

DEVELOPMENT, GROWTH, and FOOD HABITS of the  
WHITE SUCKER, CATOSTOMUS COMMERSONII  
LESUEUR ..... By Norman Hamilton Stewart

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# DEVELOPMENT, GROWTH, AND FOOD HABITS OF THE WHITE SUCKER, CATOSTOMUS COMMERSONII LESUEUR



By NORMAN HAMILTON STEWART

## CONTENTS

	Page		Page
Introduction .....	147	Development of the larva—Continued.	
Description and distribution of Catostomus .....	148	Histology of the intestine .....	163
Breeding habits .....	149	Adult condition ---	165
Development of the egg .....	152	Coiling .....	167
Condition at laying .....	152	Determination of age .....	168
Number of eggs laid .....	152	Relation between growth of scales	
Spermatozoa .....	152	and size of fish .....	168
Fertilization .....	153	Seasonal irregularities in the circuli .....	170
Water hardening .....	153	Annual growth .....	172
Cleavage .....	153	Food and the feeding habits of the white	
Period of incubation .....	154	sucker .....	173
Cleavage stages .....	154	Review of the literature .....	173
Newly hatched larva .....	157	Food .....	174
Development of the larva .....	158	Periods into which feeding habits	
Digestive tract .....	158	may be divided .....	175
Pigmentation --	158	Detailed account of feeding habits	
Fins .....	158	and food .....	176
Peculiar change in location of mouth .....	159	Summary .....	181
Histology of the mouth. Oral epithelium .....	161	Economic status of the sucker .....	183
		Bibliography .....	183

## INTRODUCTION

It is the aim of the present paper to present an account of the development and biological relationships of the white sucker. Not many papers dealing with single species of our fresh-water fishes have appeared up to the present, but the complex problems of the interrelationships of aquatic organisms will be simplified only by more complete knowledge of the lives of individual species. The rôle played by any species of fish in the economy of stream life varies with its age and feeding habits; hence it is profitable to consider the part played by such a species at every stage of its life. This is attempted in the present paper by bringing together observations extending over a year, and thus including an account of the activities of the sucker during each year of its life and at each season of the year.

As this species is remarkable for its adaptability as well as for its general abundance, it becomes one of the factors that may alter the environment in which the

From the deep, narrow gorge the inflowing creek spreads out over a delta of gravel and stones. The fish described as in deep water were in the portion of the stream at the mouth of the gorge, from which they went over the submerged delta into the shallower water of the lake to spawn. They always retreated ~~upstream~~ into deeper water when disturbed. As many as 40 were counted at a time, and their length ran quite constantly from 10 to 13 inches. Why smaller ones do not frequent this spawning bed remains a question, as we know the species does spawn when about 6 to 7 inches long. I am inclined to believe that this spot is chosen only by the fish that prefer the very deep water of the gorge as their home.

Professor Reighard found suckers breeding in April and early May in southern Michigan. On April 9 wire cage traps were placed in Beebee Lake and visited almost daily thereafter. The season was cooler than usual and we may conclude that spawning was retarded. The following facts encourage this view. Leaving out of consideration one warm day (April 21) the average daily atmospheric temperature was 5.6° F. below the normal from April 9 to May 18, the period during which breeding was in progress. On April 27 ripe fish of both sexes were found in traps located in about 3 feet of water between the deeper water and the spawning grounds proper. Previous catches were made only in 6 to 8 feet of water, and of these none contained ripe fish. Thereafter ripe females and males were taken at short intervals up to May 18. The observations should have been continued, but from May 9 to 18, 75 to 100 per cent of the specimens taken were partially or wholly spent. It ~~would~~ therefore seem that the height of the spawning season at this place was about May 5. If May 25 is taken as the approximate time when spawning ceased, the breeding period extended over 29 days.

An interesting habit, closely related to temperature, was frequently observed. Beginning April 22, whenever the water temperature reached 54° F. suckers were ~~seen~~ rather leisurely swimming up to the surface and breaking the water. Frequently they leaped out of the water for most of their length and then swam back to the bottom. This apparently was not a case of pursuit or of ~~flight~~, and its significance is uncertain.

As Reighard found, so here on this shoal from one or two to four or five males pursue the female fish that wanders over the gravel, even where the water is but 13/ feet deep. Whenever the female stops the whole group of males stops with her. Owing to the presence of fishermen on the high rocky bank near by, I never could see the spawning act.

For several mornings areas of the bottom, from 1 to 2 feet in their greatest extent, were found to ~~be~~ swept clean of debris. Probably the eggs were laid here. The yellow-white stripes along the backs of the fish, peculiar to the breeding season, were very conspicuous.

Subsequent to these observations at Ithaca, the spawning of a group of white suckers was seen to great advantage in Little Buffalo Creek, Union County, Pa., on April 26, 1925. There a company of three males followed a distinctly larger female as she swam upstream into a short, stony rapid. Upon overtaking her the four stopped in swift water of but a few inches depth. So vigorously did the males contest to crowd against the female and to strike her with their heads and tails that the

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surface of the water was broken by the splashing of the whole group. This lasted but a few seconds, whereupon the female retreated into deeper water downstream. In five minutes she returned, and the spawning was repeated, though this time she stopped not over 15 feet from where the observer was stationed.

That the dates given above for Beebee Lake can not be taken as applying to other habitats about Ithaca is evidenced by the fact that in streams accessible to suckers from the colder waters of Cayuga Lake breeding continues much later. Estimated dates when eggs were laid in such streams run as follows: Mouth of Taghanic Creek, May 25; mouth of Six Mile Creek, June 4; the inlet above Buttermilk Creek, June 9; mouth of Trumansburg Creek, May 25; mouth of Butternut Creek, June 25, and lower Salmon Creek, June 4. These dates were obtained by computing back from the date when fry of a determined length and age were collected. For example, if fry 18 millimeters in length were taken as late as August 10, we arrive at the spawning date by subtracting the age, in days, of such fry—viz, 45 days—from the date of capture, giving us June 26. From June 10, throughout the summer, collections were made twice or three times a week, which gave ample opportunity to learn of the average size of fry in the various streams.

This method is open to error, of course, as the basis for the computation of age was made upon eggs and fry raised under slightly unnatural conditions. However, the estimate is probably close to the truth and seems to indicate that suckers in the warmer, shallower, upland streams breed considerably earlier than those coming up out of the colder water of Cayuga Lake. Averages give us May 6 as the approximate close of spawning in the upland streams and June 5 for six streams accessible from the lake. These streams differ in temperature within the two groups here contrasted, which would alter the rate of development in each case, yet the difference of a month between the spawning in these two types of streams points to the coldness of the lake as the cause of the delay.

While no ripe females were taken in any habitat before April 27, it is of interest to note that ripe males were taken as early as March 23. One taken on that date, 6½ inches long, was so ripe that the milt flowed on handling the fish to remove it from the trap. A male taken February 7 was so nearly ripe that spermatozoa removed by dissection were active when placed in a drop of water.

Probably the white sucker does not breed until at least 6 inches in length. They are 4 or 5 years old at this size, and upon most sucker scales the circuli then formed show peculiarities, to be described later on, which doubtless register the physiological activities peculiar to spawning. For a clear account of the breeding behavior the reader is referred to Reighard's excellent paper (1920).

That the pearl organs of the males of this species are effective to roughen their sides and render the escape of the female difficult is witnessed by the fact that females taken from Beebee Lake after spawning showed their sides quite denuded of epidermis, the scales being bare from the caudal to the dorsal fin. Here we have one case of true effectiveness of these problematical structures, the pearl organs, though it seems doubtful that a use can be found for them as they occur on many of the Cyprinidae.

## DEVELOPMENT OF THE EGG

## CONDITION AT LAYING

When expressed from the body of the ripe female the eggs are perfect spheres 2 millimeters in diameter. They are pale yellowish in color and of such translucency as to be easily overlooked in the water. When first laid they are slightly adhesive, clinging to each other and to surrounding objects, but this quality is lost as soon as they are "water hardened"; that is, rendered turgid by the absorption of water.

Like other fish eggs, those of this species are telolethical, the heavier yolk lying below the caplike disk of protoplasm, which therefore is seen plainly from above. This disk is whitish and covers about half of the surface that can be seen from the "animal" pole. (Fig. 1.) At this stage the egg membrane, or shell, everywhere rests closely upon the egg and is so thin and colorless as to escape detection easily. Its thickness is 15 microns. Of this, the inner *zona radiata* comprises 9 microns and is made up of alternate light and dark bars each 1 micron in thickness. The outer layer is very similar to the *stratum villosum* of the egg of *Lepidosteus*, described by Mark (1890), and is 6 microns thick. The micropyle is easily seen under the microscope. At first it is a funnel-shaped depression of the shell, which, when the egg is beginning to swell, reaches nearly to the egg proper (germinal disk). A very slight implantation cone is seen on the disk opposite it. After 20 minutes in water the space between the egg and the shell has swelled so much that the micropyle dips down but one-third of the distance. By 13½ hours it is withdrawn with the shell, now reaching but one-eighth of the intervening distance. The yolk mass consists of evenly distributed yolk globules, which, after dehydration, measure from 8 to 14 microns in diameter. There is no layering of the yolk, as in birds' eggs. No large oil drops are found in the sucker's egg, but numerous very clear droplets of minute size are seen both in the yolk about the edges of the blastodisc and contained in the cells of the latter after segmentation begins.

## NUMBER OF EGGS LAID

From one 12-inch female 150 cubic centimeters of eggs, weighing 165 grams, were removed, each egg measuring 2 millimeters across before water hardening. By reference to the tables of von Bayer it will be found that this volume contains 18,000 eggs of this size. Single eggs weigh between 6 and 10 milligrams. A still larger female (15 inches long) contained 31,200 eggs.

## SPERMATOZOA

The sperm cells measure 24.7 microns in length, the ovoidal head or nucleus being 5.7 microns. The neck or middle piece is exceedingly small, less than 0.5 micron, and is seen with difficulty. The nucleus is sometimes blunt at the ends but is circular in cross section, resembling that of a trout. It could be seen after staining with hematoxylin. The flagellum was evident when iodine was used. The

von Bayer, R.: "A method of measuring fish eggs." Paper presented before the Fourth International Fishery Congress held at Washington, September 22 to 26, 1908. Bulletin, U. S. Bureau of Fisheries, Vol. XXVIII, 1908 (1910), Part 2, pp. 1009-1014. Washington.

spermatozoa are motionless when removed by dissection from the body of the freshly killed fish and examined with the microscope, but the instant a drop of water is added they reveal an activity not exceeded in its rate and pandemic nature by the most active assemblage of protozoa or bacteria. One is reminded of chemical reactions in which every particle is thrown into violent motion.

Spermatozoa from a male trapped on February 7 and measuring  $8\frac{3}{4}$  inches in length showed the following periods of such activity in various media: Tap water, 40 seconds; water from a goldfish aquarium, 45 seconds; melted snow, 45 seconds; human saliva, 5 seconds. The spermatozoa from a male that had been dead for one hour were nearly as active as this, though those from a fish four hours dead were inactive. In view of the excessive activity with which the male germ cells seek and fertilize the eggs during the minute or so of their swimming actions, it is possible to appreciate the advantage of both elements being discharged at the same time and over the same spot on the gravel.

#### FERTILIZATION

In nature this occurs during the moments following the discharge of eggs and sperm by the group of suckers engaged in the act of spawning. To obtain fertile eggs for study, a pair of ripe fish were taken from the traps on April 28 and removed to the Cornell University Fish-Cultural Experiment Station. Here the eggs and sperm were, by gentle pressure, expressed from the bodies of the live specimens into a small clean dish. The combined elements were stirred and allowed to stand for three minutes, after which water was added. Fertilization of well over 90 per cent of the eggs took place. That this occurred before the addition of the water, as is frequently assumed, can not be stated with certainty, as microscopic examination was not made until after the water was added. At that time the micropyle and implantation cone were clearly seen on several eggs.

#### WATER HARDENING

The egg when laid measures 2 millimeters in diameter. When water is added it begins to swell. The water enters through the shell or egg capsule, no doubt by way of the pores of the *zona radiata*, and lodges between the capsule and the egg. Within 30 minutes the eggs are quite turgid, have lost their partial adhesiveness, and may be handled without danger of causing injury. The capsule now stands one-half millimeter from the egg, giving a total diameter of 3 millimeters. The imbibed water probably functions to afford added protection from impact of sand, etc., prevent sudden changes of gases or liquids through the shell, and to permit movement of the embryo before hatching.

#### CLEAVAGE

A Meehan hatching jar was used with complete success. Such a jar provides a constant circulation of water from the lower end of an inserted glass tube upward through the eggs. The water used was from the creek, which is the source of supply for the station, so that conditions were as nearly natural as they could be made. A dozen eggs were taken daily, or oftener at first, fixed in Gilson's or Perenyi's fluid, and preserved in 70 per cent alcohol. Examination was made of them in the alcohol

for surface views, while many were embedded in paraffin, M. P. 54°, sectioned, and stained with Mayer's hematoxylin and eosin. A nonfertilized egg sections like hyaline cartilage, and fry with the yolk still unabsorbed, that were fixed in formalin, sectioned well. However, only a very small percentage of good sections of the cleavage stages were obtained. Those obtained nevertheless add much to the picture of the cleavage process.

#### PERIOD OF INCUBATION

The eggs in the Meehan jars hatched in 21 days. This is probably a little longer than the average time for the following reasons: About 5 per cent hatched at the end of 12 days, after which a period of cold weather delayed both eggs and fry for about a week. Then all hatched in two or three days. Cold weather is common at Ithaca even in May, so that probably 18 to 20 days is the normal period. Reighard (1915) gives 8 millimeters as the length of the newly hatched fry, but mine exceeded this by a millimeter or two, due, perhaps, to delayed hatching. The mean temperature of the water over the whole period was 50.5° F.

#### CLEAVAGE STAGES

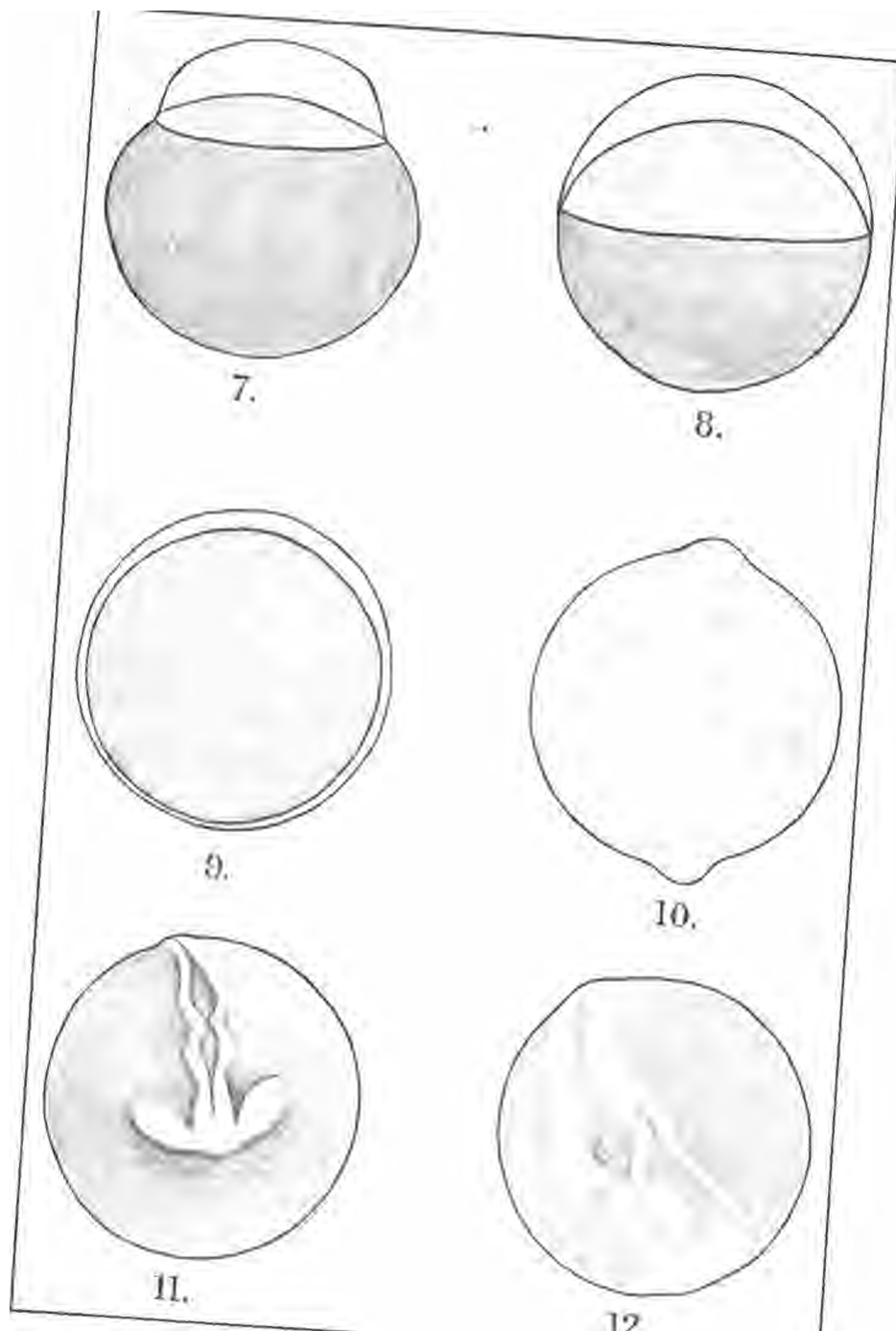
*One-celled stage.*—*Two* and one-half hours. (Figs. 1 and 2.) Samples taken two and one-half hours after fertilization are still in the one-celled stage. The shell must be removed carefully with dissecting needles. This done, the germinal disk appears white and covers about half of the top of the egg, extending down the sides about 45° from the pole. The contour of the *egg* is still that of a sphere, and the protoplasmic portion is but one-half millimeter thick at the pole and thins out laterally. Pseudopodialike branching processes of the disk extend down into the central region of the yolk. Clear droplets (oil?), twice the diameter of the yolk spheres, are found in the protoplasm, especially near its upper surface. Yolk spheres are sparsely but rather evenly scattered throughout the disk. These evidently are contributed from the densely packed yolk mass on which the disk rests.

*Four-celled stage.*—*Six* hours. (Fig. 3.) At the end of four hours the germinal disk contracts and arches up as a conspicuous white dome, leaving distinct shoulders to the egg when seen from the side. By six hours this dome-shaped disk is crossed by the first two cleavage furrows placed at right angles. These furrows extend one-third to one-half the distance through the disk, and sections show the continued wall below each one passing on to the yolk. The nuclei are centrally located in the cells, which are quite sharply demarked from the yolk laterally as well as below, as seen in sections. No cytoplasmic ~~extensions~~ of the disk were observed ~~beyond~~ the one-celled stage.

No observations were made upon the eight-celled stage.

*Eighteen-celled stage.*—*Eight* hours. (Fig. 4.) The cell cluster is sharply outlined, the cells being of nearly equal size. Cleavage planes are irregularly radial, resulting in an outer ring of about 11 cells surrounding the remainder, which are irregularly placed centrally. The outer cells are slightly larger.

*Thirty-six celled stage.*—*Ten* and one-half hours. (Fig. 5.) The centrally placed cells show by their relatively smaller size the more active cleavage. Up to this time the general contour of the egg is as in the four-celled stage—namely, a dome-shaped blastodisc surmounting the spherical yolk mass.



FIGS. 7-12.—Development of the eye of the white sucker, *Catostomus commersoni*. In each case the shell has been removed. 7. At 40 hours (both eyes cleared in yolk). 8. Extent of the blastoderm at 51 hours. 9. Same phase in development of eye at 92 hours. 10. Dorsal ridge and head process at 109 hours. 11. Development of the brain as seen at 171 hours. 12. The same at 192 hours (8 days).

*Investment of the yolk*  
(Fig. 6.) The blastodisc has begun to extend slightly. The cytoplasm shows a distinct granular texture and oil droplets are seen within.

Forty-four hours. (1)

Fifty-four hours. (1)

begins to thin out at its edge. The thickness is perhaps one-third as that of the sphere.

Seventy hours. The blastoderm may stand slightly above the yolk.

Ninety-two hours.

that while the blastoderm is only one or two cells thick at the vertex.

*Embryo.*—One hundred hours. No indication of the embryo.

One hundred and forty hours. A straight white line is visible as a straight white line. At one end (the anterior) a shallow groove was seen, and Balfour's theory of many teleosts, which is that the embryo is a straight white line.

One hundred and seventy hours. In surface view, have occurred. The optic evaginations are primary cerebral vesicles. The expansions of the neural tube (myelencephalon) is more or less a temporary series of sections of tissue present. It is all of 48 hours. The blastoderm becomes the body of the embryo out over the yolk.

One hundred and ninety hours. The head and body are seen. The limit of the head.

Two hundred and twenty hours. The embryo is reduced to two regions lying around the former core in the tail process.

Two hundred and forty hours. The embryo lies either to right or left of the head. Pigment has appeared. This time, though the millimeter in length of



*Investment of the yolk by the blastoderm up to 92 hours.—Twenty-one hours.* (Fig. 6.) The blastodisc now consists of three layers of rounded cells, and its margin **has begun** to extend slightly farther over the yolk. In each of its 100 or more cells the cytoplasm shows a disposition to radiate from the nucleus, and yolk spherules and oil droplets are seen within the cells. The cells measure 0.1 millimeter in diameter.

Forty-four hours. (Fig. 7.) The disk of cells is becoming flat on top.

Fifty-four hours. (Fig. 8.) At this stage in development the blastoderm **begins** to thin out at its edge, which has reached nearly the equator of the egg. It is perhaps one-third as thick as in the four-celled stage. The whole egg is again a sphere.

Seventy hours. The yolk is now half covered. The advancing rim of the blastoderm may stand slightly above the surface level of the yolk.

Ninety-two hours. (Fig. 9.) The yolk is entirely invested. Sections show that while the blastoderm is six to eight cells thick at the animal pole, it is but one or two cells thick at the vegetative pole.

*Embryo.*—One hundred and twenty-six and one-half hours. Surface views give no indication of the embryonic axis.

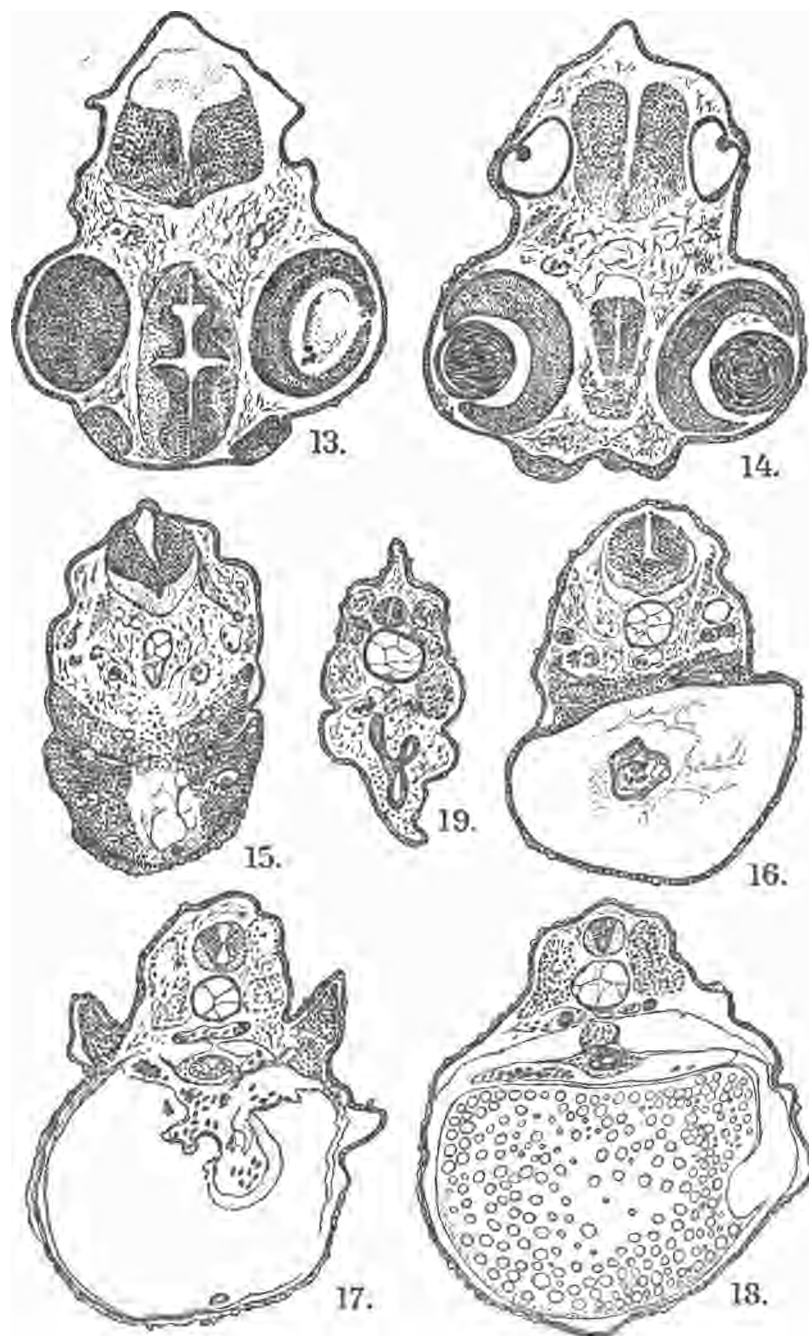
One hundred and forty-nine hours. (Fig. 10.) The body of the embryo fish is visible as a straight white ridge, narrow and rather high, nearly encircling the egg. At one end (the anterior) it terminates as a flat, rounded expansion. No open neural groove was seen, and Balfour (1881) reported the omission of that stage in the *embryology* of many teleosts, which has been well confirmed.

One hundred and seventy-four hours. (Fig. 11.) Marked changes, visible in surface view, have occurred in the anterior axial region. The brain is clearly seen. The optic evaginations are pear shaped and extend outward and backward from the primary cerebral vesicle. The other two cerebral vesicles are present as hollow expansions of the neural tube, the second being about as wide as long, while the third (myelencephalon) is more elongate and has a diamond-shaped ventricle. Fragmentary series of sections indicate that the neural tube is the only well-differentiated tissue present. It is almost solid, but otherwise resembles that of a chick embryo of 48 hours. The blastoderm abruptly passes from the thick ridge, which will become the body of the fish, to the portion, but one or two cells thick, that spreads out over the yolk.

One hundred and ninety-eight hours. (Fig. 12.) The lateral boundaries of the head and body are seen now. The tail process almost reaches around to the anterior limit of the head. The limits of the yolk sac are indicated caudally.

Two hundred and twenty-four hours. The yolk, which has been spherical, is now reduced to two regions. The anterior is spherical but the posterior portion, arching around the former, is cylindrical. The notochord is visible as a clear central core in the tail process, which process extends well beyond the yolk sac.

Two hundred and forty-six hours. The embryo forms more than a circle; its tail lies either to right or left of the head or is bent at a right angle across the front of the head. Pigment has appeared in the eyes. Five per cent of the eggs hatched at this time, though the majority were delayed for some days. The latter gained 1 millimeter in length over those hatching at this time, but were otherwise like them.



Figs. 13-19.—Development of the larva of the white sucker, *Catostomus commersoni*. Cross sections through a larva of 8 millimeters. 13. Olfactory placodes. 14. Eyes and otocysts. 15. Region of the branchial clefts. 16. Ventral aorta and pericardial cavity. 17. Heart. 18. Body and yolk sac. 19. Cloaca region. The Wolffian ducts are seen joining the intestine.

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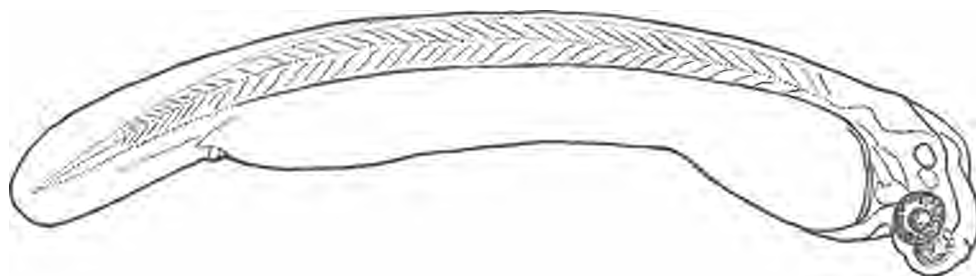
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## NEWLY HATCHED LARVA

The newly hatched fish is about 8 millimeters long but only one-sixth as deep. (Fig. 20.) The slender, whitish body extends along the cylindrical yolk sac, and the decurved head projects 0.8 millimeter in front and the tail 1.5 millimeters behind. The proportionate lengths of head, body, and tail are 1:6:1M, using the vent as the posterior limit of the body proper. The eyes are large and slightly elliptical, the long axis being parallel to the axis of the embryo. The otocysts are as yet simple ovoid sacs. The dome-shaped pericardial cavity containing the small S-shaped heart fits like a cap over the anterior end of the yolk sac.

The mouth is still in the oral pit stage. Myotomes are visible along the back and tail. The anus lies immediately posterior to the yolk sac. A low median fin fold arises in the mid-dorsal region and sweeps around the tail to end at the vent. In the portion that will persist as the caudal fin, delicate rays or actinotrichia are seen in some of the specimens. The pectoral fins begin at this stage as rather thick flaps of undifferentiated mesoderm overlaid with ectoderm. Pigment is present only in the *retinae*.



20.—Sac fry at the time of hatching, rendered partly transparent. The oral pit is ventral, the caudal fin homocercal.  
8 millimeters

Serial sections add much to our study of this stage. (See figs. 13 to 19.) The epidermis is seen to be but two cells thick. The olfactory placodes are but circular thickenings of the epidermis, five or six cells in thickness. No mesodermic coats of the eye are yet present, and the *orbital* musculature is barely outlined. The cornea resembles the general epidermis, while the lens itself still shows the vestige of its cavity and is relatively so large as nearly to fill the optic cup. The heart wall (myocardium) is but four or five cells thick, the heart occupying only the dorsal quarter of the pericardial cavity. The vitelline veins, the aorta and its arches, may be traced. Alongside the large notochord the slender nephric ducts maintain an even caliber as they pass back to join the digestive tube close to the vent.

The intestine itself is considerably smaller in section than the notochord, being a tube of columnar epithelium the cells of which contain very large, clear vacuoles. Just back of the heart is the junction of the anterior end of the yolk sac with the digestive tube, which is flattened. The fore-gut is mostly solid, though the branchial evaginations are well marked. The mouth as yet is not open. In this condition the larva lies on the bottom or swims upward, to sink again to the bottom of the hatching jar. Placed in an outdoor pond, they swam at the surface at the end of the second day after hatching.

## DEVELOPMENT OF THE LARVA

## DIGESTIVE TRACT

The yolk sac is present for but six to eight days, when the larva is 11 millimeters in length. A few complete the absorption of the yolk sac somewhat earlier. As the sac disappears the gut rapidly expands and enlarges from a size smaller than the notochord to that of the yolk sac itself. The mouth becomes open at about 9 millimeters and the branchial apparatus is completed. Food may be taken as early as the 9-millimeter stage, though this is rare. Up to 17 millimeters the gut is a straight tube from mouth to anus. The subsequent changes in the structure of the intestine will be described hereafter.

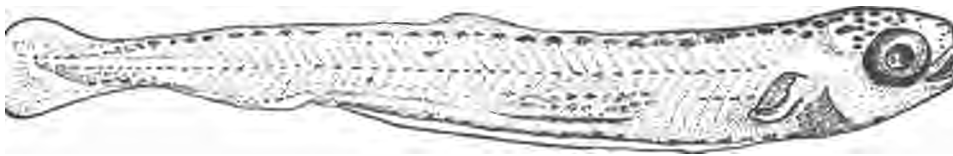


FIG. 21.—9-millimeter fry showing the terminal mouth, the exposed gills, and early condition of the fins and of the pigmentation

## PIGMENTATION

After the appearance of pigment in the eyes (see p. 157), the next to form occurs as a double row of large chromatophores along the mid-dorsal region and about 30 smaller ones on the top of the head. (Fig. 21; 9 millimeters.) A row of smaller ones appears along the mid-lateral line and a double row along the mid-ventral region. By the time the embryo is 12 millimeters long (fig. 22) chromatophores appear in the caudal fin on each side of each ray. At 14 millimeters (fig. 24) the same is true of the dorsal, at 18 millimeters of the pectoral (fig. 25), and at 20 millimeters all fins contain pigment.

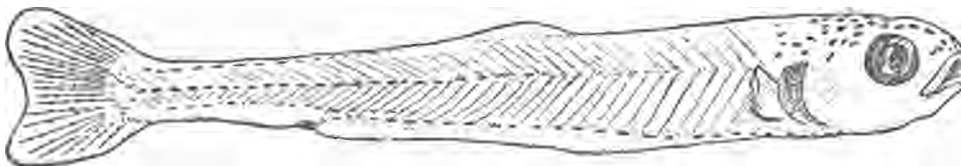


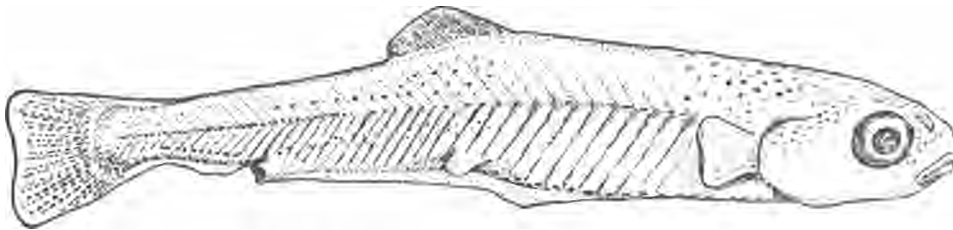
FIG. 22.—Specimen of 12 millimeters. The caudal fin is notched; the operculum covers more of the gills

At 20 millimeters scattered pigment is seen all over the body, which later (at 25 millimeters) begins to follow that of the scales by outlining the area over each scale. At this stage young white suckers begin to appear mottled, as the pigment is intensified in several laterally located spots or blotches. A yellow color appears on the sides, also, giving a distinct golden iridescence.

## FINS

Upon hatching, only the ~~homocercal~~ caudal fin and the pectoral fins are present. The ~~caudal~~ is but the terminal portion of the median fin fold, which passes from the middle of the back around to the vent below. By 9 millimeters the dorsal is defined,

the remainder of the dorsal median fin fold having disappeared. (Fig 21.) The yolk sac, having rapidly reduced in size, appears as only a thin ridge along the mid-ventral line. In the same mid-ventral line the anal fin is seen back of the vent. The caudal fin begins to show its two lobes (homocercal type) at 12 millimeters. (Fig. 22.) It is not difficult to render larva of this length transparent and to see the upturned end of the notochord—a reminder of the heterocercal nature of this fin in

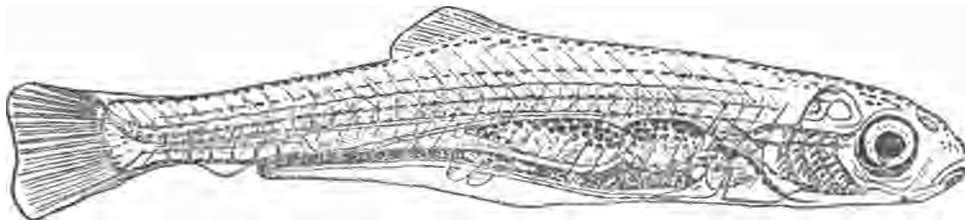


23.—Specimen 15  $\frac{1}{4}$  millimeters long. The gills are almost covered

the ancestor. In the adult male the lower lobe of the caudal is larger than the upper lobe. The pectoral fins are present at hatching, but are so transparent as easily to escape detection except in the examination of stained sections. They function for some time before the relatively smaller ventral fins appear at 15 millimeters. (See Figs. 23 and 24.)

#### PECULIAR CHANGE IN LOCATION OF MOUTH

At hatching (8 millimeters) the mouth is not yet open, the fore-gut being nearly solid. (Fig. 20.) At 9 millimeters, however, the terminal mouth, characteristic of the early top-swimming stage, is completely formed and open. (Fig. 21.) The facial expression of the larva, viewed from directly in front, is as interesting as it is grotesque. The horseshoe-shaped mouth lies in an almost vertical plane, arching up between the very large eyes so that its opening is actually as high as the center of



24.—Specimen 14 millimeters in length rendered transparent. The mouth is becoming inferior, the pelvic fin buds are evident, and the upturned notochord is seen at the base of the caudal fin

the eyes themselves. The eyes, it may be recalled, are contained but three times in the length of the head at this time, whereas they are contained seven times in the head of a 10-inch adult. The nares are each a single oval depression located in the angle between the eye, laterally, and the upper lip below. From its high terminal position the mouth cavity slopes steeply downward and backward to the pharynx. Hyaline cartilage already forms the skeleton of the head.

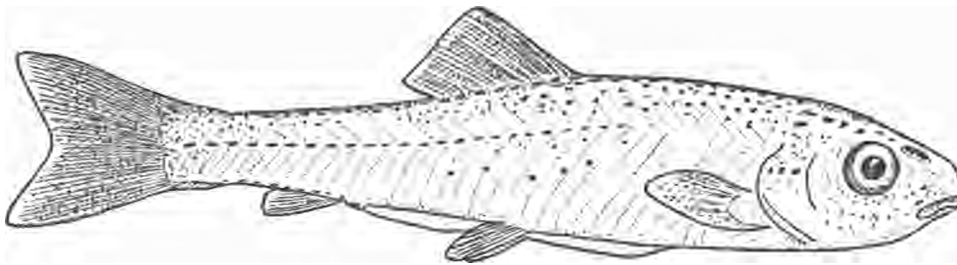


FIG. 25.—Specimen 18 millimeters long, showing the appearance of rays in the ventral and anal fins

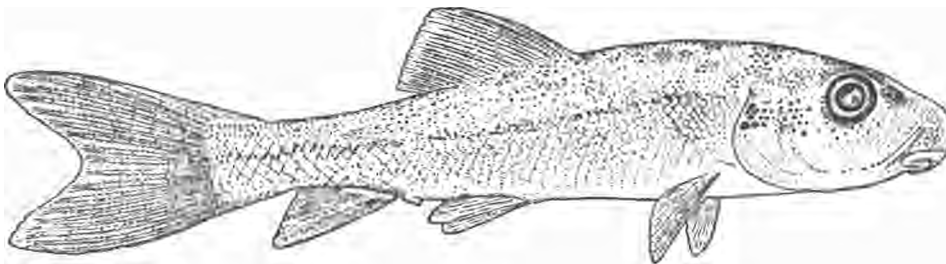


FIG. 26.—Specimen 25 millimeters long. The pigment pattern begins to follow that of the scales. The nostril is divided

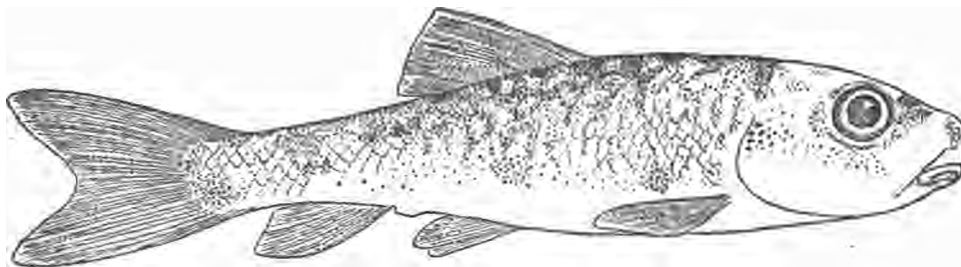


FIG. 27.—Specimen 30 millimeters long

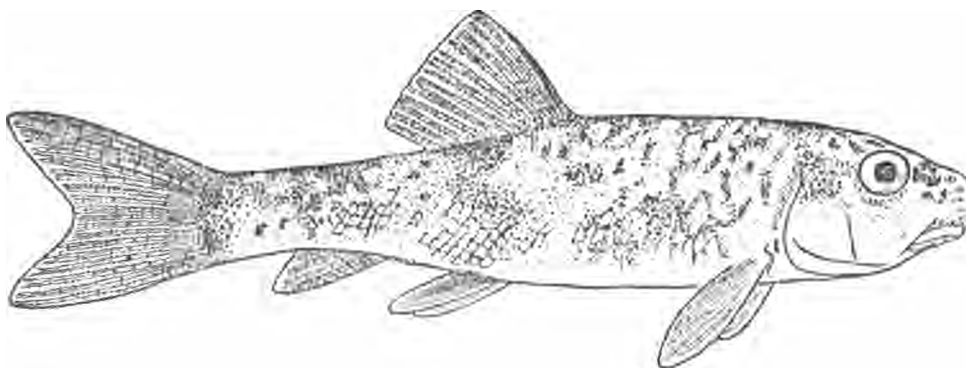


FIG. 28.—Specimen 50 millimeters long, with eye becoming relatively high, the mouth strongly inferior, and showing characteristic pigmentation

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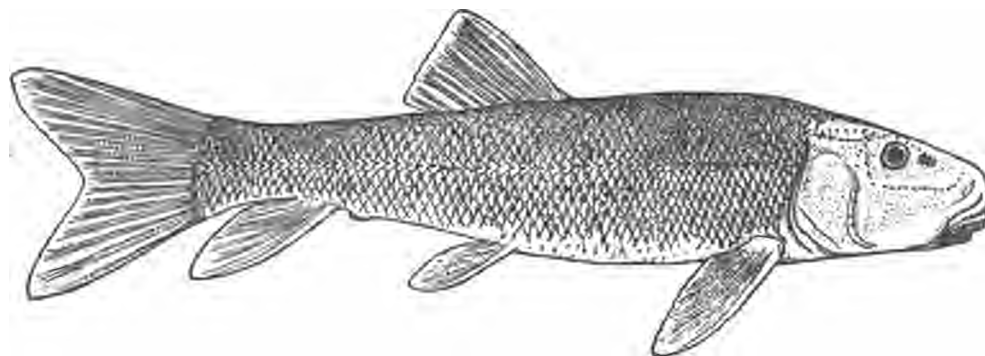
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As the fish grows, the relative positions of eyes, **nares**, and mouth are greatly altered in a manner peculiar to this family of fishes. Probably the eyes and nares are the more fixed in position, while the mouth descends to its inferior position. At 14 millimeters the mouth opening is on a level with the lower rim of the eyes (fig. 24), and by 16 millimeters it is entirely below this level. Its position now apparently interferes with feeding on floating particles, for before attaining a length of 18 millimeters the fish adopts the habit of feeding on the bottom. This change of habit will be discussed in more detail later.

In the 43-millimeter **larvæ papillæ** are present on the lips, which are now thick and swollen. In fish exceeding 16 millimeters in length the mouth may be described as still a crescent but lying more and more in a plane approaching the horizontal. In an adult 12 inches in length this crescent is 20 millimeters wide and 15 millimeters from front to back, including the lips. The lips are covered with dome-shaped **papillæ**, five rows of them on the anterior lip and nine on the posterior. This pos-



29.—Adult sucker, showing relative size of fins and relative position of the eye, nostril, and mouth. 10 inches long

**terior** lip is deeply notched behind and is flattened out at its posterior margin and also laterally.

These lips are capable of much protrusion, assuming the form of a funnel, extending downward and forward. When the mouth is closed the anterior end of the head is decidedly blunted in side view. The eye in the adult is relatively quite small and high up in the head. (Fig. 29.) The nares lie just anterior to the eyes and are divided by a vertical earlike flap 2 millimeters high.

#### HISTOLOGY OF THE MOUTH. ORAL EPITHELIUM

At 10 millimeters the mouth and pharynx are lined with a stratified epithelium, the cells of which are rounded, some of the superficial cells being flattened. There are but two to four layers of cells in this epithelium, which is 20 microns thick. The nuclei are basal in the cells. Taste buds of striking size are found here and there throughout the mouth and pharynx. They are conical or mammiliform and extend above the surface of the epithelium for another 20 microns. (Fig. 31.)

These flasklike taste buds show, in each section, about six columnar nuclei in the basal portion and a clear upper neck, which, being finely striated, doubtless contains processes of the sensory cells. In one **case** seventeen of these sense **papillæ**

are well formed. While the mouth and pharynx show cubic or polygonal cells in two and three layers, this condition gives way to three layers of columnar epithelial cells in the region of the heart. Also, there is a very conspicuous sphincter of striated muscle at this level. This muscle ends abruptly as we pass backward, the gut having an exceedingly thin muscular coat.

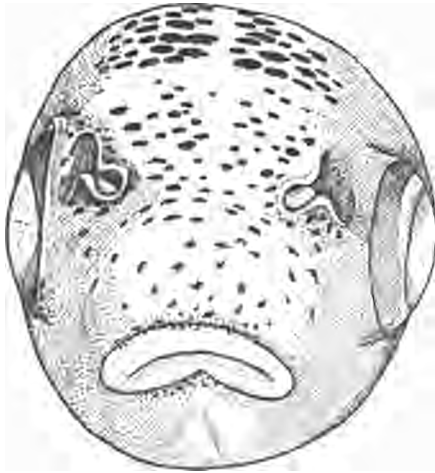


FIG. 36.-16 millimeters

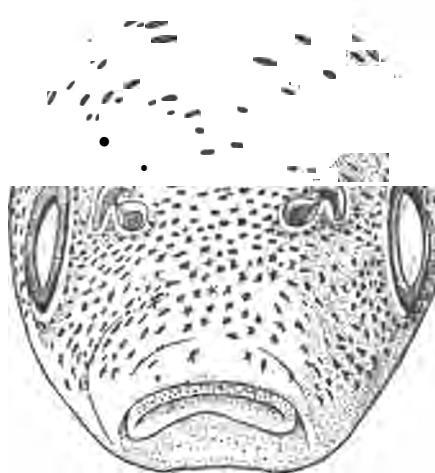


FIG. 37.-22 millimeters



FIG. 38.-42 millimeters

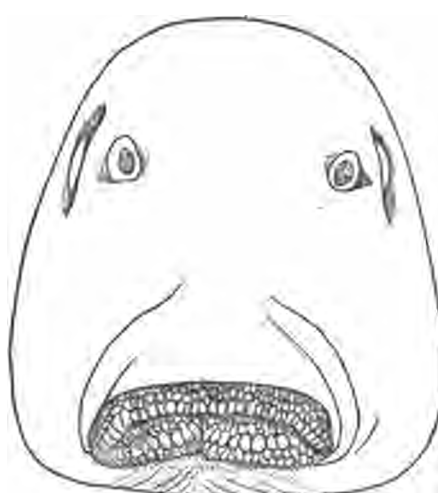


FIG. 39.-250 millimeters

Descent of the mouth, division of the nasal pits, and appearance of the labial papillae, as seen in a series of anterior views of the developing sucker.

At the anterior region of the liver, which is located just back of the heart, the epithelium changes to the simple columnar type. The gut is a narrow tube while passing through this region, and is placed high in the body. It expands, however, before the posterior end of the liver is reached, and its lining mucous membrane is



thrown into high narrow longitudinal ridges. The duct to the air bladder leaves the gut in the mid-dorsal line, while the latter is surrounded by the liver. At the same level we see the larger duct from the liver (and pancreas?) entering in the mid-ventral region. Both are lined with columnar epithelium, the latter having the greater caliber and ending in a rounded gall bladder embedded in the liver substance. The air duct curves to the left and then returns to enter the air bladder in the median line. The bile duct curves to the opposite side and upward.

Back of the liver there are no folds in the intestinal epithelium. The diameter of the intestine rapidly increases posterior to the liver and occupies the entire body



40.—Sac fry, 8 millimeters in length, rendered transparent. The yolk sac has been drawn in solid black (camera lucida)

cavity. Its wall is of simple columnar epithelium, the cross section of the organ being an almost perfect circle.

At 14 millimeters the longitudinal folds of the epithelium are found much farther back; that is, to the posterior end of the swim bladder. The latter has grown so rapidly as to occupy twice the cross-section area occupied by the intestine and one-third the entire cross-section area of the fish. This may be a potent factor in inducing the top-swimming habit of fry under 17 millimeters. Back of the swim bladder the intestinal epithelium is not yet elevated into folds.

The intestine shows the folds, or rugæ, throughout its entire course at 17 millimeters. Also the first intestinal loop is formed and the epithelial cells of the region



FIG. 41.—Fry of 11 millimeters, showing the straight digestive tract, the development of the caudal fin, and the simple swim bladder

involved appear much more closely packed as if division were proceeding very rapidly. This, for several reasons, including the change in form of the intestine, I have called the critical period in the life history.

#### ADULT CONDITION

The digestive tract, as in the *Cyprinidae*, has no true stomach; that is, no region containing special gastric glands. To be sure, the sucker appears to have a stomach, the first  $\frac{4}{16}$  inches of the gut of a 12-inch specimen being of wider diameter and



FIG. 42.—Fry of 13 millimeters. Dorsal and caudal fins show an advance, the swim bladder is becoming divided

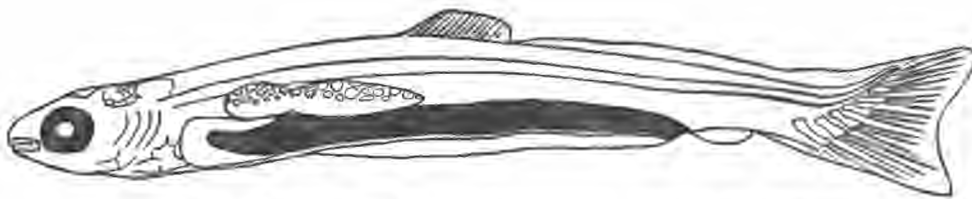


FIG. 43.—Fry of 15 millimeters. Anal fin is demarked. The gut is still straight



FIG. 44.—Fry of 16 millimeters, showing the first coiling of the intestine. The paired fins are also present



FIG. 45.—Fry of 17 millimeters, similar to that of 16 millimeters

having stronger muscular walls, but sections show that there are no glands anywhere in the digestive tract except the liver and pancreas. The entire tract is lined with a rugose mucosa consisting of simple columnar epithelium. These *rugæ* are coarse and high ( $\frac{1}{4}$  millimeter) at the beginning of the tract and reduce so as to be barely visible in the rectal region. They follow a zigzag course, running about 3 millimeters in each oblique direction.

Sections at any level are similar to those of any other region except for measurements. In the straight anterior region there are about 25 *rugæ*, each about one-half



FIG. 46.—Fry of 20 millimeters, showing beginning of the laterally placed loops

a millimeter high. Below the epithelium is a densely cellular connective tissue. About one-tenth of a millimeter outward from the bottom of the *rugæ* lies the hyaline *stratum compactum*, 20 microns in thickness. This is a dense nonnuclear layer of connective tissue fibers peculiar to the intestine of fishes. Immediately outside of it is the circular muscle layer, one-sixth millimeter thick, and outside of this is the longitudinal muscle layer, which is only one-quarter as thick as the layer of circular fibers.



FM. 47.—Fry of 21 millimeters, slightly more advanced

#### COILING

By studying a series of young fish from 9 to 25 millimeters in length, which had been rendered transparent by slow clearing in xylol, the changes in the form of the intestine could be seen with surprising clearness. (Figs. 40 to 47.) From hatching up to 17 millimeters the intestine is straight and occupies a median ventral position back of the level of the liver.

It is at the critical period (17 millimeters), when the mouth is becoming inferior and the diet is changing, that the first loop of the intestine is formed. It is located

about the middle of the body. The intestine bends so as to return forward for a distance and then curves backward to continue its course to the vent. From this time on the intestine continues to increase in length rapidly, the coils lying chiefly on the right side of the body and taking the form of a circle.

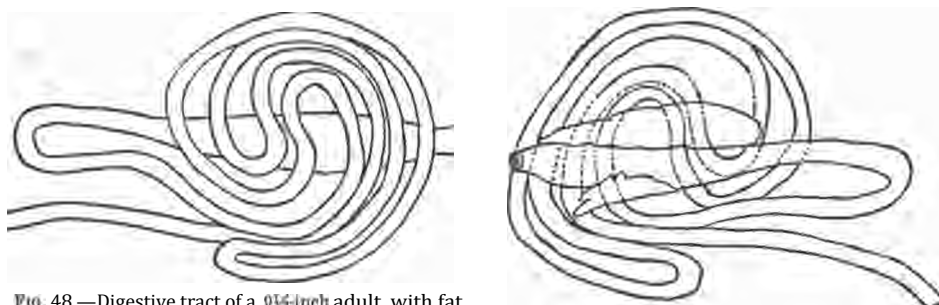


FIG. 48.—Digestive tract of a  $9\frac{1}{2}$ -inch adult, with fat and liver removed to show its coiling, viewed from the right side

49.—Same, from the left side

When the fish is 17 millimeters in length the entire digestive tract equals the length of the fish; at 24 millimeters it equals nearly twice its length; while adult specimens 6 to 12 inches long show that it falls little short of being as great as three times the fish's length.

## DETERMINATION OF AGE

### RELATION BETWEEN GROWTH OF SCALES AND SIZE OF FISH

The scale of the white sucker is of the cycloid type. While circular or **elliptical** the first two years, it gradually assumes a quadrilateral form, developing straight sides and a rounding base and apex. The focus is centrally located, though nearer the posterior edge during the first year or two. In about 30 per cent of the scales examined the focal area showed very irregular markings. Instead of concentric circuli, a reticulium of ridges had been developed. Such scales are not useful in age determination, though reported by nearly all authors and of wide distribution among species.

In this species the radii are confined principally to the anterior and posterior quadrants, very few being truly lateral. They seldom if ever branch, and but a small percentage fails to extend the whole way from edge to focus. Nothing of value resulted from a careful count of radii in about 200 scales taken from specimens from 28 to 250 millimeters body length. While the furrows are very shallow in young scales they are deeper and straighter in larger ones and maintain the clear appearance characteristic of the newly formed margin of the upper surface of the scale.

The circuli are fine, narrow, parallel ridges, separating relatively wider furrows. They are concentric and nearly always parallel with the true edge of the scale. If they run obliquely to the edge they always do so along the sides of the scales. Their distance from one another varies with the time of year but averages about one twenty-fifth of a millimeter.

The scales have a smooth edge except for a slight indentation of the margin at the end of each radius. I have found that this is not true of scales taken in the late winter and early spring, however, in which the edge is straight.

Attempts to photograph scales were not successful, but drawings made carefully to scale are presented in illustration of certain features of scale growth.

Scale formation begins when the fry are somewhat less than 22 millimeters in length (40 days from hatching). However, none could be removed in specimens under this length, even by scraping the surface. Those first obtained measure one-third of a millimeter in diameter, and it is probable that they represent scales from the region of the lateral line, for in fishes generally it is known that the scales first appear in this region. By the time the fry are 25 millimeters long scales seem to be everywhere present. While the first showed but three circuli, on an average four are now present. It is also noticeable that the pigment in the dermis follows the edges of the scales, forming a cross-hatched pattern. This pattern is limited at first to the sides of the fish in the first and last third of the body. When 28 millimeters long the scales show five circuli, there being a striking uniformity in this respect. The pigment pattern mentioned above now occurs over the entire scale-bearing portion of the fish.

By autumn of the first season the scales average about 10 circuli each. (Fig. 50.) This figure is important, in that we know definitely the time in which they have formed this number. One can detect, even at this time, that the circuli formed during the summer and fall are more closely crowded than those of the spring. It is in the very early spring that sucker scales show the widest spacing of circuli. In some species, such as the carp, this is said to be true of those formed in midsummer.

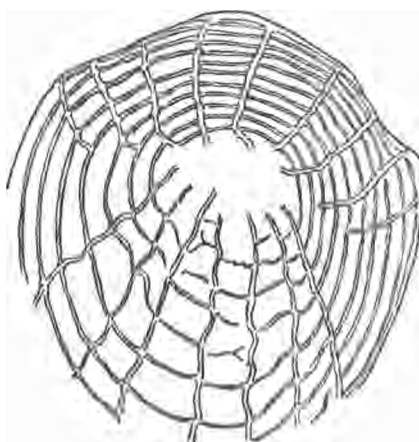


FIG. 50.—Scale of first season, taken in August from a specimen 40 millimeters in length

If we now take the scale of a larger fish, say 5 or 6 inches long, we find that it is correspondingly larger and shows many more circuli. These are seen to fall into groups or zones, each zone containing a band of widely spaced circuli followed by another band in which the circuli are more closely crowded.

In other species these zones of circuli are known to indicate the annual growth of the scale. They are spoken of as "annuli," and by counting them the age is determined. The question arises as to the evidence that they represent such annual growth in this species.

By frequent collecting throughout the summer there is left no doubt but that fingerlings 1 $\frac{1}{4}$  inches in length are but one season old. Their scales show but one zone of circuli, widely spaced at first but becoming narrowly spaced in the fall. This is, then, a true annual zone. The fact that in later years zones of about the same width and containing about the same number of circuli are present, but in greater numbers, points to the conclusion that they are repetitions of the process

of growth of the first year. Again, the marginal circuli of specimens taken in the spring or in the fall show the spacing characteristic of the season in which the fish were taken.

While the number of circuli per zone or the total number on the scale is an unreliable basis for age determination in many species and also in old specimens of the sucker, it is a striking fact that in suckers 4 or 5 years old the number of circuli per zone is quite constant—namely, about 10.

White suckers of the same age, in terms of years, vary in length within fairly narrow limits, but they have the same number of zones of circuli. This number is a more accurate index of the age of the fish than is the length. Such are the conclusions to which the following observations appear to lead.

A series of specimens was selected, ranging from 60 to 300 millimeters in length, with an interval of 10 millimeters between specimens. Ten scales of each specimen were examined, and the annual zones and number of circuli in each zone were

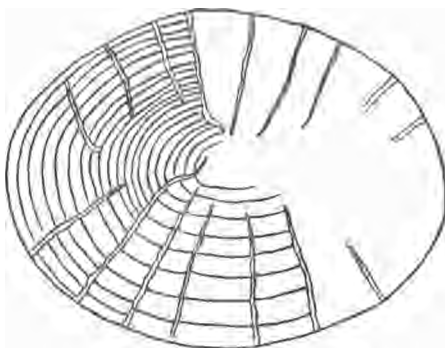


FIG. 51.—Scale of second year, taken in November from a specimen 60 millimeters in length

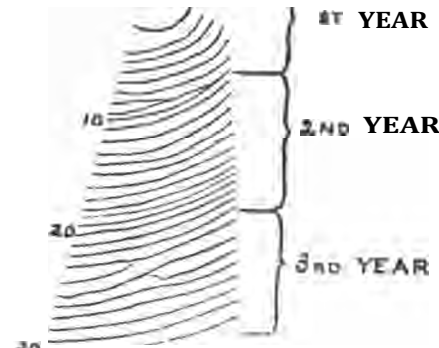


FIG. 52.—Sector of scale of the third year, from specimen 90 millimeters in length

counted. It at once became evident that the fish belonged to various groups determined by the number of annual zones, and that their age could be thus fixed.

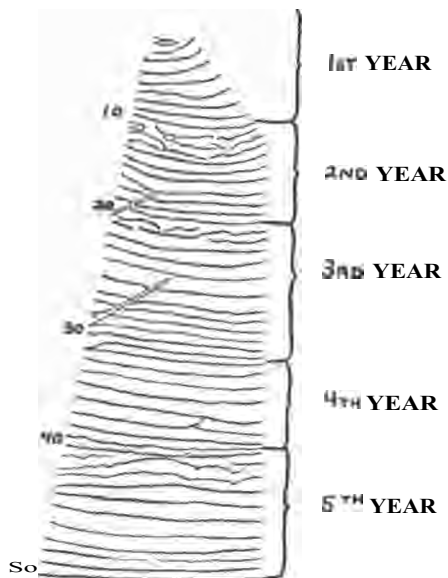
Specimens measuring 60, 70, and 80 millimeters showed two zones (annuli) and were therefore 2-year fish. (Fig. 51). It is interesting to note that the number of circuli averaged 19 (30 scales). This is in accord with the finding that about 10 are added in each new zone. Fish of 90, 100, 110, and 120 millimeters showed three zones and belonged to the third year. (Fig. 52.) The number of circuli varied within the narrow limits of 28 to 32, or approximately three times 10. In the larger specimens similar results obtained, except that as the fish becomes older the zones tend to become narrower and contain a smaller number of circuli. (Figs. 53 and 54.)

#### SEASONAL IRREGULARITIES IN THE CIRCULI

Not all the circuli are even and continuous lines. Those of early spring (February and March) are quite irregular. This irregularity may consist of sinuous curvings, interruptions of the ridge, or branching. More rarely a chainlike condition is produced by junctions between two parallel ridges. These early spring circuli usually

are the most widely spaced. However, equally wide spacing may occur in those of the middle part of the annual zone, which form during the summer. As a rule they show a progressive crowding from spring to late fall, when they probably cease to form. (Fig. 55.)

Scale growth in the white sucker appears to be nearly at a standstill from November to late February. The evidence supporting this conclusion consists in finding that the number of circuli in the current annulus appears to be the same throughout this season, the full year's quota being present in the fall. Again one frequently finds scars on the scales—that is, eroded edges—which apparently have thickened during the winter while growth was at a standstill.



53.—Sector of scale of the fifth year, specimen 160  
millimeters

Hoffbauer believed that when a carp was poorly nourished growth proceeded more slowly, and that this was evidenced by the crowding of the circuli. Others have believed that temperature regulated the spacing phenomenon. The sucker feeds well in November and February and probably all winter, though I have not observed it. The wide circuli observed for all specimens taken in early spring, even before the ice is out of the streams, can not be assigned to temperature as stimulating growth.

The sucker spawns in April and May, and the gonads of the male are ripe as early as February. It may be that the ripening of the germ cells interferes with the nutrition of the other tissues of the body, and that this condition is responsible for the irregularity in the form of the circuli of early spring. Coupled with this is the

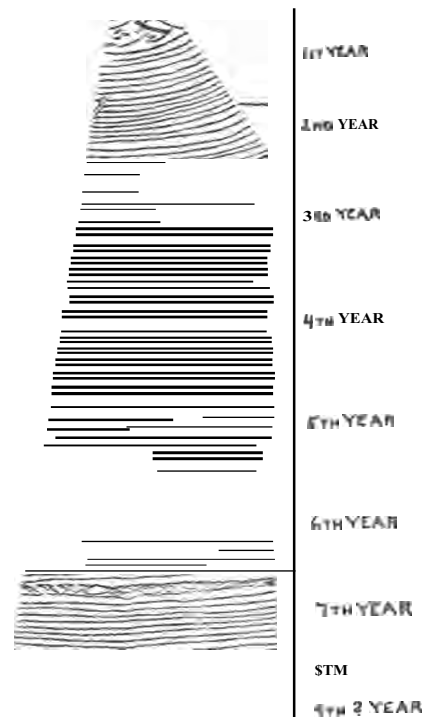


FIG. 54.—Sector of scale of the eighth or ninth year, specimen 371  
millimeters

fact that these irregularities in form are more constantly present and more emphasized at the beginning of the fourth year than during the previous springs. This age is determined from the scale, which shows these markings at the beginning of the fourth annual zone. The fish then measured from  $4\frac{1}{2}$  to 6 inches. It is in specimens of this size that ripe gonads have first been found, and Reighard reports that the smallest ones seen spawning by him were about 6 inches long. However, other factors besides either the sexual cycle, food, or temperature alone must operate to cause the variations described each year. Otherwise we would have difficulty in



55.—Detail of the last two annual zones on a scale of a 13-inch specimen taken in April

accounting for such facts as the variation in spacing from May to October of the first and second summers.

A very interesting local variation was observed in suckers seined in November from a large spring, where they probably lived the year round. Their scales showed virtually no seasonal variations of the sort described as usually present. Though sexually mature 6 to 10 inches, not even the markings so pronounced in the fifth and sixth springs were noticeable.<sup>8</sup> This fact, taken alone, would point to the direct regulative effect of an evenly cold temperature. Again, the greatest contrasts in spacing have been observed in fish from pools from the exposed and shallow creeks emptying into the pools.

### ANNUAL GROWTH

On the basis of the annual zones on the scales we can determine the average lengths of specimens at each year of their lives. The following table is a summary of the average lengths of specimens showing from one to seven annual zones on the scales. Not over a dozen of each age were averaged, and the record is incomplete, as the white sucker is known to attain a length of 22 inches. The specimens used were taken in the late summer or fall. The first season is therefore but half a year.

	Inches
First season	$1\frac{1}{2}$
Second season	3
Third season	4
Fourth season	6-6
Fifth season	6-8
Sixth season	8-13 $\frac{1}{2}$
Seventh season	$13\frac{1}{2}$ -15 $\frac{1}{2}$

The rapid growth during the sixth and seventh years seems surprising and would be interesting to test upon fish confined or tagged and recovered.

<sup>8</sup> Scales from these and other suckers could be separated on sight, even when purposely mixed.



## FOOD AND THE FEEDING HABITS OF THE WHITE SUCKER

With respect to their food, fishes may be divided into several groups. For example, we have plankton feeders, mud feeders, insectivorous species, fish eaters, mollusk eaters, **and** herbivorous species. Probably very few fishes confine their diet to one of these types of food, yet the classification is useful and may be applied in a broad sense. The factor that usually causes fishes to deviate from one type of food is their size. Obviously very small fishes must subsist upon still smaller organisms, so we are not surprised to learn that microorganisms form the early food of most species.

Some fishes pass through more than two stages in their feeding activities. The bass, for example, is a plankton feeder at first; later it pursues such Crustacea as the water shrimps and also insects, and as an adult it feeds largely upon smaller fishes, frogs, and crawfish.

The case of the sucker is peculiar in that a new factor—namely, the position of its mouth—enters in to alter its range of feeding. As its mouth changes from a terminal to an inferior position, the fish must alter its diet, losing those forms that swim or float and sucking in the fauna of the stream bottom. This, together with its wide range of taste, makes it almost omnivorous, and it is difficult to classify it according to the system mentioned above. While, of the various groups listed, we would be obliged to consider the sucker principally insectivorous, yet in an **interesting** way many insects escape it entirely. On the other hand, it does not exclude entirely any of the types of food upon which other fishes subsist.

### REVIEW OF THE LITERATURE

Examination of the stomach contents of the white sucker has been made by Forbes (1890), Hankinson (1908), Reighard (1915 and 1920), Baker (1916), and Pearse (1918). Two or three facts are at once evident in reviewing this work. The number reported upon by each author ranges from 5 to 42, which seems a small number upon which to draw conclusions in the case of a fish of such varied feeding habits. Again, in most cases the size of the specimens does not cover a wide range from any one locality, which is necessary in giving a picture of the biological relationships of the organism throughout its life; and the time of year frequently is not mentioned, yet we know that age, season, and available food all influence the selection of items in the diet of fishes.

It is striking to note how much disagreement exists in the accounts referred to above. Forbes and Baker report mollusks as forming 42 per cent and 30 per cent, respectively, of the food eaten. Pearse mentions no mollusks, while Hankinson notes their presence but gives no percentages. Again, while Pearse gives chironomid **larvæ** as forming 40 per cent of the food, Forbes reports but 3 per cent; and while Baker (1916) found "mud and plant remains" making up 49 per cent (3 adults), Pearse finds "**algæ** and silt" composing but 6.6 per cent. Similar variance could be shown in the reports on Protozoa, May-fly nymphs, rotifers, etc. The observations of the authors in question probably are reliable, so we must assume that the disagreement is due to the difference in place, age, and season.

The following illustrations will make clear the fact that suckers vary in their food according to place, age, and season.

In respect to the influence of locality, which possibly is associated with variations in the distribution of food organisms, we may cite such instances as the following. Of two suckers of the same length and collected on the same date but from two different streams, one contained 100 per cent *Entomostraca* and the other but 5 per cent. The direct influence of the size of the fish is seen in a case where, at the same time and in the same creek, a 1-inch specimen was found to contain 90 per cent chironomids while a 4-inch fish had taken 80 per cent caddis-fly larvæ.

The effect of season is illustrated by the fact that in summer one may find suckers that are full of *algæ*, while in winter this item seems quite absent from their diet. Moreover, it has become increasingly apparent and equally puzzling that even small fry exhibit what we can assign at present only to individual taste. In the same small nursery pond (3 by 5 feet) the following diet was selected by fry that measured 17 to 19 millimeters in length. On June 9 one specimen contained 80 per cent sand, another 80 per cent chironomids; on June 12 one specimen contained 80 per cent Rotifera; and on June 16, one individual contained 80 per cent *Diffugia*, and another 70 per cent *Entomostraca*. It is obvious that limited observations here would lead to widely divergent conclusions. Even among 4-inch suckers taken the same day and in the same lagoon one showed 90 per cent Odonata nymphs while another showed 60 per cent chironomids and no Odonata.

While the factors here considered evidently alter the feeding habits of this species, there are probably others that likewise enter in. Of these may be suggested floods with their resulting debris, burying the bottom fauna; parasites that attack the sucker, filling its alimentary tract; and local differences in temperature of the stream or lake. Seasonal changes in the time of the appearance of its food organisms also would play a large part.

The diverging conclusions hitherto reached regarding the food of the sucker can be understood, therefore, and it is obvious that an extended survey of its feeding habits alone would afford a basis for generalizations on this point.

It is the aim of this paper to record the results of such a survey, which, while limited geographically in the wider sense, is probably more extensive in respect to numbers examined, age, and season than any previously recorded.

#### FOOD

It was necessary to use several methods in collecting the material utilized. For fry up to about 20 millimeters in length a dip net of very fine mesh, such as one made of cheesecloth, was necessary to prevent the escape of the tiny fish. From this size to fingerlings of 2 to 3 inches the fish were taken by means of a stout-handled dip net of coarser mesh—viz, eight meshes to the inch.

For fishes over 3 inches in length other methods had to be used. The wire-cage trap proved the best of these. These were made of both fine and coarse mesh—viz, one-third-inch square mesh and 1-inch round mesh. They had one or two funnel-shaped entrances, the passage narrowing down to about 4 inches in diameter. Such traps were baited with bread and placed in deep spots in the stream known to be frequented by suckers. A few were secured by a minnow seine 8 feet long and of

one-third-inch mesh, but only where the bottom was smooth. A seine 100 feet long and of 1-inch mesh was used in Cayuga Lake and the lagoons of Fall Creek, where specimens 10 to 15 inches in length were taken. About 40 specimens were taken by hook and line, the bait always being earthworms.

For food analysis the material from the smaller specimens was fixed in the field, while from the larger ones it was prepared immediately upon arriving at the laboratory. Either 4 per cent formalin or 70 per cent alcohol was used as a preservative. For sectioning, either Gilson's, Bouin's, or Perenyi's fixation fluid was employed with equally good results.

The region about Ithaca affords unusual opportunities to observe aquatic organisms under varied conditions, combining, as it does, cold, spring-fed brooks, gravel and boulder-bottomed streams, areas of clay, cataracts with deep pools, sluggish waterways through cat-tail marshes, and the lake with shallow or deep waters near the shore.

The material examined was taken between June, 1922, and August, 1923. Some collections were made every week except during December and January, when the ice made collecting very difficult. All the larger streams of Tompkins County were covered in collecting the fry and fingerlings, while the traps were set and seines drawn at points nearer the Cornell Campus—Cascadilla Creek, Fall Creek, and the lagoons of the latter and Cayuga Lake.

#### PERIODS INTO WHICH FEEDING HABITS MAY BE DIVIDED

The life history of the white sucker shows five periods that can be distinguished on the basis of its feeding activities. This is peculiar to the sucker to the extent that its feeding is correlated with the change in its mouth from the terminal to the inferior position. Some fishes show three or four periods, due to increase in their size and the correlated need for more nourishing diet. For the sucker the following periods may be distinguished, both by the general behavior of the fish and by the actual analysis of the contents of the alimentary tract.

*First or yolk-food period.*—In a sense this period begins with segmentation and ends when the yolk has been entirely consumed. The fry is approximately 8 millimeters long at hatching, and the yolk is found to be its food up to a length of 12 millimeters. This may be called the "yolk-sac stage," though the sac actually is reduced, so as not to appear in surface views, before feeding through the mouth begins.

*Top-feeding period.*—From the time the fish begins to feed (12 millimeters), up to the change in the position of its mouth at 16 to 17 millimeters, it feeds upon organisms at or very near the surface of the water. This constitutes a very clearly-defined period in its life history, and the fry at this stage play a very different role in the economy of the stream life than do the older fingerlings and adults.

*Critical period.*—This term is used to designate the actual period during which the feeding habit changes. It extends from the time when the fish begins to go to the bottom occasionally to pick up food to the time when it ceases to feed anywhere but on the bottom. It is a brief period, only a few days in duration, when the fish is 16 to 18 millimeters long.

*Fingerling period.*—This period extends from the critical period (17 or 18 millimeters body length) to approximately 75 millimeters in length. The fish during this stage comes nearest to being what is suggested by the term "mud feeder." Limited by its size to small particles of food, and by the position of its mouth to the bottom as a source of nourishment, it takes a varied diet of the bottom-inhabiting organisms.

*Adult period.*—Fish longer than 75 millimeters may be considered adults as regards their feeding. They are no longer "mud feeders," in the sense used above, for while a fish may take mud and sand into its mouth only organisms are swallowed, and these consist principally of insect nymphs or larvæ. The almost complete elimination of microorganisms and the high percentage of macroorganisms, nymphs, mollusks, etc., distinguish this stage from all the others.

#### DETAILED ACCOUNT OF FEEDING HABITS AND FOOD

*Yolk-food period.*—The newly hatched fish has a well-filled, cylindrical yolk sac extending from the heart to the anus. The mouth is not yet open, and all nourishment is obtained from the yolk. The fish lies on the bottom but makes erratic motions that elevate it a few inches from time to time. Within two or three days the yolk sac has been reduced so that the fish apparently has no yolk left. This is so at 9 millimeters; at 11 millimeters the mouth is open; and at 12 millimeters the first food is taken.

*Top-feeding period.*—While fry of 12 to about 25 millimeters were collected from 62 points scattered along 10 streams in Tompkins County, it was thought wise to make daily observations of these early stages on fish confined in a pond, also. Accordingly, a pond 4 by 6 feet was dug where there was a slow seepage, both in and out, through the soil. The pond averaged 16 inches deep, with sides and bottom made of earth. Early in the spring it was fertilized by the addition of 1 quart of well-rotted manure and 1 pint of dried milk albumen. No organisms were intentionally introduced, yet the young suckers found a rich fauna and flora there in May.

To observe the earliest feeding, young fry were put into this little pond on May 22. They were but 2 and 3 days old, having been reared to this point in the Meehan hatching jar indoors.

During the first day many of them lay on the bottom, though a few maintained themselves near the surface by swimming. Soon all were swimming at the surface, and on May 27, when 9 days old (12 millimeters in length), the yolk was all gone and yet no food except a single diatom was present in the individuals examined. When 14 millimeters long or 11 days old (on May 29), samples showed food in the digestive tract. This earliest food, taken in the nursery pond, showed no important difference from that taken in the various streams of the region, and consisted of Protozoa (Euglena), Entomostraca (Cyclops adults and nauplii), chironomid larvæ, Rotifera, and diatoms. The following list gives the percentages of each organism entering into the food of fry between 12 and 16 millimeters in length, both in the nursery pond and in four of the principal streams of the county:

In the nursery pond (9 specimens): Chironomid larvæ, 15; Entomostraca, 37; diatoms, 1.3; Protozoa (Euglena), 27; Rotifera, 18.

In the streams (23 specimens): Chironomids, 62; Entomostraca, 4; diatoms, 8; Protozoa (Diffugia), 6; Rotifera, 7; fragments of arthropods, 7.

The latter is the truer picture of the diet during this second stage. The differences are due to the lack of current in the pond, increasing the proportion of Euglena and Entomostraca (Cyclops and Bosmina), which flourish in still waters. It will be shown presently that chironomid *larvæ* are common as floating objects in the streams.

Sucker fry can be distinguished in the field, after a little practice, by their form and actions. They are more slender than dace and shiners of the same length, and seem always to prefer a slight current, in which they maintain a rather fixed position by a very characteristic motion, which deserves a word in passing. Whereas many other fry swim by swinging the whole body, the sucker fry move only the tail. Thus they never show the jerky darting so characteristic of young minnows. Preferring a moderate current, they are not to be found in the rapids nor in still ponds, but in intermediate situations—that is, where the stream enters deep, quiet stretches. Knowing this, one can predict with some certainty what portions of a stream will harbor the young fry. Also, they swim within 6 inches of the surface. While dozens of pools entirely cut off from the streams were examined and were often found to be teeming with minnows, sucker fry under 17 millimeters never were discovered in them. They are often found associated with the plant Elodea.

During the stage from 12 to 16 millimeters, the fry, as we have said, maintains its position in the moderate current within 4 to 6 inches of the surface and waits until food organisms float to it. Constantly they swim here and there (a matter of an inch or so), feeding on particles in suspension. On an average of once in a minute and a half they touch (taste?) or take organisms floating by. They are in small groups of 2 or 3 to 8 or 10.

Of the food eaten, it is of interest to show that it may all be obtained in the floating condition. To establish this the following tests were made:

The surface mud of the bottom taken below a school of 10 fry contained Protozoa (Stylonichia), Gastrotricha, diatoms, and rotifers, but no chironomid *larvæ*. Evidently the latter were not obtained from the bottom. Then a handful of Elodea collected 4 inches below the surface, where 10 fry were feeding, was violently stirred in a shell vial of water, allowed to settle, and the sediment examined. This contained 20 chironomid *larvæ* per cubic centimeter of sediment.

To show that these *larvæ* do become detached and float free in the water, a Birge net was set for 24 hours a few inches below the surface. By centrifuging and examining, two *larvæ* were obtained in addition to Cyclops, rotifers, and desmids. The fry may pick these *larvæ* from the weeds, though this was not observed. It is well known that Diffugia also floats.

The sucker begins feeding when 12 millimeters long, approximately 9 days after hatching. The mouth is terminal but in process of becoming inferior. For 10 or 11 days it is a top feeder or feeds close to the surface on floating microorganisms, principally chironomid *larvæ*, Entomostraca, diatoms, rotifers, and Protozoa.

*Critical period, 16 to 18 millimeters.*—As observed in the nursery pond, this period covered nine days. On June 7 (20 days old) the fry were seen to make occasional excursions to the bottom (16 inches) and pick up mouthfuls of the sand, etc.

For a day or so preceding this they had fed farther from the surface, but not at the bottom. On June 12 (25 days old) three-fourths of the time was spent at the bottom. On June 16 (29 days old), none was feeding above the bottom. While microscopic examinations of the contents of the alimentary canal were made almost daily, the following average percentages of the more important constituents of the diet, derived from nine examinations, will suffice to show the facts: Chironomid *larvæ* and *pupæ*, 19 per cent; Entomostraca, 15 per cent; diatoms and desmids, 10 per cent; Protozoa, 2 per cent; Rotifera, 20 per cent; sand, 27 per cent; unicellular *algæ*, 2 per cent. Total—animals, 56 per cent; plants, 12 per cent; sand, 27 per cent.

The presence of sand is noticeable. Some of this is found in every specimen (even as much as 70 or 80 per cent of the volume in some cases), but it is also noticeable that diatoms and desmids are the only other items constantly present. These three items together form 37 per cent of the food.

With the change in feeding habit there appears also a new instinctive reaction. Whereas the early fry never enter the deeper water when alarmed, these later fry retreat to the bottom when one approaches them. Quite a few specimens of this age show that the alimentary canal is entirely empty, but when the bottom-feeding habit is established it is regularly well filled, if only by sand and diatoms.

*Fingerling period.*—This stage covers the time during which the young fish (25 days to 2 years old, 18 to 75 millimeters long) feeds upon bottom forms but can not separate them from the sand, which, therefore, constitutes nearly 25 per cent of its intestinal contents. It differs from the critical period in the fact that the bottom-feeding habit is firmly established. It is separated from the following or adult period by the fact that the food includes only microorganisms and no nymphs and *larvæ* of the larger insects.

The feeding habits are now quite different from those of the previous periods. The bottom selected for feeding is usually a stretch of uniformly fine sand or silt, covered with a thin film of such organic matter as diatoms, desmids, Protozoa, etc. The feeding grounds for fish of the first summer (up to a length of about 40 millimeters) is in water 6 to 18 inches in depth along the shores of *lagoons*, eddies, or ponds connected with the stream. For those 40 to 75 millimeters in length the feeding grounds are in the swifter-flowing water, as in the case of the adults, but in smaller, shallower streams.

New instincts are manifested and others are emphasized. In this stage a strong gregarious habit is apparent, especially during the first summer. The fingerlings of the first summer invariably are found in schools. These contain from a dozen or so to four or five hundred individuals. When feeding they usually spread out like sheep, advancing slowly, all facing the shore and keeping side by side. They retreat into deeper water when alarmed, but return within a few minutes to continue their almost constant plucking at the bottom ooze.

They ~~are~~ very protectively colored at this stage, being a mottled, sandy gray above and quite translucent. The sides are yellowish and greenish and flash when turned upward. Occasionally in very still water a large school (200 to 500) will be seen resting within an inch of the surface. They then face in all directions and are motionless. At the least cause for alarm the whole school disappears and remains in deeper water.

Feeding is most continuous on bright warm days. The fear of being exposed to view, which seems such a powerful instinct in the adults, does not prevent feeding in shallow places in the daytime during the first summer; but after the first winter suckers are inhabitants of the deeper places in the stream, except at night or during their migrations.

The food of 57 specimens of this stage was examined with the following results:

	Percentage
Chironomid larvæ and pupæ	28
Diatoms and desmids	22
Rotifers.	4
Entomostraca.	3
Protozoa (Diffugia)	9
Algae	2
Fragments of arthropods	1
Sand	21
Unidentified (largely mucus)	10
	<hr/>
Animals	45
Plants.	24
Total Sand	21
Unidentified	10

This is virtually identical with the diet characteristic of the critical period. There is no item of food taken near the surface which is not also found at the bottom, whereas sand is taken only at the bottom.

The striking facts here are that up to 3 inches in length (2 years) the sucker continues to be limited to microscopic matter and that the indigestible sand is not eliminated from the diet. The habit of almost continuous feeding (by day at least), and the fact that the alimentary canal is seemingly never empty become intelligible when we consider how little of the matter eaten is actually available to the fish as nourishing food. The following is an attempt to estimate the nonnutritious waste matter:

	Percentage
Sand	21
Protozoa (shells of Arcella and Diffugia)	5?
Entomostraca (chitin)	2?
Rotifers (chitin)	2?
Diatoms (silicon)	10?
Chironomids (chitin)	12?
Total	52

This estimate may be far from exact, but it is not without significance.

To test whether suckers can, after the critical period (17 millimeters), catch floating organisms in sufficient quantity to maintain life, a number (12 to 15) of them, measuring 22 to 25 millimeters, were placed in a hatching tray with screen bottom and ends. This was set in one of their favorite haunts but 8 inches off the bottom. For a control, dace of equal size were placed with them. The latter survived well upon particles floating in through the screening of the ends and bottom of the tray, but the suckers all died within eight days (two in five days). Examination showed the alimentary canal to be nearly empty (a few diatoms only), and the fish were very thin.

*Adult period, 75 millimeters.*—Suckers of this period (3 to 15 inches in length) are shy fish, lurking among the stones on the bottom of the deeper holes along the creek, and probably in the deeper shoal waters of the lakes. While perch, bass, minnows, etc., frequently are seen leisurely feeding or resting in moderately shallow water, the white sucker is not seen unless the pool be approached cautiously, and only during the spawning season are large suckers found in shallow water in the daytime. They exhibit a shyness characteristic of trout, making off with great haste when disturbed. It is next to impossible to take them in a seine if the bottom is rough, for they escape through any gap, finding such places with great rapidity. Reighard (1915) reports seeing suckers feeding in the early morning. Suckers are taken on hook and line baited with earthworms, but mostly on cloudy days or when the water is turbid. Specimens removed from the traps in the morning regularly showed a well-filled intestine. From this and the extreme shyness of the fish it seems probable that its feeding is done in the darker hours.

While gregarious in the adult stage, one finds individuals of all sizes between 2 or 3 to 10 or 12 inches inhabiting the same pool or lagoon. In the lakes and larger streams, those of larger size—8 to 15 inches in length—appear to feed and travel in bands of a score or more. These larger ones have been seen resting quite motionless some 4 to 6 feet below the surface of the lake, and they refuse all bait.

The food of the adult is not mixed with sand to any extent. Only 0.9 per cent of the food of 52 specimens was sand, as against 21 per cent in the case of fingerlings. At the beginning of this stage (3 inches) the sucker begins to hold the food particles in its mouth and to spit out the sand. This ejecting of the sand has been reported by Reighard (1915). The diatoms doubtless are ejected in this cleaning process, as they constituted but 3.6 per cent of the intestinal contents in 52 cases. The holding of the food is possible because it now consists largely of insect larvæ and nymphs. These facts are summarized in the following percentages, based on a study of 52 specimens:

	Percentage
Chironomidae	30
Diatoms and desinids	3.6
Rotifera	0
Arthropod fragments	5.4
Entomostraca	5
Protozoa	.1
Algae	2.4
Sand	.9
Mollusk shells	.2
Larger insect larvæ and nymphs <sup>4</sup> ■■■■	31
Debris (principally mucus)	22

While the most distinguishing items of diet are the immature aquatic insects of large size (31 per cent), the total of these, together with the omnipresent midge larvæ and fragments of insects, brings the total quantity of insects eaten by the adult fishes to 66.4 per cent. The adult sucker in this region must then be classed as an insectivorous species. Of the organic food but 6 per cent consists of plants, hence the fish is distinctly carnivorous in this as in the earlier stages.

Most of the insect larvæ and nymphs occur whole in the digestive tract, even larger ones, such as dragon-fly nymphs, being swallowed without fragmentation.

Odonata, 9 per cent; mayflies, 9 per cent; and caddis flies, 13 per cent.



## SUMMARY

For 162 fish heretofore listed by groups only, the average percentages are as follows:

The variation in capacity of the fish is not taken into account here. Obviously the larger the fish the more insects necessary to make up a given percentage of the volume of its intestine. The greater numbers of smaller suckers in a stream would, however, make up in part, at least, for their smaller capacity.

(Figures are average percentage)

Food	Top-feeding period; 12 to 16 millimeters, inclusive	Fingerling period; 17 to 75 millimeters, inclusive	Adult period; 3 to 12 inches	Food	Top-feeding period; 12 to 16 millimeters, inclusive	Fingerling period; 17 to 75 millimeters, inclusive	Adult period; 3 to 12 inches
Number examined .....	25	57	52	<del>Algae</del>		2	2.4
<del>Chironomids</del>	<del>12</del>	28	30	Sand -----		21	.9
Diatoms and desmids	8	22	3.6	Odonata			9
Rotifera	7	4		May fly -----			9
Other arthropod fragments	7	1	5.4	Caddis-fly larvae			11
Entomostraca	4	3	5	Mollusca			.2
Protozoa -----	.8	9	.1	Unidentified (mucus) ----	11.5	10	21.4

In the ~~above~~ table is presented a comparison of the constituents of the diet during the three principal periods. The figures given are percentages of the volume of the food, and it is important to bear this in mind in obtaining a picture of the role played by the sucker as a consumer. The number of chironomids eaten is enormous. It was estimated that one sucker, 5 inches long, contained 1,200, and in addition to this 800 caddis-fly ~~larvae~~ and 60 May-fly nymphs were eaten. A daily ration of 1,200 chironomids means that 36,000 are consumed in a month, or 216,000 in six months.

It is possible to suggest some reasons that may account for the three following periods in the feeding habits—namely, the yolk-food period, the top-feeding period, and the bottom-feeding period.

The first is obviously determined by the amount of food stored in the egg when laid. Factors external to the egg, such as temperature, will determine the rate of development of the ~~larvae~~, and hence the length of time before the yolk is exhausted.

The top-feeding period presents a greater problem. The air bladder is relatively very large at this time, and up to a length of 14 millimeters it is connected to the gut. It may be that control of the gaseous content of the air bladder is not possible to the fish during this period, and that they are actually unable to submerge themselves below a depth of 6 inches.

Bottom-feeding is related to the metamorphosis of the mouth, but implies also that the content of the air bladder permits swimming at lower levels.

The separation of sand from insects, etc., and its elimination before the insects are swallowed may be merely a matter of the relative size of food and sand. As long as the food consists of ~~microorganisms~~ it can not, apparently, be separated from the sand; but when such insects as caddis-fly ~~larvae~~ are taken they are held in the mouth while the sand is ejected. The following organisms were identified in the food of the white sucker (210 specimens):

Algae:	Cladocera:
Mougeotia.	Chydorus.
Spirogyra.	Scapholeberis.
Desmids:	Mona.
Closterium.	Alonella.
Cosmarium.	Daphnia.
Diatoms:	Eurycercus.
Gomphonema.	Ostracoda:
Diatoma.	Cypris.
Cymbella.	Cypridopsis.
Navicula.	Malacostraca:
Surirella.	Gammarus.
Nitzschia.	Cambarus (fragment only).
Epithemia.	Rotifera: Various species.
Stephanodiscus.	Nematoda: Ascaris (?).
Fragilaria.	Annelida: <del>Seta</del> only.
Protozoa:	Mollusca: <del>Sphaerium</del> (?).
Diffiugia.	Cestoda: Proteocephalus (?).
Arcella.	Trematoda: Crepidostomum (?).
Euglena.	Insecta:
Copepods:	Chironomid <del>larvae</del> and pupae.
Cyclops.	Chironomus.
Canthocamptus.	Tanytarsus.

## Insecta—Continued.

Caddis-fly larvæ (Neuronia).

May-fly nymphs:

Heptagenia.

Chironomus.

Ecdyru.

Iron.

Blasturus.

Dragon-fly nymphs:

Libellulidæ.

Æchnidæ.

Ori-fly larvæ.

Halophilid larva.

## Insecta—Continued.

Tipulid larva.

Black-fly larva (Simulium).

Chauliodes larva.

Dytiscid larva.

Corixa nymph.

Stone-fly nymphs:

Perla.

Isoperla.

Capnia.

Mosquito egg.

Weevil.

Fish scale.

## ECONOMIC STATUS OF THE SUCKER

The white sucker, being principally an insectivorous fish, is a rival of the trout and bass—two species of prime importance to man. While the sucker eats many May-fly nymphs and the trout may depend more largely upon the adult May flies, the rivalry is no less keen. The sucker has been reported as a "spawn eater," devouring the eggs of the log perch (Reighard, 1920). It has been reported as eating small fishes and fish eggs. In November, 1922, twenty 6 to 8-inch suckers were collected directly over the newly made nests of brook trout, where eggs were doubtless abundant in the gravel. As not a single fish egg was found in these or in over 200 other sucker stomachs examined it seems safe to assume that fish eggs are rarely taken by this species.

As a food fish the white sucker is considered of little value. In the spring its flesh is firm and of agreeable flavor, but by June it becomes soft and undesirable. When the life histories of all fish parasites are better known it may be found that this species is a carrier of infection. A single 8-inch specimen taken near the University Experiment Station contained 145 cestodes and 50 trematodes, while the intestines contained nothing else, being filled with these parasites.

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