | = | 83.02 | + | 0.663 | (1st An.) |
| July | " | " | " | = | 74.95 | + | 0.819 | " " |
| Aug. | " | " | " | = | 171.02 | + | 0.495 | " " |
| Sept. | " | " | " | = | 165.32 | + | 0.706 | " " |
| Oct. | " | " | " | = | 233.99 | + | 0.225 | " " |
| Nov. | " | " | " | = | 209.74 | + | 0.339 | " " |
| Dec. | " | " | " | = | 257.85 | + | 0.198 | " " |
| Jan. | " | " | " | = | 192.2 | + | 0.678 | " " |
| Feb. | " | " | " | = | 235.01 | + | 0.302 | " " |
| Mar. | " | " | " | = | 233.68 | + | 0.357 | " " |
| Apr. | " | " | " | = | 259.82 | + | 0.107 | " " |
| May | " | " | " | = | 231.02 | + | 0.262 | " " |

Table 8. Monthly Formulae for Scale edge/1st
Annulus for II-yr. Shad.

It is noted from Figure 20 that compensatory growth is most rapid earliest in the season. The data for each monthly representation of compensatory growth were obtained from ten male and ten female shad whenever possible. To meet this number, sometimes shad collected during the same month but in different years were used. Too, the same shad population was not sampled throughout the year. I think it is largely because of these failings that the compensatory growth picture shown by the slope and the distance of scale edge regression line E does not progress more smoothly.

The older shad give the same type of compensatory growth picture during the year. The amount of compensation, however, becomes more and more reduced as the fish grows older.

Figure 21 shows theoretical monthly growth curves (produced from the formulae of Table 8) for shad of 100 mm and 175 mm S. L. at the first annulus.

The smaller shad (at first annulus) grows faster and more during the year after the first annulus was produced than does the larger one.

Figure 22 shows the original 75 mm differences between the large and small shad being reduced until by December it is about 21 mm.

While compensatory growth in length during the interim between the 1st and 2nd annuli formations is quite obvious, there is no such compensation in weight during this same period. The weight advantage of the 1st year is maintained and strengthened during the 2nd year.

Figure 23 shows a comparison of the weight progress of the 100 mm and the 175 mm (at 1st annulus) shad. The weights were calculated by means of the length/weight formula $\text{Log } W = -4.71241 + 3.02313 (\text{log } SL)$. The fish lengths during the months were obtained by adding the monthly increase derived from the curves of Figure 21, to the beginning lengths, i. e. to 100 mm and 175 mm.

Compensatory growth in length can likewise be followed from year to year. Here the calculated length at one annulus is compared with those at other annuli. The larger shad at 1st annulus maintain their length advantage

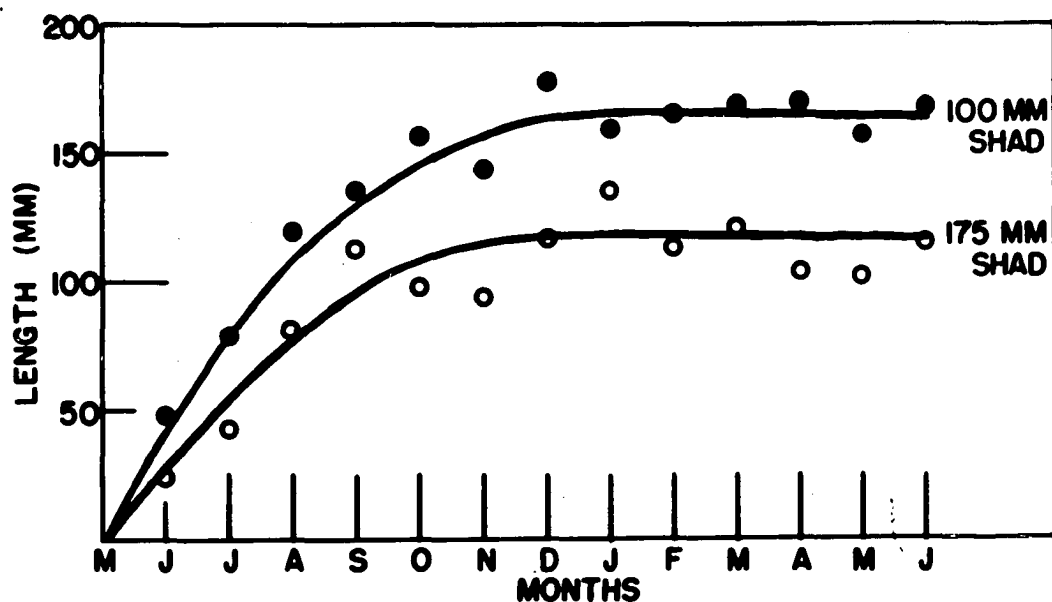


Figure 21. Seasonal Growth Curves Constructed from Formulae of Table 8 Showing Compensatory Growth in the 100 mm (length at first annulus) Class as Compared with the 175 mm Class. Theoretical) (Curve Shows Length Acquired between Times of 1st and 2nd Annulus Formation).

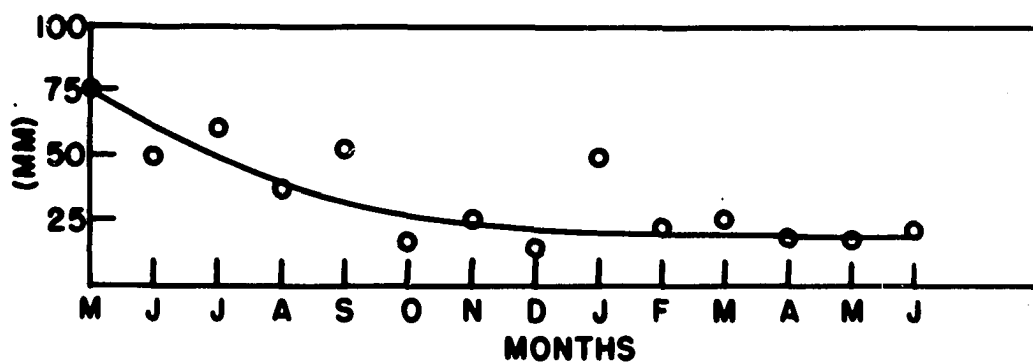


Figure 22. Seasonal Differences in Length between Shad having Lengths of 100 and 175 mm at the Time of First Annulus Formation. (Theoretical).

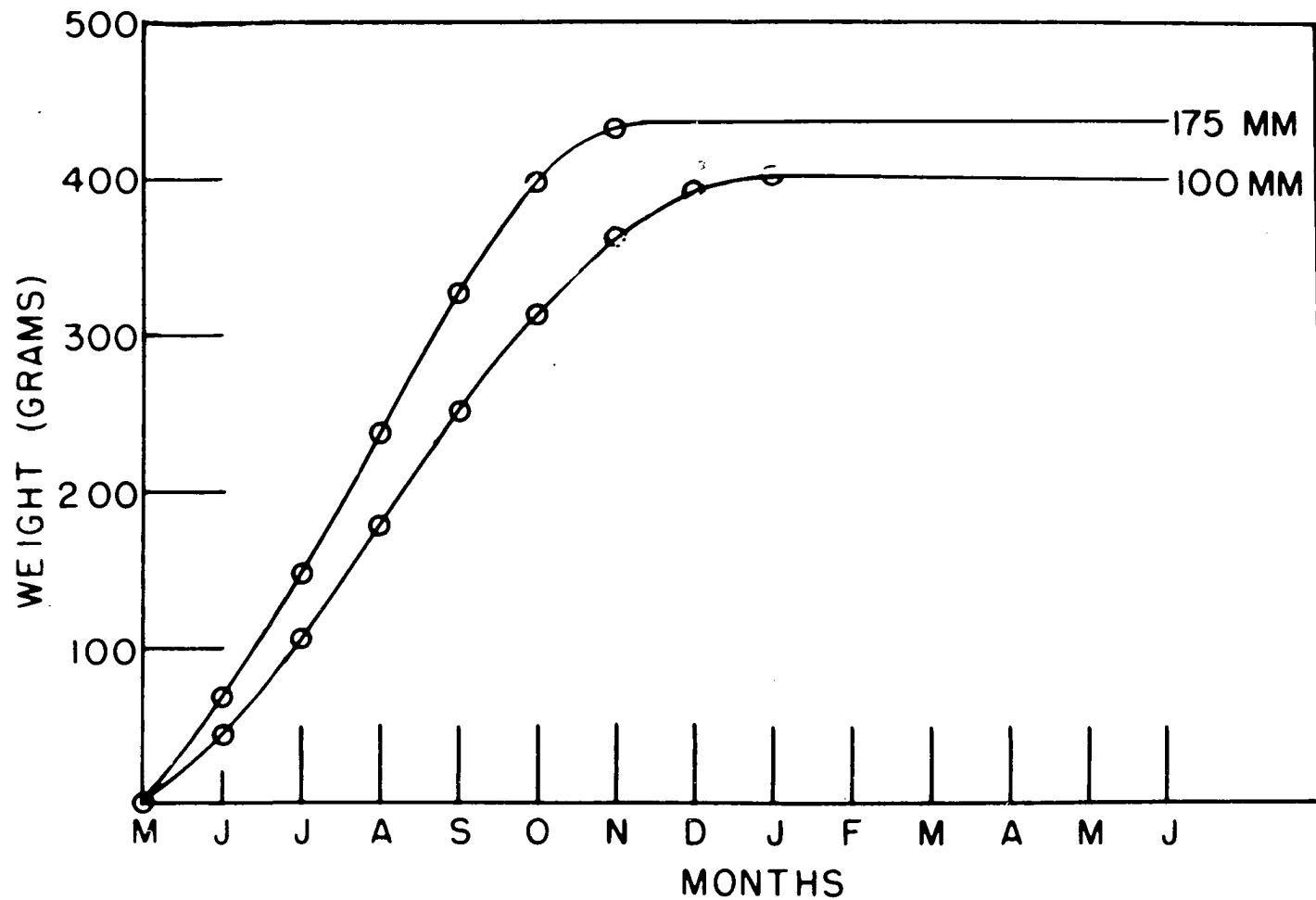


Figure 23. Seasonal Growth in Weight of Shad in the 100 mm (Length at 1st Annulus) Class Compared with That of the 175 mm Class. (Curve Shows Weight Acquired Between Times of 1st and 2nd Annulus Formations).

for two or three years. The smaller ones at 1st annulus 'compensate' year by year and finally overtake the larger shad between the time of fourth and fifth annuli formations.

Using all ages of fish and grouping them by centimeters of length at the time of their first annulus formation I get the averages shown in Table 9. By the method of least squares I arrived at the regression line formulae (for lengths at annuli subsequent to the first annulus) given in Table 10. Regression lines drawn by means of these formulae show 'over compensation' occurring between the time of fourth and fifth annuli formations. (Figure 24).

| AVERAGE LENGTHS OF EACH (1st ANNULUS SIZE) GROUP | | | | |
|--|---------|---------|---------|---------|
| 1st An. | 2nd An. | 3rd An. | 4th An. | 5th An. |
| 76.0 | 250.5 | | | |
| 87.9 | 259.7 | | | |
| 96.4 | 255.0 | | | |
| 106.0 | 269.1 | 316.0 | | |
| 115.4 | 271.3 | 326.0 | 343.0 | 354.0 |
| 125.3 | 275.2 | 320.0 | 347.0 | |
| 134.7 | 282.7 | 327.0 | 357.0 | 384.0 |
| 146.1 | 281.4 | 328.0 | 359.0 | 380.0 |
| 155.4 | 288.3 | 331.0 | 337.0 | 349.0 |
| 164.8 | 285.0 | 338.0 | 354.0 | 383.0 |
| 175.5 | 291.5 | 330.0 | 357.0 | |
| 184.6 | 301.0 | 328.0 | 348.0 | 355.0 |
| 192.0 | 301.0 | | | |
| 202.5 | 306.0 | | | |

Table 9. Average Lengths of Shad at Different Annuli Compared with Size at First Annulus.

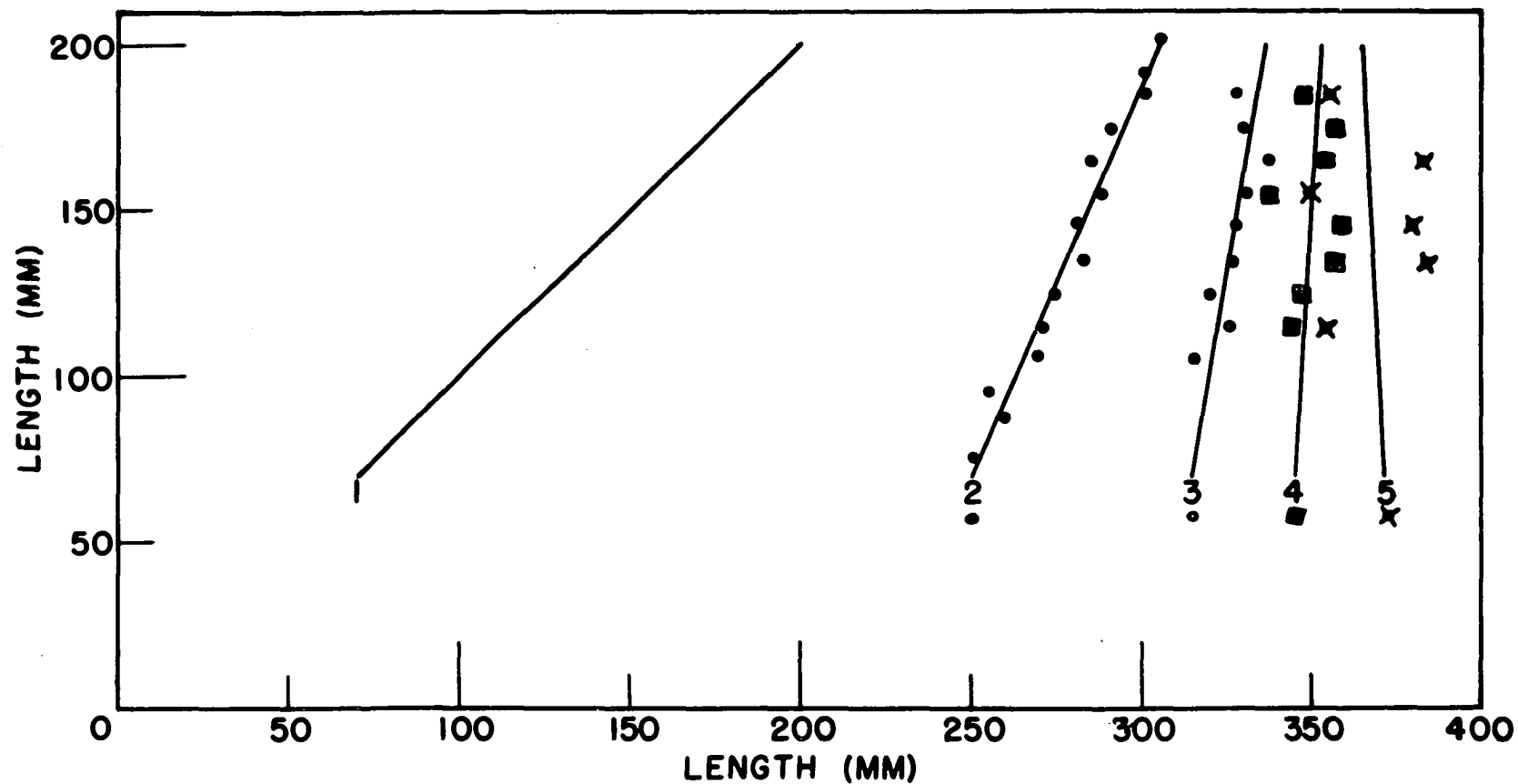


Figure 24. Length at 1st Annulus vs. Length at Succeeding Annuli, Showing Compensatory Growth.

• = 2nd Annulus
 ○ = 3rd Annulus

◼ = 4th Annulus
 ✕ = 5th Annulus

| | | | | | |
|-------------|---|--------|---|-----------|---------------|
| 2nd Annulus | = | 221.18 | + | 0.4184 | (1st Annulus) |
| 3rd Annulus | = | 302.64 | + | 0.1684 | (1st Annulus) |
| 4th Annulus | = | 340.89 | + | 0.0623 | (1st Annulus) |
| 5th Annulus | = | 375.0 | + | (-0.0501) | (1st Annulus) |

Table 10. Length at n Annulus/1st Annulus
(Based on Table 9).

If, however, only fish with four annuli are followed through their years of growth it is noted in Figure 25 that these fish have 'over-compensated' between the time of third and fourth annuli formations. Comparing only fish with five annuli (Figure 26) it is noted that these fish 'over compensated' between the time of second and third annuli formation! Data for these ages of shad are meager--for the four annuli shad, 19, for the five annuli ones, 7--but there seems to be the tendency for those shad which compensate the fastest and most to live the longest.

Tracing the growth in length of the theoretical 100 mm and the 175 mm shad through five years (Figure 27) we note that the greatest yearly increment of growth was during the first year for the larger class and during the second year for the smaller one.

Compensation in weight begins between the second and third annuli and over compensation occurs between the fourth and fifth annuli. Incidentally the greatest yearly increment of growth in weight occurs between the first and second annuli for both. See Figure 28.

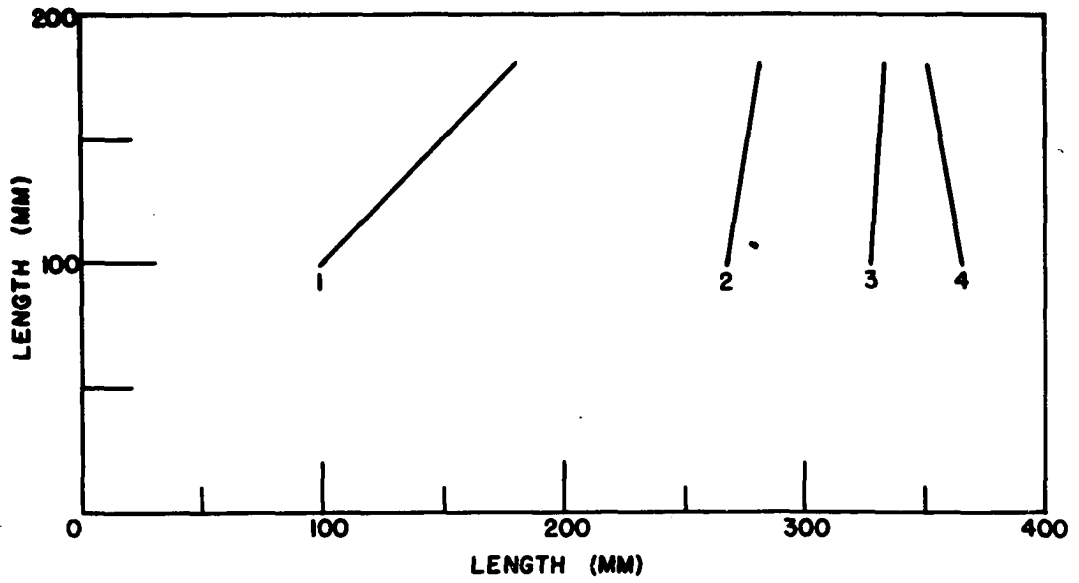


Figure 25. Annual Compensatory Growth in Length
(Based on IV-yr. Shad).

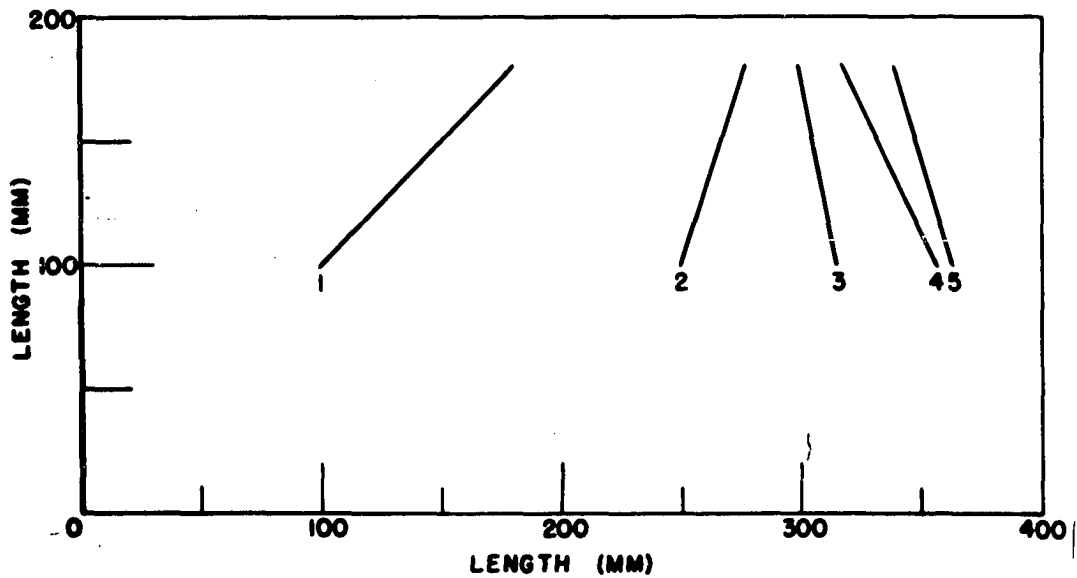


Figure 26. Annual Compensatory Growth in Length
(Based on V-yr. Shad).

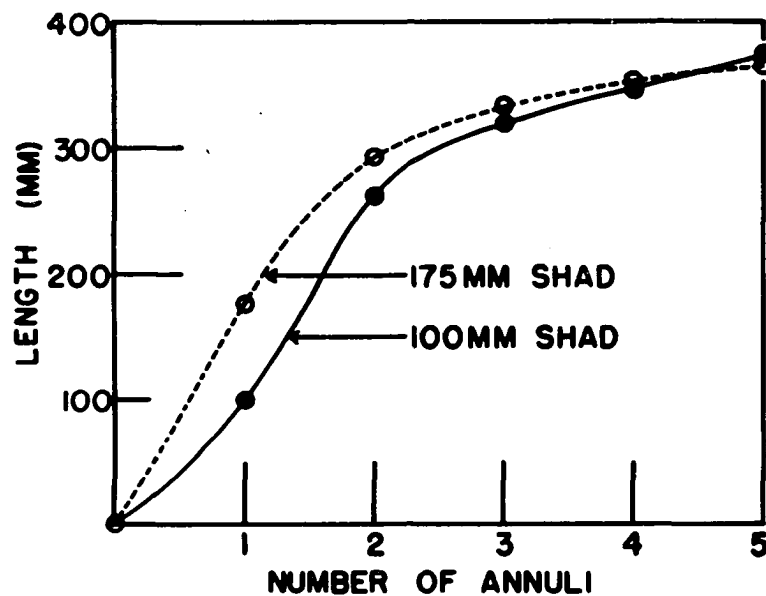


Figure 27. Graph of Length vs. Annulus Number. Curve of 175 mm (Length at 1st Annulus) Class Compared with That of the 100 mm Class. (Theoretical).

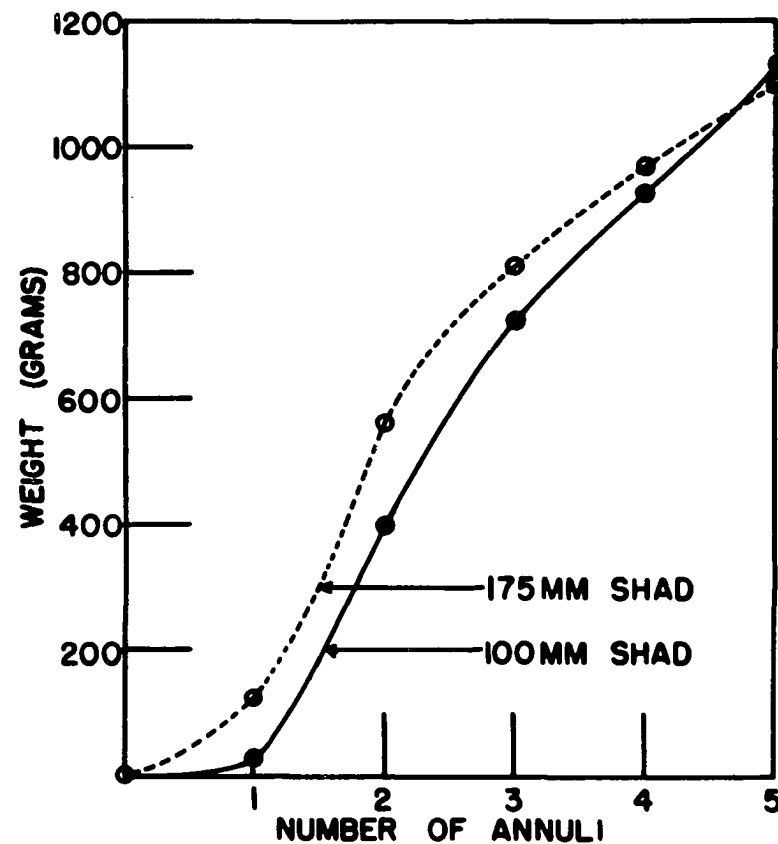


Figure 28. Graph of Weight vs. Annulus Number. Curve of 175 mm Class Compared with That of 100 mm Class. (Theoretical).

AGE COMPOSITION

Age Composition and Site.

The shad collections were made within a half mile from island and mainland shores. It must be recognized that the age composition as derived from these collections may not be an accurate one for the whole of Lake Erie--nor for the western end of this lake. The nearer one approaches shore, especially in shallow water, the more the age composition veers from a 'normal'.

In Lake Erie, the small young shad are found close to shore, usually in shallow water. As the young become larger they move into deeper water further from shore. Except during the spawning season, the III-yr. and older shad are rarely found in the shallower waters, or close to shore. Nor do the oldest shad come into the very shallow waters. See Figure 29.

The shad grow so rapidly that, except for the young-of-the-year (mostly for June, July, and August) the nets used will get all age groups, neither trap nor gill netting having shown selectivity.

Age Composition and Season.

In the following tables and graphs those 0-yr. gizzard shad which were caught by means other than trap or gill nets were largely excluded. I found no way to get reasonably accurate numerical ratios between these 0-yr.

fish and those caught by the nets since both gear and site selectivity are extremely great between the small and large members of this group. Suffice it to say that in general the 0-yr. shad appear in June, rise to greatest abundance in late July and taper gradually until after November when the drop in numbers is precipitous, after which it remains as we find it from January on in our table as I-yr. fish.

Although they were present in greatest numbers in late July, none of the 0-yr. shad had acquired a large enough size to be caught by gill and trap nets (2 inch bar measure) until August. The numbers of 0-yr. shad coming into this larger size range increased until they reached a peak in November. From here they gradually declined. The percents of 0-yr. shad from the time of their first capture by gill and trap nets as compared to all other ages of shad follow in Table 11.

| Month | Number of Fish | 0-yr. | All Other Ages |
|-----------|-------------------|--------|-------------------|
| August | 526 | 46.01% | 53.99% |
| September | 1,212 | 76.40% | 23.50% |
| October | 818 | 70.90% | 29.10% |
| November | 1,852 | 91.04% | 8.96% |
| December | 814 | 87.47% | 12.53% |

Table 11. Percent Young-of-the-year Shad of All Shad Caught Monthly by Gill and Trap Nets.

Table 12 shows the age composition by months of

the pooled shad collections of 1952 to 1955. This probably does not represent the actual age composition of shad in Western Lake Erie since the age compositions vary from site to site and season to season, but it is the closest estimate I have been able to make. From this table we note that as the year progresses, older and older shad enter the collections until, in June and July, VI-yr. shad are present. Thereafter the collection peaks include younger and younger shad until by November and December the oldest fish present are only II-yr. olds. See Figure 30.

In Figure 31 (data from Table 12) we also note that from December of the previous year the percent of I-yr. shad decreases, month by month, until a low of 13.63% is reached in June. I feel that the low percentage during March was a result of inadequate sampling. During the early part of this month, the ice breaks up, and the lake is generally very rough, hence collecting is largely halted. Commercial fishermen put their twine into the lake during the latter part of March but few shad are caught.

The age composition for the entire year, given in percentages at the bottom of Table 12, shows that ages I and II make up more than 96% of the fish collected. We note that age II is more abundant than is age I. The II-yr. shad, as will be seen later, are mature fish. They have a physiological urge to get close to shore when spawn-

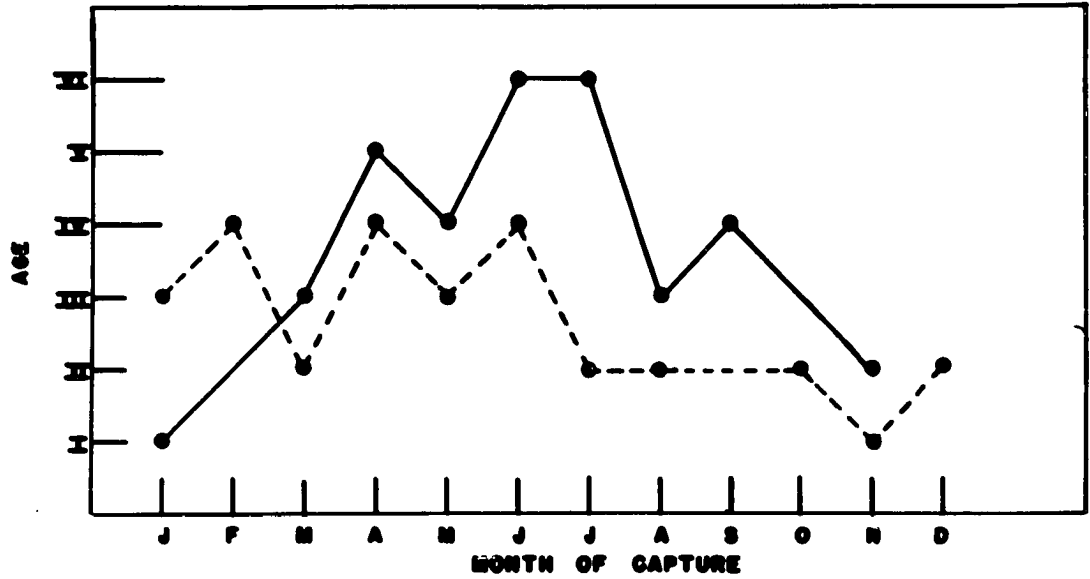


Figure 29. Age Limit Variations of Shad by Season and Site.
 Solid Line = Lake Caught
 Dotted Line = Shoal Caught

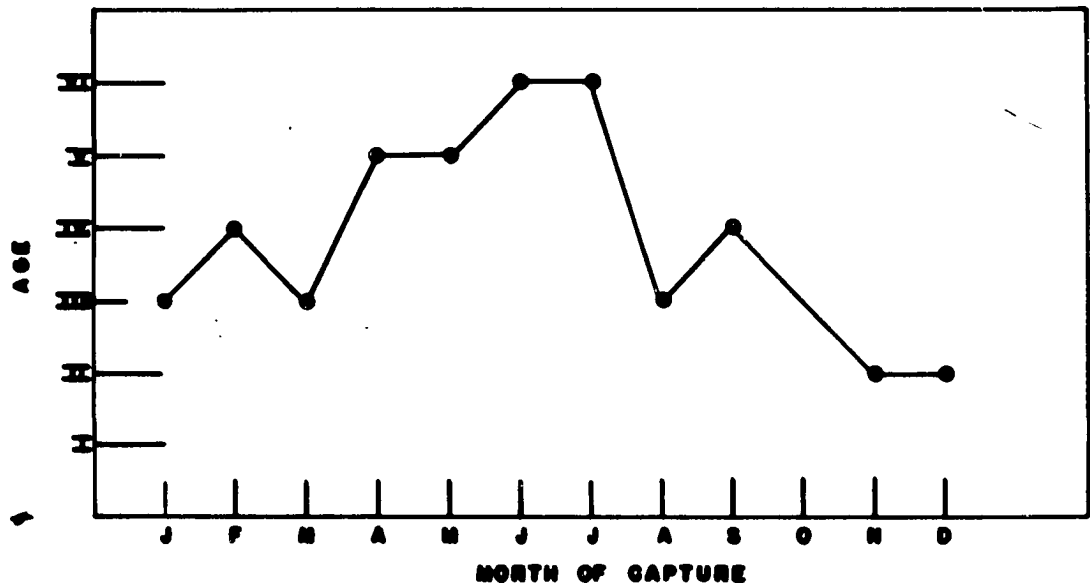


Figure 30. Seasonal Age Limit Variations.
 (Lake and Shoal Capture Pooled).

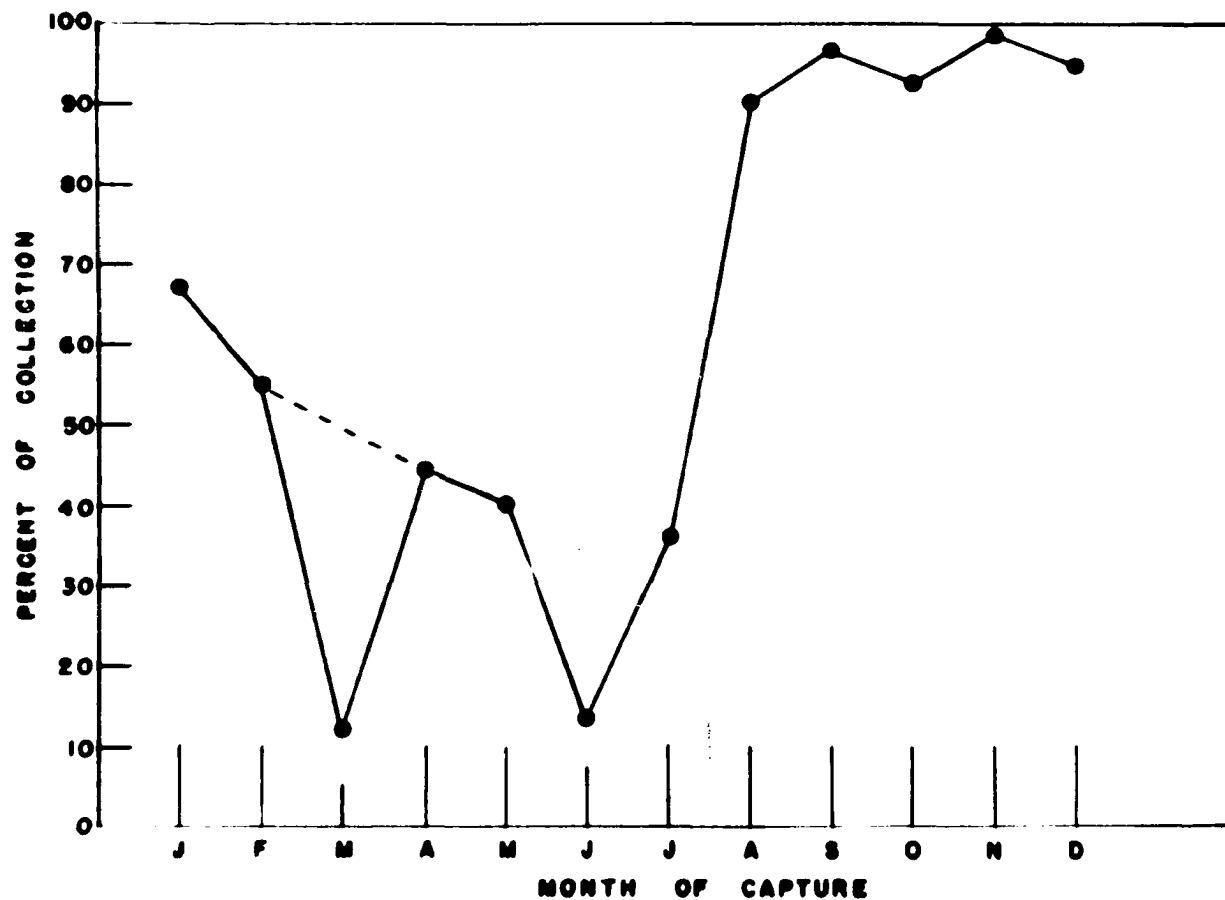


Figure 31. Percent of I-yr. Shad in Monthly Captures.
 (Excluding Young-of-the-year).
 Dotted Line Indicates Probable Course.

| MONTH | NUMBER of FISH | PERCENTAGE COMPOSITION OF COLLECTION BY AGE (EXCLUSIVE OF YOUNG-OF-THE-YEAR) | | | | | |
|-------------------------------------|----------------------|---|--------|--------|-------|-------|-------|
| | | I | II | III | IV | V | VI |
| January | 143 | 67.83% | 31.47% | 0.70% | | | |
| February | 144 | 55.56% | 40.28% | 2.08% | 2.08% | | |
| March | 25 | 12.00% | 68.00% | 20.00% | | | |
| April | 710 | 44.37% | 49.44% | 5.06% | 0.99% | 0.14% | |
| May | 216 | 40.32% | 56.92% | 1.98% | 0.39% | 0.39% | |
| June | 1,321 | 13.63% | 81.45% | 3.94% | 0.68% | 0.15% | 0.15% |
| July | 825 | 35.88% | 59.88% | 3.52% | 0.48% | 0.12% | 0.12% |
| August | 284 | 90.14% | 9.51% | 0.35% | | | |
| September | 286 | 96.85% | 2.45% | 0.35% | 0.35% | | |
| October | 237 | 93.25% | 6.33% | 0.42% | | | |
| November | 166 | 98.80% | 1.20% | | | | |
| December | 102 | 95.10% | 4.90% | | | | |
| Total Annual % of All Ages | 4,389 | 46.71% | 49.62% | 2.92% | 0.57% | 0.11% | 0.07% |

Table 12. Monthly Variations in the Age Composition of Gizzard Shad in the Western Lake Erie Collections of 1952 to 1955 (Pooled).

ing, and are then caught there. They have special business within our sampling area, whereas the I-yr. shad are for the most part merely wandering. Spawners appear in greatest numbers in June and taper to less than 5% by September or October while the I-yr. shad are present in about the same numerical abundance throughout the year but suffer, percentagewise, during this period because of the influx of spawners.

Rate of Disappearance.

Since the gizzard shad is neither a game nor a commercial fish, the only continuous record I have been able to obtain of it lies in my collections from the fall of 1952 to the early summer of 1955. Consequently I can only conjecture on the rate of disappearance of year classes. Although the pooled data of the captured shad do not present a satisfactory age ratio picture of shad in this region I believe that collections made during certain seasons give a fairly reliable picture of age ratios among select age groups. For example, collections made during May, June, and July, when the II-yr. and older shad have in common the drives related to spawning, I think, give a good indication of the age ratios existing among them. Collections made during September, October, and November probably give a reasonably accurate age ratio existing between the I-yr. and the II-yr. shad--the II-yr. shad have gotten over their spawning drives and the water is not cold enough to force either of them to leave the collecting sites.

Judging from various reports (not actual counts) we can assume that the shad population is not static--it more than maintains itself--it is slowly increasing. Over a long period of years it is not, however, doubling itself yearly. The female spawns in her third year of life (see under spawning). If these II-yr. shad just maintain them-

selves, the increase due to the spawning of shad older than the II-yr. ones would probably cover whatever increase the shad has been making. Estimating the number of eggs spawned by a female as 400,000 (see under spawning), and assuming a one to one ratio between males and females we could estimate that the ratio of eggs spawned to II-yr. old shad is 200,000 to one. The values for the II-yr., III-yr., IV-yr., V-yr., and VI-yr. shad obtained from the May, June, and July collections are: 1649, 83, 14, 4, and 3 respectively. The numbers of I-yr. and II-yr. shad collected during September, October, and November are 652 and 24 respectively.

In table form the following information would appear:

| <u>Ages</u> | | <u>Number Relationships</u> | | <u>Ratios</u> |
|-------------|-------------|-----------------------------|--------|---------------|
| Eggs | : II-yr. = | 200,000 | : 1 = | 200,000 : 1 |
| I-yr. | : II-yr. = | 652 | : 24 = | 27.17 : 1 |
| II-yr. | : III-yr. = | 1,649 | : 83 = | 19.87 : 1 |
| III-yr. | : IV-yr. = | 83 | : 14 = | 5.93 : 1 |
| IV-yr. | : V-yr. = | 14 | : 4 = | 3.5 : 1 |
| V-yr. | : VI-yr. = | 4 | : 3 = | 1.33 : 1 |

Since Eggs : II-yr. = 200,000 : 1 and I-yr. : II-yr. = 27.17 : 1 then Eggs : I-yr. must be 7361.1 : 1.

The ratios between eggs and each age would be:

| | | | |
|------|-------------|-------------|-----|
| Eggs | : I-yr. = | 7,361 | : 1 |
| Eggs | : II-yr. = | 200,000 | : 1 |
| Eggs | : III-yr. = | 3,974,000 | : 1 |
| Eggs | : IV-yr. = | 23,565,820 | : 1 |
| Eggs | : V-yr. = | 82,480,370 | : 1 |
| Eggs | : VI-yr. = | 109,973,830 | : 1 |

The oldest shad I have gotten from the western end of Lake Erie from 1952 to 1955 were those in their seventh year of life--and only three of these. Patriarche (1952) found X-yr. gizzard shad in Lake Wappapello, Missouri in 1951.

The greatest loss in this series is for the period from the spawned eggs to the I-yr. shad. This is due largely to predation pressure. Unfertilized eggs and adverse meteorological conditions have also taken their toll during this period.

The period (fall I-yr. to fall II-yr.) encloses the first spawning season, during which the loss ratio is the next highest, associated undoubtedly with the phenomenon of spawning. After this age, losses are probably related largely to spawning.

REPRODUCTION

Size and Age at First Spawning.

In 1954 I found three I-yr. (second year of life) female shad which were mature--their S L's were 197, 225, and 236 mm. Some twenty-five or thirty I-yr. males, ranging between 190 and 230 mm, were also found to be mature. The milt and eggs produced by this age fish were scanty. See Figure 32. Invariably, these precocious fish arrived on the spawning site at the tail end of the spawning season--in July. They were not the largest of their age group, whose size range extended to 254 mm during this time. What percent of the I-yr. population they represent could not be determined since site selectivity during the spawning season appears to be very great.

The greatest number of spawners were in their third year of life (II-yr.). Size appeared not to be a determining factor--many of this age group were immature, yet were of larger size than were some of the mature ones. Here, again, the percent of II-yr. shad which were mature could not be determined because of the selectiveness of site. However, based on observations of gonads throughout the year, I am of the opinion that about 90% of the shad are mature at this age in Western Lake Erie.

At the same time, I feel that shad remaining elsewhere in the lake where temperature and food conditions are not favorable, would probably not spawn (regard-

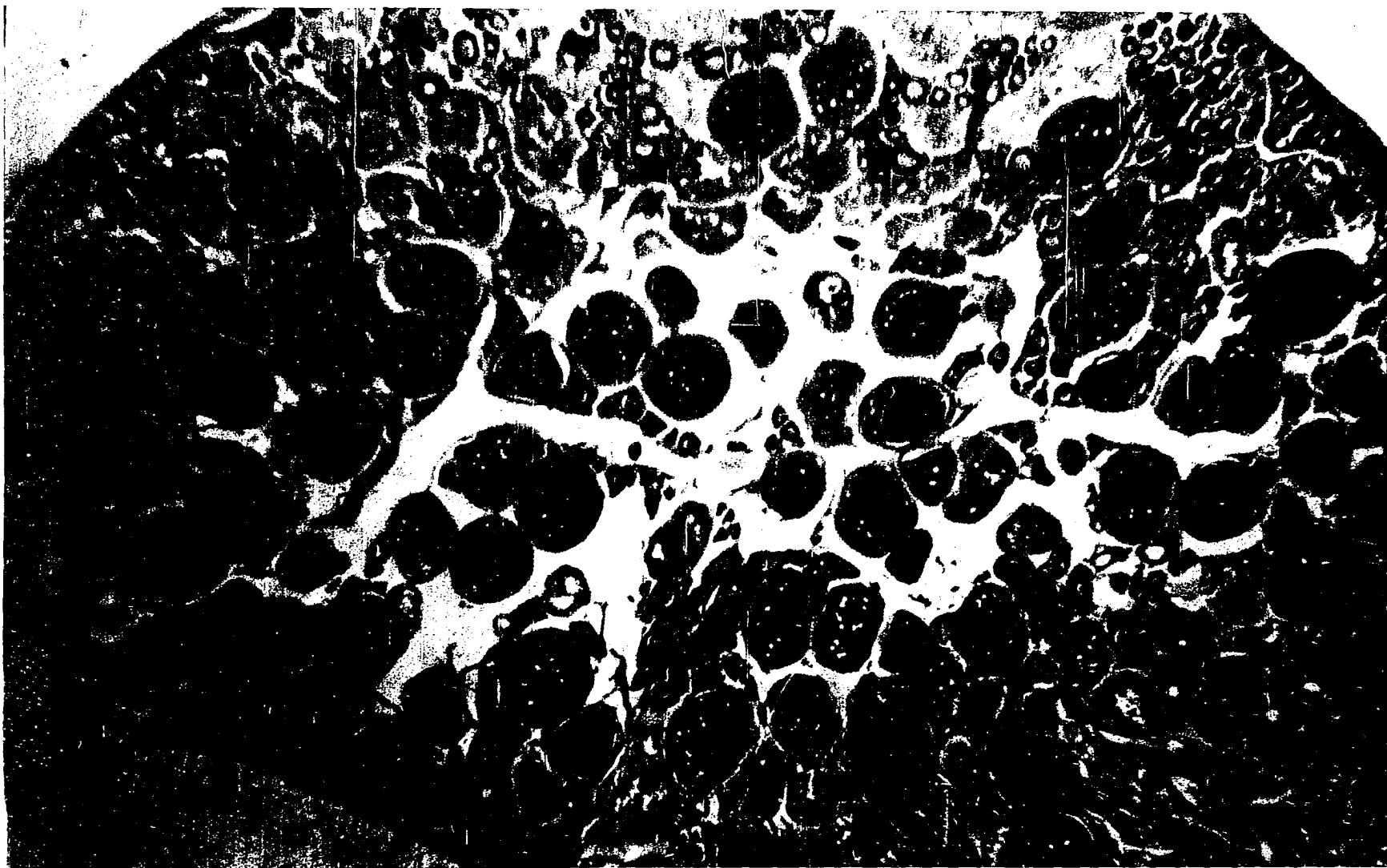


Figure 32. Ovary of A Mature I-yr. Shad Showing Relatively Few Near Mature Eggs.
I-yr. Gizzard Shad (7/6/54) (Dissecting Scope--Medium Power).

less of age) until they enter a more favorable environment. Shad of this age in Fishery Bay were practically all mature while many of those brought in from the lake were immature.

A few of the older fish (III-yrs. and older) had gonads which had not developed or had been resorbed. That some were definitely resorbed is shown by histological preparations of some of these ovaries. The inter-ovule space is filled with connective tissue and the egg count is scanty. See Figure 33.

Occasionally, the mature eggs were not spawned--probably because the fish entered an unfavorable environment during spawning season or because the eggs matured too late in the season. These eggs were absorbed. See Figure 34.

Spawning Site.

A spawning site for gizzard shad in the vicinity of Fishery Bay is a bar, covered by two to four feet of water, and extending from Oak Point half way to Gibraltar Island. See Figure 4. This bar is topped with sand, gravel and boulders. *Cladophora*, *Myriophyllum* and *Butomus* (forma *vallisneriifolius*) are present here in abundance during the spawning season.

Shad were not found on this bar prior to, nor after, the spawning season (May--July inclusive). To get

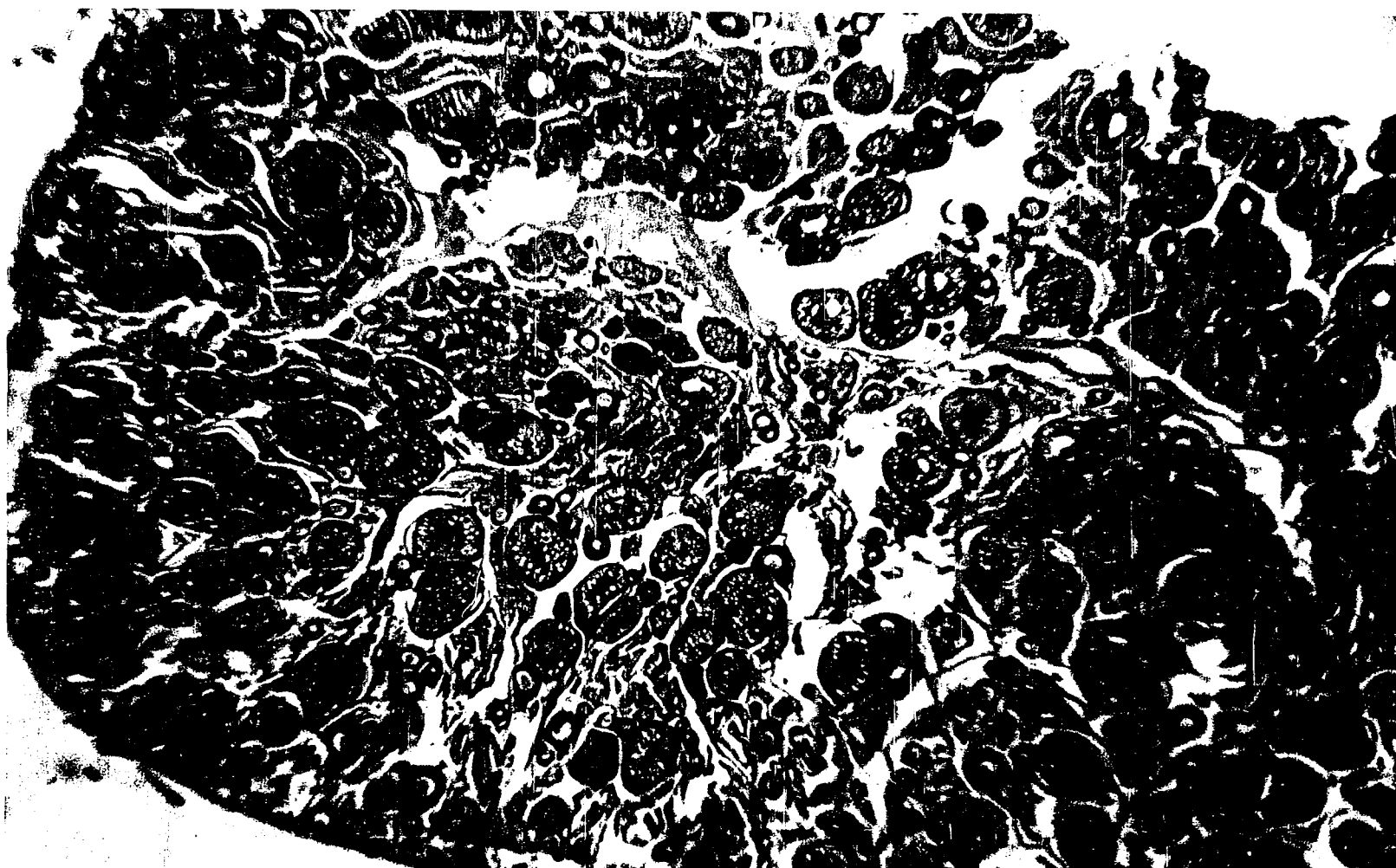


Figure 33. Ovary Becoming Senile III-yr. Gizzard Shad (6/10/54).
(Dissecting Scope--Medium Power).

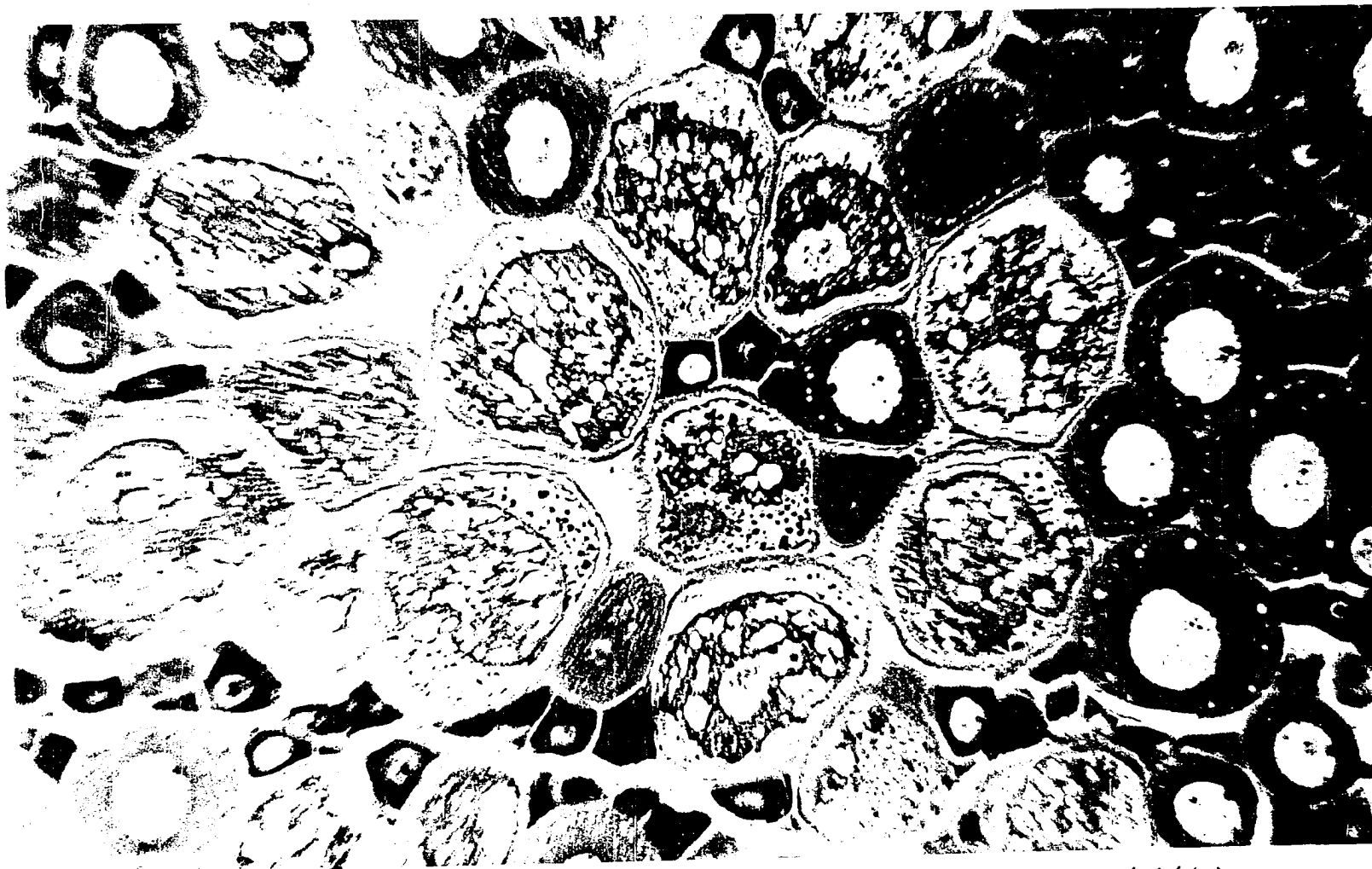


Figure 34. Unspawned Eggs Being Absorbed 1-yr. Gizzard Shad (12/16/53).
(Compound Scope--Low Power).

some idea of the day-to-day variations of the shad population here, a 100 ft., 2 inch mesh (bar measure) gill net was set nightly along the top of this bar from May 9, 1955 to the time of this writing (June 30). For results see Table 13. It will be noted later that the female shad does not spawn her entire egg holdings in the course of one visit to the bar. Consequently, many shad would have come to the bar on subsequent dates but for having been caught. The shad also exhibit greater activity at the height of spawning than just prior to and after spawning; consequently, a greater percentage of those present are likely to swim afoul of the net at this time. The table must be interpreted with these in mind.

In an effort to pinpoint the site more accurately, gill nets were set transversely across the bar. In every case most shad were caught in that portion of the net which crossed the highest area of the bar, while fewer shad, but more carp, were caught at either end of the nets where they sloped gradually into deeper water.

Spawning Season.

The ovary/body weight ratio of shad collected throughout the year in conjunction with the capture of shad actually spawning is used here as an index of spawning season. See Table 14.

At the beginning of the spawning season some shad

| MAY (1955) | CAUGHT SHAD | TEMP. (°F) OF WATER | JUNE (1955) | CAUGHT SHAD | TEMP. (°F) OF WATER |
|---------------|----------------|------------------------|----------------|----------------|------------------------|
| | | | 1 | 4 | 64 |
| | | | 2 | 6 | 65.5 |
| | | | 3 | 20 | 67 |
| | | | 4 | 10 | 66 |
| | | | 5 | 12 | 66 |
| | | | 6 | 21 | 67.5 |
| | | | 7 | 23 | 66.5 |
| | | | 8 | 24 | 65.5 |
| | | | 9 | 5 | 66.5 |
| 10 | 0 | 58 | 10 | 10 | 66.5 |
| 11 | 0 | 59 | 11 | 16 | 66 |
| 12 | 0 | 58.5 | 12 | 6 | 65.5 |
| 13 | 0 | 60 | 13 | 4 | 65 |
| 14 | 0 | 60 | 14 | 1 | 65.5 |
| 15 | 0 | 59 | 15 | 1 | 65.5 |
| 16 | 0 | 61.5 | 16 | 14 | 68 |
| 17 | | 59.5 | 17 | 57 | 70 |
| 18 | 0 | 59 | 18 | 35 | 71 |
| 19 | 1 | 59 | 19 | 38 | 71.5 |
| 20 | 0 | 60 | 20 | 20 | 72 |
| 21 | 0 | 61 | 21 | 10 | 71 |
| 22 | 0 | 61 | 22 | 10 | 71.5 |
| 23 | 0 | 61 | 23 | 4 | 72 |
| 24 | 0 | 61 | 24 | 33 | 72.5 |
| 25 | 0 | 61.5 | 25 | 24 | 73 |
| 26 | 0 | 61 | 26 | 5 | 73 |
| 27 | 0 | 62.5 | 27 | 10 | 74 |
| 28 | 0 | 63 | 28 | 5 | 73.5 |
| 29 | 1 | 63 | 29 | 18 | 73.5 |
| 30 | 0 | 62 | 30 | 17 | 73 |
| 31 | 0 | 63 | | | |

Table 13. Daily Variations of the Shad Population
at a Spawning Site.

PERCENT

| GONAD WT. BODY WT. | 1954 April | 1954 May | 1954 June | 1954 July | 1954 Aug. | 1953 Oct. | 1953 Nov. | 1953 Dec. |
|-----------------------|---------------|-------------|--------------|--------------|--------------|--------------|--------------|--------------|
| 0-1 | 2 | - | 2 | - | 4 | 6 | 7 | - |
| 1-2 | 3 | - | 3 | 1 | 5 | 10 | 16 | 15 |
| 2-3 | 1 | 3 | 2 | - | - | - | - | 3 |
| 3-4 | 2 | 3 | 1 | - | | | | |
| 4-5 | - | 4 | 3 | 1 | | | | |
| 5-6 | - | 3 | 4 | 1 | | | | |
| 6-7 | - | 3 | 12 | | | | | |
| 7-8 | 2 | 6 | 6 | | | | | |
| 8-9 | - | 3 | 7 | | | | | |
| 9-10 | - | - | 8 | | | | | |
| 10-11 | - | 3 | 9 | | | | | |
| 11-12 | - | - | 6 | | | | | |
| 12-13 | - | - | 2 | | | | | |
| 13-14 | - | - | 2 | | | | | |
| 14-15 | - | 1 | 3 | | | | | |
| 15-16 | - | - | 2 | | | | | |
| 16-17 | - | - | 4 | | | | | |
| 17-18 | - | - | 3 | | | | | |
| 18-19 | - | - | 3 | | | | | |
| 19-20 | - | - | - | | | | | |
| 20-21 | - | - | - | | | | | |
| 21-22 | - | - | - | | | | | |
| 22-23 | - | - | 1 | | | | | |

NUMBER OF INDIVIDUALS

Table 14. Monthly Ovary/Body Weight Ratios for Shad in Western Lake Erie.

with an ovary/body weight ratio of 5% have been observed to spawn. Shad with a ratio of 10% at this time are generally spawners. At the close of the spawning season, shad with a ratio of 5% have not yet completed their spawning. Assuming that the 10% ratio begins the spawning season and that the less than 5% ratio closes it, we have a spawning season at Western Lake Erie which extends from May to July inclusive. It is evident from this table and from data presented later as well as from captured fish whose ovary/body weight ratios had not been determined that most of the spawning occurs during June--perhaps 90% or more.

In an effort to learn the time of peak spawning during June, 1954, the daily average ovary/body weight ratios were plotted as percentages in Figure 35. The highest averages (using sufficient data) occurred during the latter part of the first week and the earlier part of the second week. Thereafter it rapidly dropped, reaching the 'less than 5%' level by the third week of the month.

To learn whether the age of the shad influences its spawning time, Table 15 was prepared, showing the percent of each age group which had begun spawning prior to capture during June and July, 1954. In order to include the older shad, lake collections were pooled with the Fishery Bay ones. It appears that the II-yr. shad have a long-

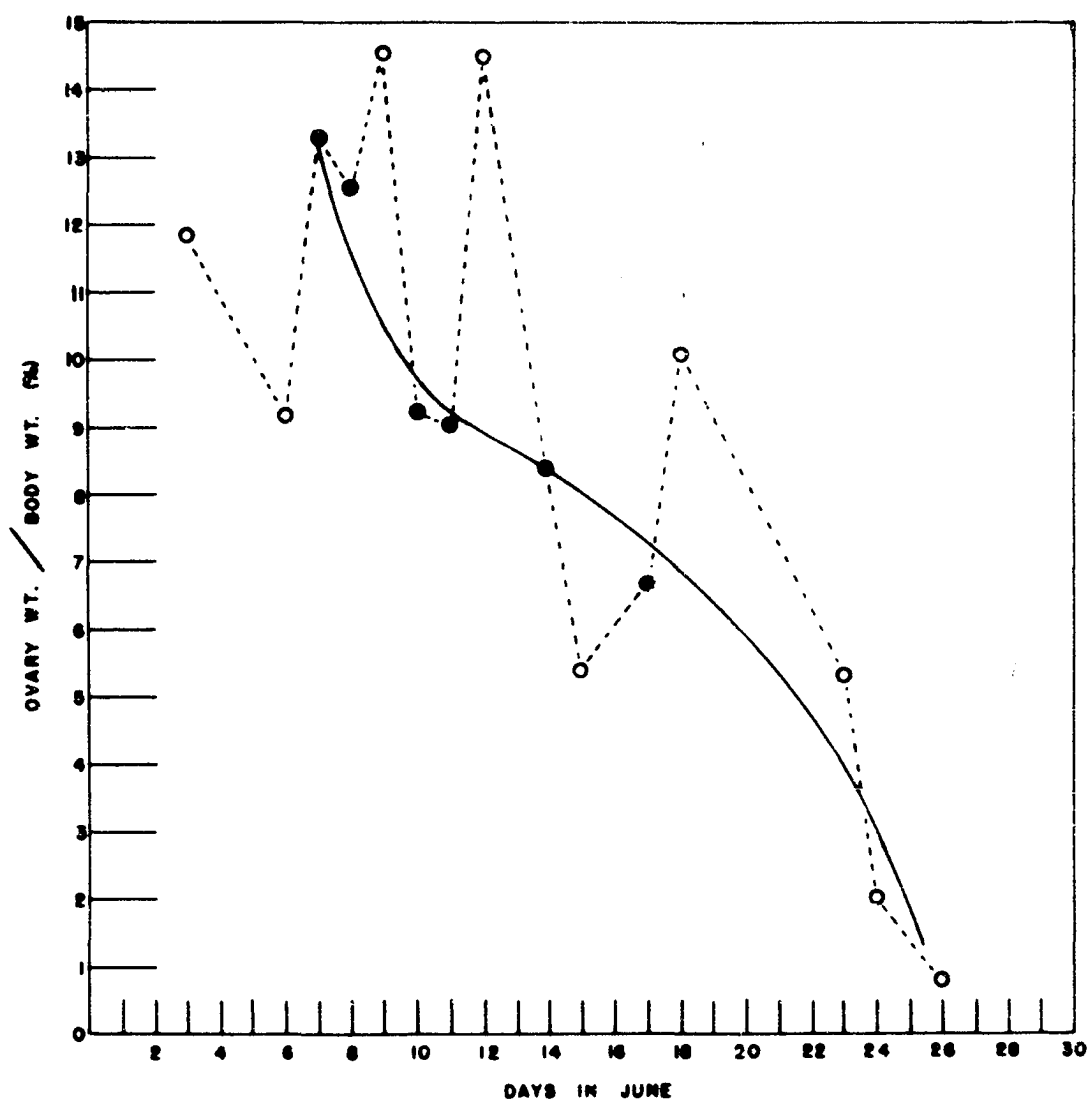


Figure 35. Average Ovary/body Wt. Ratios During Successive Days in June, 1954.

○ = Less Than 5 Individuals.
 ● = More Than 5 Individuals.

| June 1954 | | | | | JULY 1954 | | | |
|-----------|------------------|-------------------|--------------------|--------------------|------------------|-------------------|--------------------|--------------------|
| Age | June 1 June 8 | June 9 June 15 | June 16 June 23 | June 24 June 30 | July 1 July 8 | July 9 July 15 | July 16 July 23 | July 24 July 31 |
| II-yr. | 7.4% | 59.5% | 18.3% | 46.8% | 65.3% | 76.9% | 87.5% | 100%* |
| III-yr. | -- | 50%* | 40%* | 32% | 50% | 50%* | -- | -- |
| IV-yr. | -- | -- | 0%* | 0%* | 33.3%* | 0%* | -- | -- |
| V-yr. | -- | -- | 0%* | 50%* | 0%* | -- | -- | -- |

Table 15. Influence of Age on Spawning Time. Percent of Shad Which Had Begun Spawning before Capture. (Composite of Lake and Shoal Shad).

** = One Individual.

* = Five or Less Individuals.

er spawning period than have the older ones. The older shad (especially the IV-yr. and V-yr.) appear to begin spawning a week or two later than the II-yr. ones and to leave the scene a week or two earlier. Data on these older shad, however, are meager.

Incidentally, three mature I-yr. shad were captured on June 28, July 6, and July 8. The eggs (see Figure 32) were nearly ripe. These fish would probably have spawned in late July or early August--or else the eggs would have been absorbed (see Figure 34).

To learn whether fishes of different weights have different spawning times, Figure 36 was prepared, using only the II-yr. shad from Fishery Bay. Aside from the shad weighing 400 grams and less, whose curve appears erratic--probably due to the small samples, the peak ovary/body weight ratios are greatest during the first week in June. It is of interest to note that the heavier fish have the higher ovary/body weight ratios. This will be pursued further under Fecundity.

The actual time of spawning (within a 24 hour period) was sought by two methods. In one, a gill net was set on the spawning bar at about 7:00 p.m. and lifted at 12:00 p.m. Reset immediately and lifted at 6:30 a.m. Reset immediately and lifted at 7:00 p.m. The numbers of shad of each sex were tabulated for each period.

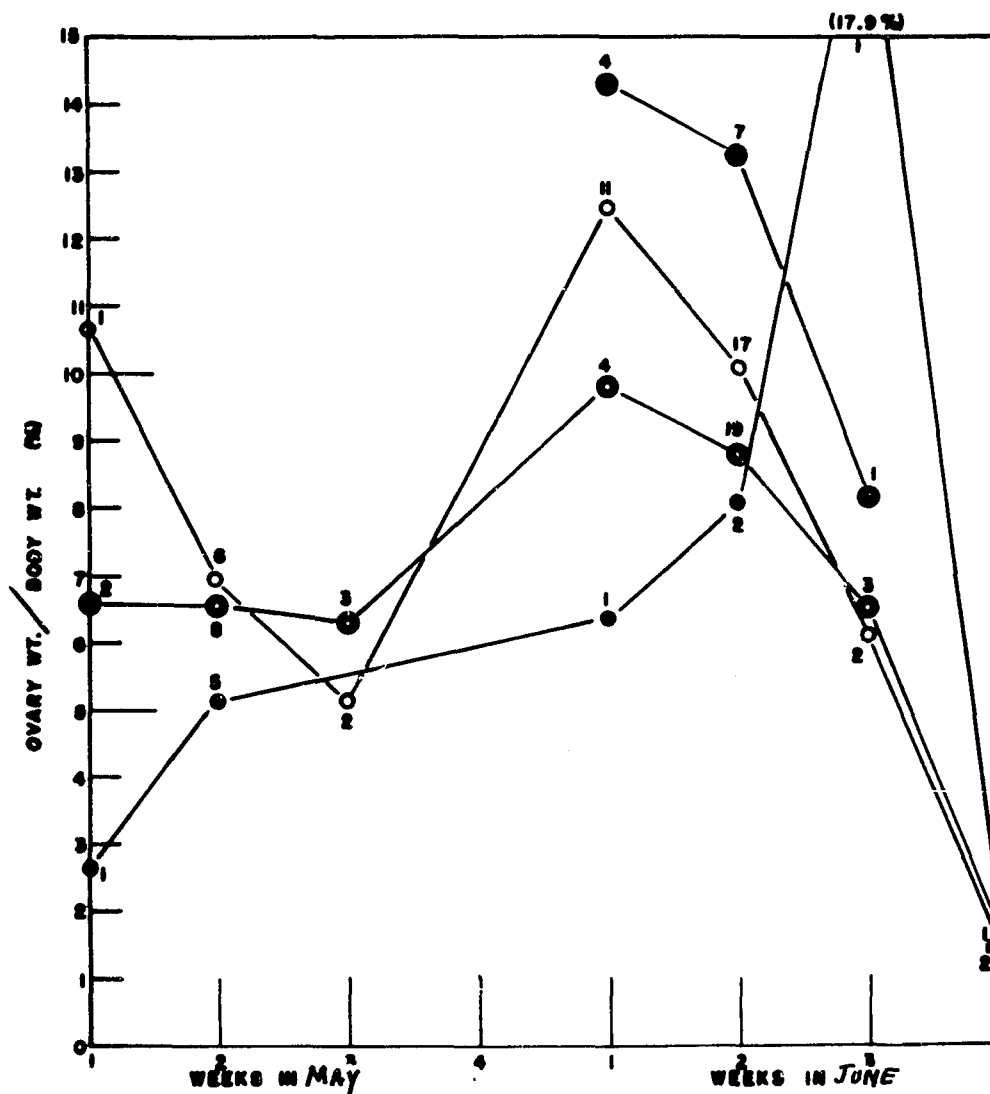


Figure 36. Effect of Fish Weight on Spawning Time (11-yr. Shad from Fishery Bay).

Numbers = Individuals Averaged.
 = Less Than 400 Grams.
 = 400 - 500 Grams.
 = 500 - 600 Grams.
 = More Than 600 Grams.

By the other method, concrete slabs having a surface area of one square foot were placed and lifted at the spawning site at the times given for the gill net in the preceding paragraph. The numbers of shad eggs adhering to the blocks were tabulated for each period.

In 1954 only three days, beginning with June 17, were tested by these methods. See Table 16 for results.

From this table, it would seem that the gizzard shad spawn most actively during the evening and early night (on that bar). Least active spawning occurred during the day. I might add that I have not seen shad engaging in spawning activities during the day time, but they appeared actively milling, frequently breaking surface, when I went to lift the net at midnight.

| | GILL NETS | | | | CONCRETE BLOCKS |
|-----------------------|-----------|---------|---------|-------|--------------------|
| | MALES | FEMALES | | | EGGS |
| | | NOT | SPAWNED | SPENT | |
| | | SPAWNED | | | |
| 7:00 p.m.-12:00 p.m. | 91 | 16 | 11 | 8 | 15 |
| 12:00 p.m.- 6:30 a.m. | 50 | 7 | 4 | 10 | 5 |
| 6:30 a.m.- 7:30 p.m. | 0 | 2 | 1 | | 2 |

Table 16. Spawning with Reference to Period of Day.

During the course of the spawning season the membership of the spawning population changes continually. But a female does not deposit her entire egg holding during one nightly visit to the bar. This is shown by the fact that while intermediate degrees of 'spentness' are encountered throughout the entire spawning season, these degrees approach complete 'spentness' for few at the beginning of the season, for more as the season progresses and finally for all at the close of the season. The state of development of the 'nearly mature' eggs found together with free ones in the ovaries of spawning shad indicate that probably days of 'rest' are interspersed between spawning periods. I am of the opinion that several days are required for complete spawning--perhaps as much as a week in some cases.

'Lake' and 'Spawning Site' Shad Compared.

In the course of collecting shad from the spawning site and from the lake, differences in the degree of maturity and percent of spawners were noted. Figure 37 and 38 were made of lake and shoal shad for comparison. These are based on gross examinations of the gonads.

Figure 37 shows very few spawning female shad captured in the lake. The data indicate that the males and ripe females migrate from the 'lake' population during the spawning season and congregate in the 'shoal' area. The rise in percentage of males in the 'lake' population

during the third week in July is probably the result of the influx of males from the spawning grounds--spawning having been mostly completed.

Spawning Behavior.

Langlois (1954) observed shad spawning in North Reservoir at Akron, Ohio in 67° F. water. They spawned close to shore in six to twelve inches of water. During oviposition, a female was flanked by a male on either side.

McQuate (1954) observed shad spawning in Sandusky Bay, Ohio on May 24, 1954, in 62.5° F. water. They spawned along a stony shore at 12:00 o'clock (noon) "spawning always taking place in the shade of an overhanging tree". Female shad were pursued by several males, frequently breaking water.

Trautman (1954) noted about twenty shad spawning in Buckeye Lake, Ohio in 73° F. water on May 23, 1939. The females, pursued by several males, swam rapidly toward a sloping stone wall, then on abruptly turning they deposited their eggs.

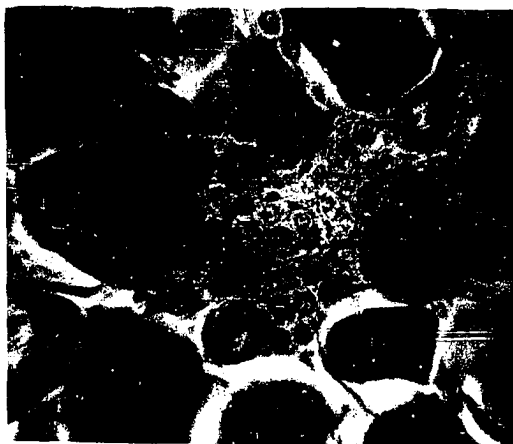
I have not seen shad spawning during the daylight hours at the spawning site--but then I have rarely caught shad there in gill nets during that time. It isn't that the gill nets are so conspicuous as to be avoided during the day (they were treated with a copper preserva-

tive which rendered them greenish, hence less visible and were set in the vegetation which almost wholly obscured them) but the shad are just not there. During the midnight lifts, however, when the moon shone brightly, I saw many shad swirling and breaking water--especially on nights when the net catches were heavy. The moonlight was not bright enough for me to tell anything about the size or numbers. Nor could I identify them further than to note that they were white and shad-like. The gill nets, however, caught many shad during those nights and the only other fish caught were a few carp.

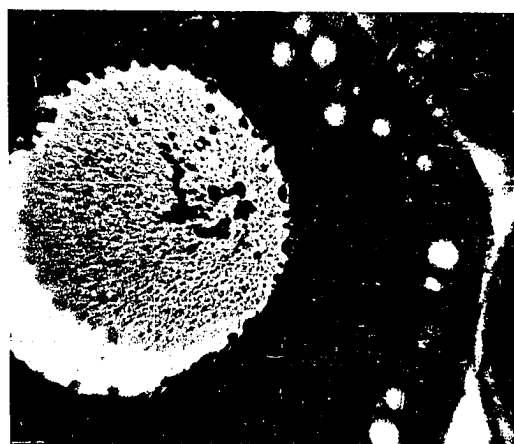
Annual Sex Cycle.

The growth and maturation of the eggs are depicted in Figure 39. The very early stages of egg development have been omitted. For convenience I have selected 'stages' which show clear-cut changes during egg development.

In the description I use the following terminology: the circular central portion of the cell is the nucleus; the dark sphere or spheres within this nucleus, the nucleolus; the portion surrounding the nucleus, the cytoplasm; the clear spheres in the cytoplasm, oil globules; the dark spheres in the cytoplasm, yolk granules; the clear membrane enveloping the cytoplasm, the zona pellucida; and the layer of large cells external to the



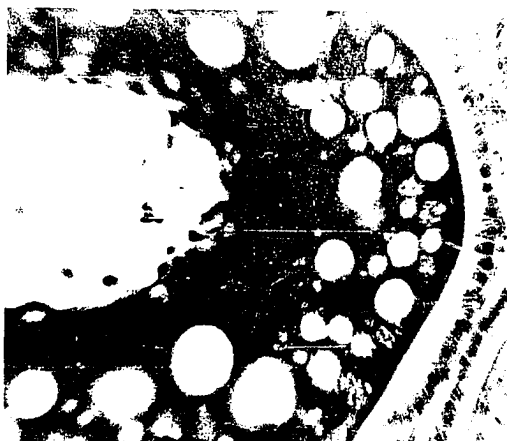
Stage 1



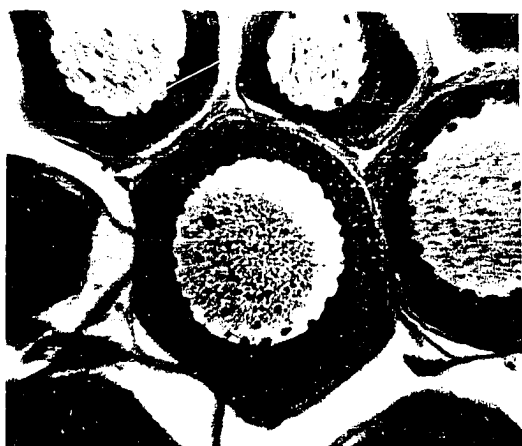
Stage 4



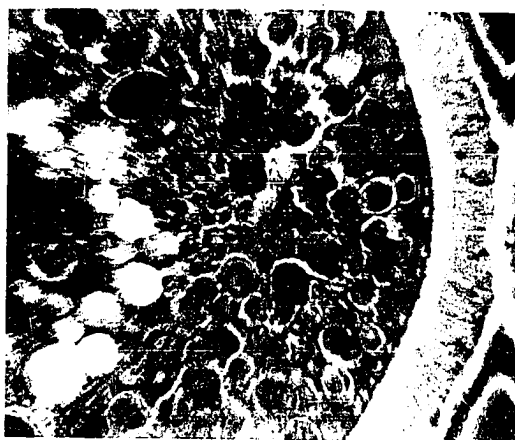
Stage 2



Stage 5



Stage 3



Stage 6

Figure 39. Growth and Maturation of Gizzard Shad Eggs
(Compound Scope--High Power).

zona pellucida, the follicular layer.

It should be mentioned that during every month (in some portion of the ovaries of all individuals) every early stage of egg maturation is represented. Those stages beyond the 'oil globule' formation stage (Stage 4 of Figure 39), however, are found only in months subsequent to January (the stages advancing with the nearing of the spawning season).

In Stage 1, we note small cells, having ample cytoplasm and one nucleolus in the center of the nucleus.

In Stage 2, the nucleus has increased in size more than has the cytoplasm, and several nucleoli are present--some of which are migrating toward the nuclear membrane. The cytoplasm is becoming granular.

In Stage 3, the nucleoli have increased numerically and have migrated to the nuclear membrane. A follicular layer, whose cells are not clearly discernible, has enveloped the cytoplasm.

In Stage 4, the nucleoli are disintegrating; the cytoplasm is increasing in quantity with oil globules forming next to the cytoplasmic membrane; and the follicular cells are well developed.

In Stage 5, nucleolar disintegration continues; the oil globules of the cytoplasm are migrating toward the nucleus; yolk granules are beginning to develop next

to the cytoplasmic membrane; and the follicular cells have begun to lay down the zona pelucida.

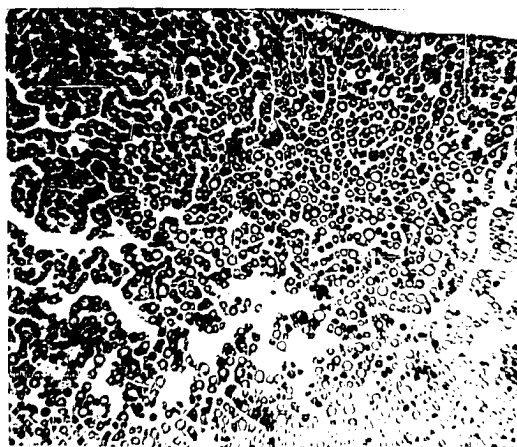
In Stage 6, the nucleus has been invaded by the oil globules and yolk granules which now almost completely fill the cell; and the zona pellucida is well developed.

In a later stage (not shown) the oil globules have largely disappeared; the cell is completely filled with yolk granules; and the follicular cell layer has begun to separate from the zona pellucida.

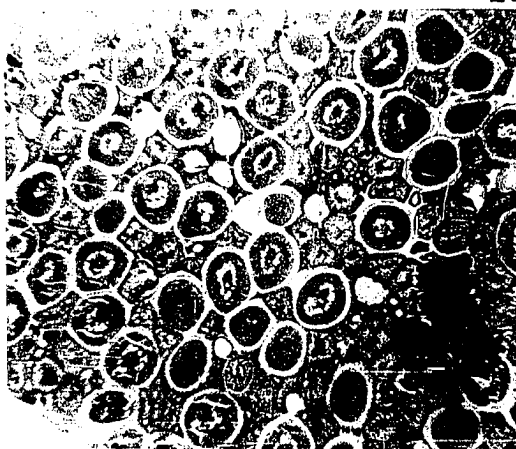
What happens to the nucleus? It may be dispersed throughout the cell, it may be one of the granules and thought to be a yolk granule, or it may constitute the entire cell.

When the egg leaves the ovary, the follicular layer separates from the zona pellucida and remains in the ovary where it is absorbed. The zona pellucida becomes the egg membrane--greatly distended by imbibed water after the eggs are spawned and water hardened.

The seasonal cycle of changes occurring in the ovary can be followed in Figure 40. These photomicrographs have been selected as representative of the majority of the ovaries examined. This seasonal progression of ovarian change is by no means uniform in all shad. In some the changes are months in advance of these illustrations, in others they are months tardy. Whichever the case



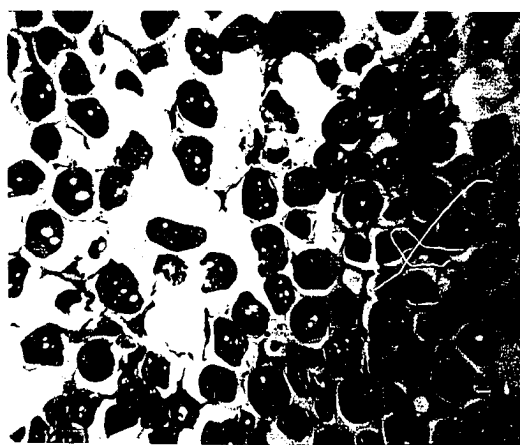
Stage 1 (8/23/54).



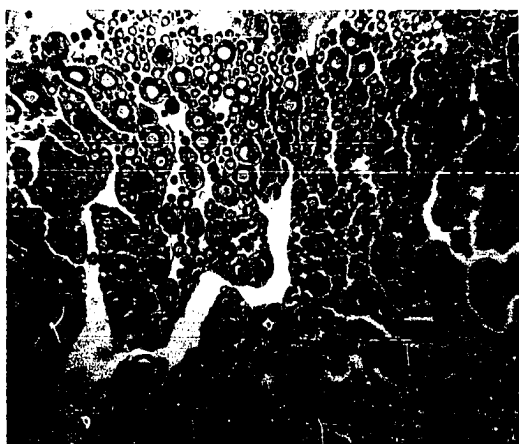
Stage 4 (5/5/54).



Stage 2 (10/19/53).



Stage 5 (6/10/54).



Stage 3 (12/9/53).



Stage 6 (7/3/53).

Figure 40. Seasonal Changes Occurring in the Ovary
of Shad (Dissecting Scope--Medium Power).

may be, they tend to become more uniform by the spawning season--the advanced ones tend to remain dormant just prior to the spawning season while the retarded ones develop rapidly at this time.

The following seasonal changes occur in the ovary:

Stage 1. (August). The follicular remnants have been absorbed and some of the small eggs are starting to develop.

Stage 2. (October). At this time most of the eggs (for the coming season) are at Stage 3 of Figure 39.

Stage 3. (December). By this time many of the coming season's eggs have reached Stage 4 of Figure 39.

Stage 4. (May). Eggs are in Stages 5 and 6 of Figure 39.

Stage 5. (June). Eggs are in a stage subsequent to the last stage shown in Figure 39--some are on their way out.

Stage 6. (July). The eggs have been spawned--eggs for future spawnings are present as well as remnants of the old follicular layers. The ovary at this time has many spaces where the eggs had been and many fissures resulting from the migration of the eggs ventward.

Incidentally, while there is no lumen in the ovary, the eggs migrate through the substance of the ovary

toward the vent. They do not leave laterally through the ovarian wall into the body cavity.

Fecundity.

In Table 17 are given the results of gizzard shad egg counts. It is noted that considerable variation exists in the number of eggs per individual. Although the number of counts is meager, the averages show definitely, a meager egg production among the precocious I-yr. shad, a maximum production by the II-yr. ones, and a slowly declining number by successive age groups.

In this connection it is noted in Figure 41, in which average ovary/body weight ratios of fish pooled within 50 gram categories were plotted against the total weight of the fish, that the ratio differed according to the total weight of the fish. The peak ovary/body weight ratio occurs at 600 grams. These data agree with the egg count data in Table 17.

Development and Hatching.

The eggs of the gizzard shad are heavier than water and slowly sink after being expelled by the female. The egg capsules adhere to whatever they come in contact with--submerged aquatic plants, stones, etc. The hatching time varies from about 36 hours to perhaps a week, depending on the water temperature (based on hatching experiments

| DATE OF CAPTURE | AGE | STANDARD LENGTH (MM) | WEIGHT OF FISH (GRAMS) | WEIGHT OF OVARIES (GRAMS) | NUMBER OF EGGS IN OVARIES (ESTIMATE) | AV. NO. OF EGGS PER INDIVIDUAL BY AGE GROUP |
|-----------------|-----|----------------------|------------------------|---------------------------|--------------------------------------|---|
| July 6, 1954 | I | 225 | 260 | 3.88 | 22,405 | 59,482 |
| July 8, 1954 | I | 236 | 305 | 14.8 | 96,560 | |
| May 23, 1955 | II | 282 | 524 | 78.6 | 543,912 | 378,985 |
| June 3, 1954 | II | 285 | 529 | 71.65 | 524,580 | |
| May 20, 1954 | II | 292 | 593 | 35.15 | 211,378 | |
| May 20, 1954 | II | 293 | 578 | 24.55 | 258,345 | |
| May 23, 1955 | II | 305 | 526 | 55.8 | 356,713 | |
| May 23, 1955 | III | 322 | 713 | 44.5 | 406,174 | 344,784 |
| June 18, 1954 | III | 328 | 700 | 62.63 | 367,670 | |
| June 24, 1954 | III | 343 | 847 | 36.21 | 260,509 | |
| June 18, 1954 | IV | 348 | 882 | 28.78 | 267,216 | 308,749 |
| June 23, 1954 | IV | 363 | 895 | 74.2 | 350,283 | |
| June 23, 1954 | VI | 355 | 1,114 | 29.8 | 215,331 | 215,331 |

Table 17. Egg Estimates Per Individual Shad.

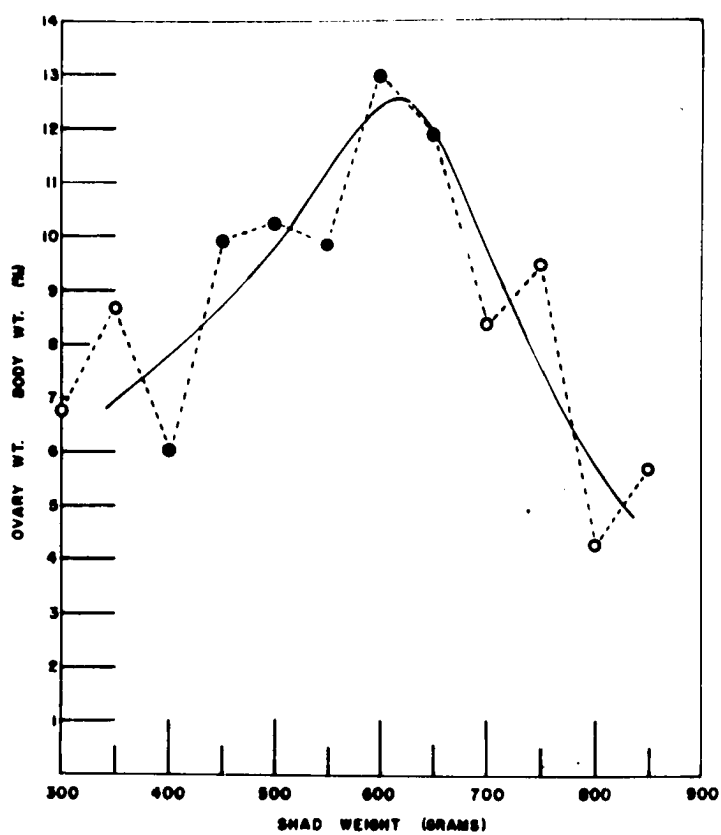


Figure 41. Ovary/body Weight Ratio Graphed Against Body Weight (June Collection).

in the State Fish Hatchery at Put-in-Bay). This agrees with Warner's (1940) observations at Buckeye Lake (Ohio).

Although for two years I tried rearing hatch after hatch of shad, using running water, aerated water, and standing water, and have varied food offerings from that found in the running water, to reared protozoa, and phyto- and zooplankton strained from lake water, I could not keep the young alive beyond the tenth day after hatching. Up to the ninth day they appeared to be doing fine with practically no mortality, then suddenly on the tenth day only a handful remained alive out of literally thousands. Those remaining perished before the day ended.

The movements of the newly hatched shad were an upward swimming and a downward settling--in each direction the head going foremost. This went on for three or four days. The whole body moved snakelike with such rapidity that the individual movements could not be followed. At this time the pectoral fins were not yet used to any great extent. On the fourth day these fry began swimming horizontally as well as up and down. In a Petri dish, under a dissecting scope, their mode of swimming at this time was observed to be largely by the pectoral fins. These 'vibrated' with the rapidity of a bee's wings in flight. The snakelike body movement was not abandoned but its frequency had slowed and one could easily follow this movement. After

adding food to the aquaria, the young shad were observed to 'flit' to and fro as though pursuing some item of food. Although the gut showed some food to be present during the fifth or sixth day, only some green algae were recognizable while peering through the thin gut wall.

Incidentally, the young congregated on the lighted side of the aquarium. If all sides were lighted and running water was used, they were found mostly close to the source of the running water facing the source.

Sex Ratio.

The sex ratios during the spawning season can be obtained from Figure 37 and 38 for lake and shoal caught shad.

The sex ratios for the different ages are given on a yearly basis in Table 18.

| AGE | MALE | FEMALE | PERCENT MALE | PERCENT FEMALE |
|-------|-------|--------|-----------------|-------------------|
| 0 | 1,873 | 2,138 | 46.70% | 53.3% |
| I | 728 | 940 | 43.65% | 56.35% |
| II | 523 | 495 | 51.38% | 48.62% |
| III | 54 | 94 | 36.5% | 63.5% |
| IV | 9 | 13 | 40.5% | 59.5% |
| V | 1 | 7 | 12.5% | 87.5% |
| VI | 2 | 1 | 66.7% | 33.3% |
| Total | 3,190 | 3,688 | 46.4% | 53.6% |

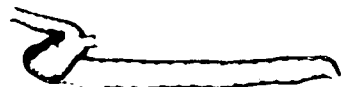
Table 18. Numbers and Percents of All Ages of Shad by Sex (Pooled Collections of 1952, 1953, 1954).

In the 0-yr - II-yr. group the sex ratios are probably not significantly different from 1. The III-yr. and IV-yr. data, however, indicate a differential sex loss--more females than males surviving to these ages.

FOOD HABITS

Digestive System.

As noted by Warner (1940) the alimentary canal of the gizzard shad larva (one or two days old) consists of a single straight tube about one-half the total length of the fish. I have been able to hatch some eggs and keep the larvae alive for ten days. Up to this age the gut appears not to have changed. The gut of an 18 mm shad, seined in Fishery Bay (age unknown), had already developed two flexures--the portion of the gut between them eventually develops into the gizzard. The 19 mm shad has begun its third and fourth flexures and the 22.5 mm one already has them completed. The caeca laden duodenum will develop between the second and third flexures. It is interesting to note, Figure 42, that as the gut continues to grow, the flexures are pushed until they reach the limit of the abdominal cavity. Continued gut growth does not push the flexed portion further to one side, or upward or downward, but rather 'secondary' flexures develop between the 'primary' ones. In other words, the flexures, once formed, are landmarks by means of which one can observe what portion of the gut continues to grow. The distal part of the gut makes a greater gain in length and its growth continues for a longer period of time than does any other portion. The first three flexures remain with



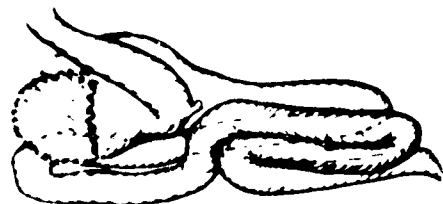
18 MM SHAD (SL)



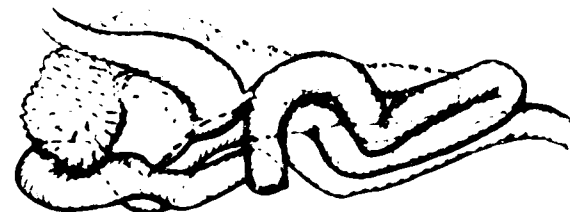
19 MM SHAD (SL)



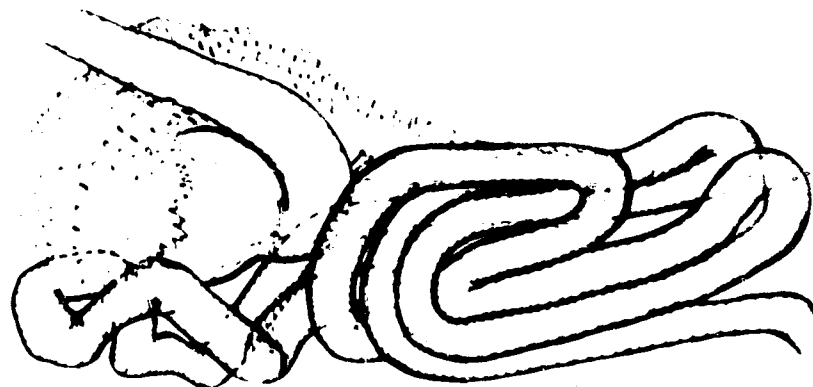
22.5 MM SHAD (SL)



27.5 MM SHAD (SL)



33 MM SHAD (SL)



51 MM SHAD (SL)

Figure 42. Development of the Shad Gut (Camera Lucida Drawings).

no 'secondary' flexures developing between them. It is from the gut segments included between them that the hepatopancreas, gizzard, and caeca develop. The 51 mm stage is relatively simple as compared to the adult of, say, 250 mm, where the convolutions are so numerous and complex as to defy being traced from a two-dimensional illustration. Indeed, the gut which began as one-half the total length of the day-old fish becomes, in the adult, three times the fish's total length and is packed in an abdominal cavity one-third of the fish's length!

A brief notation about parts of the anatomy of the digestive apparatus of the gizzard shad would not be amiss here. Forbes (1914) stated that the larva of this fish has teeth. After examining many young, ranging in size from newly hatched to 20 odd millimeters when the adult shape begins taking form, I have yet to observe these teeth!

The pharyngeal pockets, mentioned by Forbes (1888) and adequately described by Lagler and Kraatz (1944) constitute a paired muscular organ which has been wholly overlooked by students of shad food. This paired organ probably forces food into the esophagus. The action of distinct sphincter muscles at the proximal portion of the pneumatic duct probably prevents food passage into the air bladder.

The muscular and glandular esophagus, and the gizzard have been adequately described by Wier and Churchill (1945). I might add that the esophagus possesses longitudinal folds.

The numerous caecae which arise from the lateral portion of the duodenum converge in groups which have common orifices arranged in two rows which connect them with the lumen of the duodenum. The caecae are longest at the anterior portion of the duodenum and shortest at the posterior end. In a 200 mm shad these range from about 5 mm to about 2 mm. Counts were not made but there appear to be several hundred of them. They possess longitudinal folds within. Their lumen are so small as to admit only liquids and unicellular organisms. Only when the duodenum was turgid with food was there found anything in the caeca, although they appear to function as absorptive devices rather than secretory ones. The lining cells are columnar--non ciliated.

Although Wier and Churchill (op. cit.) have located and described a pancreas separate from the liver for this fish, I have been unable to identify one although I have searched for it repeatedly in many sizes of shad. They describe the liver as being composed of several lobes. I find that it has no definite form but rather seems to spread in close proximity to the gut, invading intercaecal spaces

as well as those between neighboring portions of the gut, and completely covering the anterior, dorsal, ventral, and left lateral fields of the gizzard. It is a very diffuse type of organ and intermixed, I believe, with the pancreas.

The small intestine possesses no villi, contrary to Forbes and Richardson (1908) nor does it have the large conspicuous longitudinal folds described by Wier and Churchill (op. cit.). Rather there are four ridges extending longitudinally in the gut. Attached between each of two ridges and along the circumference of the gut (consequently there are four rows) are folds which have a free edge directed toward the center of the lumen. These 'transverse lamellae' remind one of the valves found in veins. The free edge of each 'lamella' is directed slightly posteriorly. See Figures 43 and 44.

While the columnar cell lining of these 'transverse lamellae' is unquestionably absorptive and while these lamellae greatly increase the absorptive surface of the gut, they may also function in the manner suggested by Milton Trautman when I showed them to him. He suggested that during peristalsis the longitudinal ridges (by apparent lengthening and shortening due either to actual changes in length or to changes in position) may cause these lamellae to move back and forth and hence, to aid in forcing food along the tract.

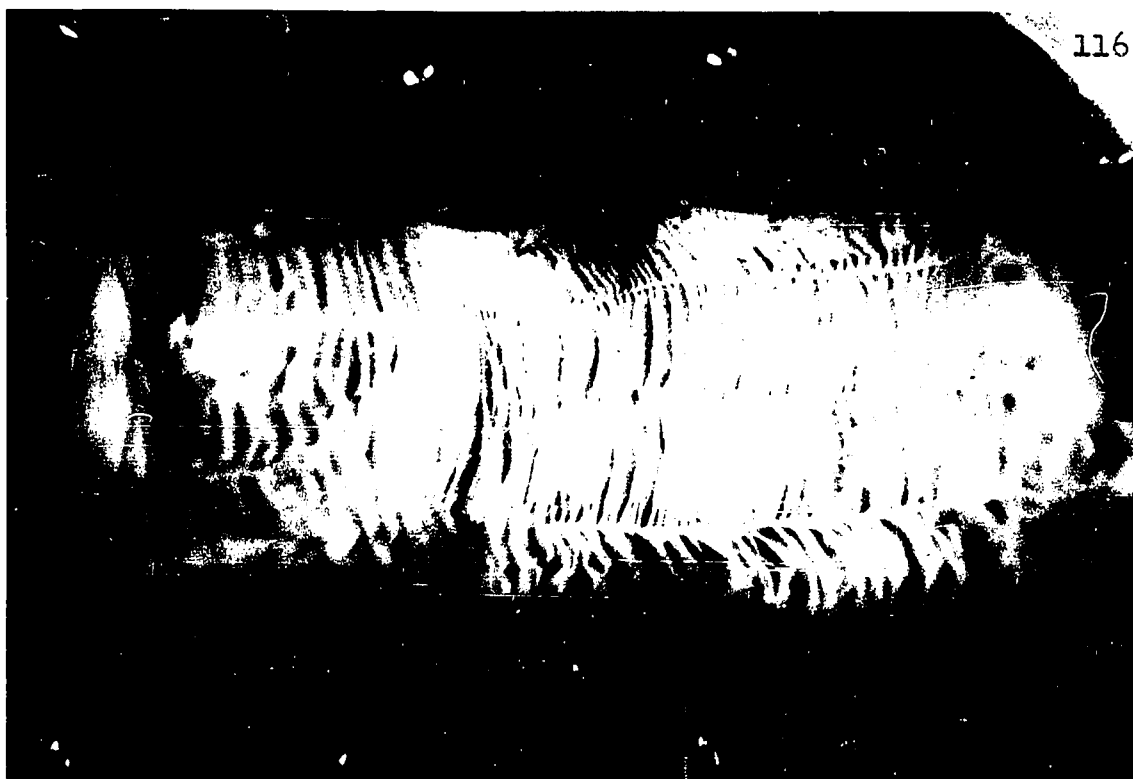


Figure 43. Inner Wall of Shad Gut Showing the Four Longitudinal Ridges and the 'Transverse Lamellae'.

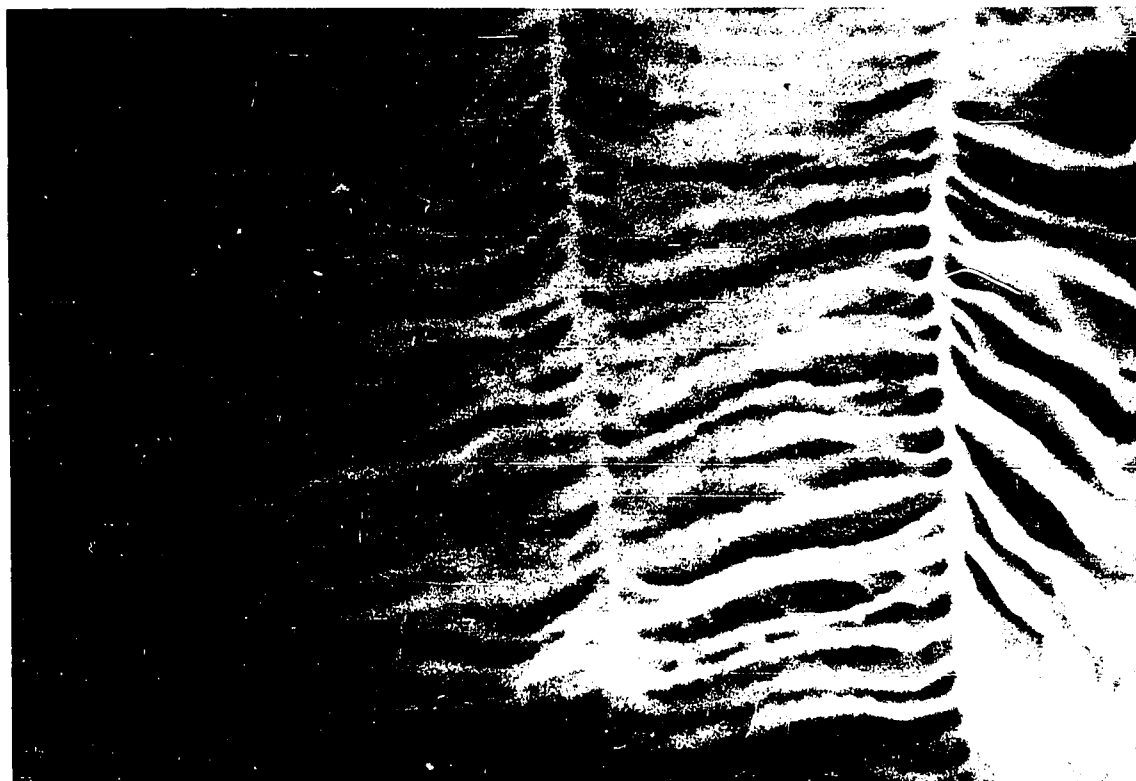


Figure 44. Enlarged View of the 'Transverse Lamellae'.

The nearest resemblance I could find to this in the literature was that by Kraatz (1924) of the gut of Campostoma anomalum, Raf. in which the folds assumed a zig-zag arrangement.

In the 22.5 mm shad the 'transverse lamellae' are present but are attached only to the circumference of the gut--there not being any of the four longitudinal ridges present as yet.

Longitudinal sections of the gut give the appearance of being villous, which may account for Forbes and Richardson's description.

I have not found the columnar cells lining the gut to be ciliated as have Wier and Churchill (op. cit.).

Incidentally an organ which I can identify only as the spleen is located at the posterior part of the visceral mass, extending on either side of the cloaca, ventrally and anteriorly.

Digestive Enzymes.

In order to understand better which of the kinds of material ingested by the shad is used as food, a qualitative study was made of its digestive enzymes. No attempt was made to determine the quantity or potency of the enzymes beyond what the qualitative tests showed.

The areas tested were: pharyngeal pockets, esophagus, gizzard, duodenum (that fore part of gut contain-

ing the caeca), hepatopaneas, bile, and the first, second, and third portions of the gut. These were prepared in the usual manner, the extraction made with 50% glycerol.

The enzymes tested for were: pepsin, trypsin, amylase, lipase, maltase, sucrase, and rennin. In addition enzymes were sought which would act on chitin and cellulose. Table 19 gives the information pertinent for the enzymes sought.

The enzyme giving the strongest reaction in the gizzard shad was amylase. See Table 20. It was found in all areas tested.

Pepsin and trypsin gave moderate reactions while that of lipase was weak. I am at a loss to explain the significance of the positive test for rennin.

The presence of enzymes in the esophagus is not new in fishes. Sarbahi (1951) found amylase, maltase and invertase in the goldfish esophagus and Kenyon (1925) gives Kingsley as reporting gastric glands in the sturgeon esophagus.

Foods and Feeding Habits.

The young gizzard shad begins feeding on about its third day after hatching. The earliest item of food is mostly protozoa. When the shad has attained a length of about twenty millimeters (age unknown) it feeds on the smaller of the zooplankters practically to the exclusion

| ENZYME | SUBSTRATE | pH ADJUSTED | TEMPERATURE | TIME | POSITIVE REACTION |
|-------------|------------------------------|-----------------------|----------------------------|------------------------|---|
| Pepsin | Carmine Fibrin | 1.5 | 37° C. Room Temperature | 24 hrs 48 & 84 hrs. | Release of color & dissolution of fibrin if enzymatic action is strong |
| Trypsin | Congo Red Fibrin | 8.0 | Room Temperature | 24 & 84 hrs. | Release of color & dissolution of fibrin if enzymatic action is strong |
| Amylase | Soluble Starch | | Room Temperature | 1 & 24 hrs. | Negative iodine test for starch & positive Benedict's test for dextrose |
| Lipase | Fresh Milk & Phenolphthalein | 8.3 | | | Fading of pink due to production of fatty acids |
| Maltase | 1% Maltose Solution | | Room Temperature | 1 hr. | Positive reaction with Barfoed's reagent (heating regulated) |
| Sucrase | 1% Sucrose Solution | | Room Temperature 37° C. | 1 hr. 24 hrs. | Positive Benedict's test |
| Rennin | Fresh Milk | | Room Temperature | 48 & 84 hrs. | Clotting of the milk |
| 'Chitinase' | Daphnia & Gammarus | Neutral 1.5 8.0 | Room Temperature | 72 hrs. | Dissolution or fragmentation of exoskeleton |
| 'Cellulase' | Filter Paper & Cladophora | Neutral 1.5 8.0 | Room Temperature & 37° C. | 24 hrs. | Dissolution or disintegration of filter paper & Cladophora |

Table 19. Information Pertinent to Enzymes Sought in the Gizzard Shad.

| ENZYME | PHARYNGEAL POCKETS | ESOPHAGUS | GIZZARD | DUODENUM | HEPATOPANCREAS | BILE | 1st INTESTINE | 2nd INTESTINE | 3rd INTESTINE |
|-------------|-----------------------|-----------|---------|----------|----------------|------|---------------|---------------|---------------|
| Pepsin | - | xx | xxx | xx | x | - | - | - | - |
| Trypsin | - | | - | xxx | xx | x | | | |
| Amylase | xx | xx | xx | xxx | xxxx | xxx | xxx | xxx | xx |
| Lipase | - | - | ? | x | xx | x | - | - | - |
| Maltase | - | - | - | ? | ? | ? | - | - | - |
| Sucrase | - | - | - | x | - | - | - | - | - |
| Rennin | - | - | ? | xx | xx | - | | | |
| 'Chitinase' | | | | | | | | | |
| Neutral | - | - | - | - | - | - | - | - | - |
| Acid | - | - | - | - | - | - | - | - | - |
| Alkaline | - | - | - | - | - | - | - | - | - |
| 'Cellulase' | | | | | | | | | |
| Neutral | - | - | - | - | - | - | - | - | - |
| Acid | - | - | - | x | - | - | - | - | - |
| Alkaline | - | - | - | - | - | - | - | - | - |

Table 20. Digestive Enzymes Found in the Gizzard Shad.

| | | | | | |
|-------|---|----------------------|------|---|-----------------------|
| Blank | = | Not Tried | xx | = | Small Reaction |
| ? | = | Not Definite | xxx | = | Considerable Reaction |
| - | = | Negative | xxxx | = | Very Good Reaction |
| x | = | Perceptible Reaction | | | |

of phytoplankton. By the time it is thirty millimeters long it has assumed the adult shape, and its gizzard is fairly well developed. About this time it is beginning to venture into deeper water where the zooplankton population is less concentrated. By choice or because of circumstances, the shad now begins to feed more and more on phytoplankton.

Throughout the literature there appear to be three schools of thought regarding the nature of the food eaten by adult gizzard shad. Some claim they eat predominately mud, others insist that they feed chiefly on phytoplankton, while still others maintain that they subsist mainly on zooplankton. All agree, however that they are filter feeders, and this alone, I believe, best describes them. They filter the water of whatever may be in it. The fish captured in open waters contained mostly free-floating phytoplankton, those captured among the attached plants such as *Cladophora*, *Myriophyllum*, etc. contained high percentages of Cladocera, Copepods, Rotifers, and small aquatic larvae, while those captured in very turbid water were filled largely with mud. That they do, however, add to their diet from the bottom debris is evidenced by the presence of sand particles of sizes in excess of 0.25 mm in diameter. This size sand is not in suspension even when the water is most turbid.

While the bottom is available to the shad at all time, I have not found sand in them from December through March. No recognizable food particles were present during this time either. The taking of sand when food is plentiful suggests its use as an aid in maceration by the gizzard.

Microscopic examination of the 'stomach' contents of adult gizzard shad revealed no appreciable differences between individual shad of a group collected in one locality at one time. There did not seem to be any selection of food within the size range they swallow. There was, however, a site and a seasonal difference, due undoubtedly, to the relative abundance of the different forms present at different times and in different places. No detailed quantitative studies were made--the forms present in abundance are indicated in Table 21. In consequence of the foregoing, individual fish samplings were soon discontinued and collection samples taken instead, i.e., the 'stomach' contents of several fish of a collection were lumped together and this was considered to be representative of the food ingested by these shad at that time and place.

The 'stomach contents' were in reality, three separate samplings--one each from the pharyngeal pockets, the gizzard, and the intestines.

Material taken from the gut is largely fragmented

| | |
|---------------|---|
| January----- | <u>Debris</u> |
| February----- | <u>Debris</u> |
| March----- | <u>Debris</u> |
| April----- | <u>Debris</u> , Diatoms, Sand |
| May----- | <u>Debris</u> , Diatoms, Sand, Copepods |
| June----- | <u>Debris</u> , <u>Diatoms</u> , <u>Rotifers</u> , <u>Green-algae</u> , <u>Cladocera</u> , <u>Copepods</u> , <u>Sand</u> Chiramonas larvae, Euglena |
| July----- | <u>Blue-greens</u> , <u>Copepods</u> , <u>Volvocaccae</u> , <u>Cladocera</u> , <u>Rotifers</u> , <u>Diatoms</u> , <u>Ceratium</u> , <u>Sand</u> , <u>Green-algae</u> |
| August----- | <u>Sand</u> , <u>Green-algae</u> , <u>Cladocera</u> , <u>Blue-greens</u> , <u>Euglena</u> , <u>Rotifers</u> , <u>Ceratium</u> , <u>Copepods</u> , <u>Diatoms</u> , Ostracods |
| September---- | <u>Greens</u> , <u>Blue-greens</u> , <u>Diatoms</u> , <u>Cladocera</u> , <u>Rotifers</u> , <u>Sand</u> , <u>Copepods</u> |
| October----- | <u>Diatoms</u> , <u>Greens</u> , <u>Cladocera</u> , <u>Rotifers</u> , <u>Sand</u> |
| November----- | <u>Diatoms</u> , <u>Greens</u> |
| December----- | <u>Debris</u> |

Table 21. Gizzard Shad 'Stomach' Contents by Months. Most Abundant are Under-scored--Least Abundant are Omitted.

and mostly unrecognizable--giving the appearance of bottom debris or mud, especially upon gross inspection. I have never found any compact matter approaching 3.0 mm in diameter in the shad, although Tendipedidae and small Leptodora were not uncommon during certain seasons. Neither have I found in them bits of attached aquatic plants, except after severe storms when small fragments of these plants were presumably torn loose.

There are three distinct regions in the alimentary apparatus where food may be found--the pharyngeal pockets, the gizzard, and the gut, especially the fore part which is beset with caeca and which is often swollen with ingested material.

The pharyngeal pockets, described by Lagler and Kraatz (op. cit.) and suggested by them to be accessory to the digestive system, has, to my knowledge, not been examined by students of shad food. Although food is frequently absent here, yet when the water--and the fish's gut, are full of food (especially zooplankton) the pharyngeal pockets contain as much food as does the gizzard. Grossly, their contents appear straw colored and consist mostly of Cladocera and Copepods along with long strands of filamentous algae. Here are found the grosser parts of the shad's diet, and they are, as yet, undisturbed. The zooplankters still have their full complement of limbs

and the filamentous algae are in long strands.

The gizzard is frequently empty--not often is it turgid with food. Food, when found here, is similar to that found in the pharyngeal pockets--except that the zooplankters are more or less dismembered and the filamentous algae are in short strands. In addition there are many unicellular algae, Rotifers, and sand present, together with plant and animal debris.

The gut usually contains food, although it is scanty in winter. Most of the material in the gut is unrecognizable. A sample of this would surely convert one to accept a 'mud feeding' habit for shad!

The contents of the alimentary tract of the shad vary according to season and locality. They are in agreement with the sediments, living and dead, found in the water with the fish. As Tiffany (1920) indicated, these fish are a living tow net. Consequently, there is little to be gained by indicating the percentage of each item found ingested by the shad. Nor is there much to be gained by indicating every organism eaten by the shad at one time or another. Therefore, I list in Table 21 only the few major groups found during the year.

As is to be expected, during the time of least shad growth--December through March--no recognizable food was found in the gut, its scanty contents were a yellowish,

slimy fluid. The pharyngeal pockets and gizzard were empty.

During the season of most rapid growth, Rotifers, Copepods, and Cladocera were major items in the diet.

Velasquez (1939) was able to culture algae taken from various parts of the shad gut. He concluded that while the shad utilized some algae, others passed through it unscathed and that the shad consequently influenced the algal composition of the waters it inhabits.

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AUTOBIOGRAPHY

I, Anthony Bodola, was born in New York City, October 1, 1914. I received my secondary school education in the public schools at Rivesville and Fairview, West Virginia. My undergraduate training was obtained at Fairmont College at Fairmont, West Virginia, from which I received the degree, Bachelor of Arts, in 1942. In 1945 I received the degree, Master of Science, from West Virginia University at Morgantown, West Virginia. In 1952 I received an appointment as Fishery Research Biologist under the U. S. Fish and Wildlife Service and in 1953 I was appointed Senior Conservation Fellow at the Franz Theodore Stone Institute of Hydrobiology where I studied the life history of the gizzard shad. I held the former appointment three years--the latter two years while completing the requirements for the degree, Doctor of Philosophy.