EXPERIMENTS IN THE CULTURE OF FRESH-WATER MUSSELS.

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CONTENTS.

INTRODUCTION.

The coming of fresh-water mussels to a position of commercial importance in America resulted in a special demand for information as to methods of propagating them. In response to this demand the U. S. Bureau of Fisheries undertook an extensive investigation of the commercial fresh-water mussels. This led to the adoption of a method of propagation that promised effectively to increase the supply of mussels. This method, briefly, is the infection of suitable fish with the young mussels in the parasitic stage. These fish are then released to spread the mussels at large under natural conditions. The investigations have been continued for the purpose of extending the application of the methods now in use, the testing of new methods, and to secure more complete information on the life history of the mussels used in pearl-button manufacture.

Since Leydig's (1866) discovery that the young fresh-water mussels are parasitic on fish, many attempts have been made to raise them in captivity. No particular difficulty has been experienced in carrying certain species through the parasitic stage, but up until the time of the present investigation there seem to have been no records of the rearing of these under observation through what is called the juvenile stage.

In aquaria, either balanced or supplied with running water, they did not seem to thrive. Even in tanks out of doors supplied with water from their usual habitat the results were negative. The majority apparently at the very beginning of their free life were eaten by predacious forms, or, if by chance they escaped these enemies, they continued their existence dwarfed. Something in the environment was unfavorable to them.

Among European investigators who have attempted to rear young mussels are the following, with the results attained as to time carried under culture: F. Schmidt (1885), 4 weeks; C. Schierholz (1888), 4 to 5 weeks; W. Harms (1907), 7 weeks; and Karl Herbers (1913), about 2 months, or to a size of 3.13 millimeters.

In America we have the following records of artificially reared mussels. Lefevre and Curtis (1912) found a young mussel two years after a plant had been made in a tank. Similar results were attained at the U. S. Fisheries Biological Laboratory at Fairport, Iowa. In this case two mussels, *Lampsilis ventricosa* (Barnes), were obtained in a pond one year after a recorded plant had been made. In these two instances no observations of the mussels were made in the period between the planting and finding of the mussel at an advanced stage of development. A. F. Shira (report in MS.) reared the Lake Pepin mucket in a balanced aquarium to a size of 4.4 millimeters.

As a part of the general plan mentioned above, the experiments described in this paper were carried on to test the possibilities of artificial culture of mussels from the earliest stages up to the mature adult. The studies were carried on at the U. S. Fisheries Biological Laboratory at Fairport, Iowa, under the direction of Dr. R. E. Coker, in charge of the investigations upon the fresh-water mussels, and later under A. F. Shira, his successor. The author wishes to acknowledge here courtesies extended and assistance rendered in the conduct of these studies to the Crerar Library, of Chicago, for use of their excellent facilities; to Bryant Walker, Detroit, Mich., for assistance in determination of mussels; to Caroline Stringer, Omaha, Nebr., and Ruth Higley, Grandview, Iowa, for determination of Rhabdocœls; to Prof. Edwin Linton, Washington, Pa., for assistance in the determination of Turbellaria; and to Prof. F. B. Isley, Fayette, Mo., for suggestions of methods.

METHODS AND PLAN OF INVESTIGATION.

After some little experimental study of developing mussels it was realized that there must be some vital deficiency under artificial conditions to account for the many failures in attempts to raise mussels. It seemed that a promising line of attack in solution of the problem would be to find some way which would depart from the natural habitat only so far as the necessity of mechanical control demanded. To rear at least one brood of the young seemed to be an objective of prime importance. Success in this would answer some unsolved questions as to growth, as well as furnish a starting point for more artificial methods if these were desirable. In our situation, where we take the mussels from the Mississippi River, the most practicable solution that offered itself was a floating crate containing baskets made of wire cloth of sufficient size to hold the fish and of a mesh small enough to retain the miscroscopic mussels.

A crate held at the surface accommodates itself to the frequent rise and fall of the river, is convenient of access, and removes the young mussels from many of their enemies prevalent at the bottom. Another advantage of a surface location is the fact that the precipitation of silt there is at a minimum. The first crate used (fig. 74) was constructed

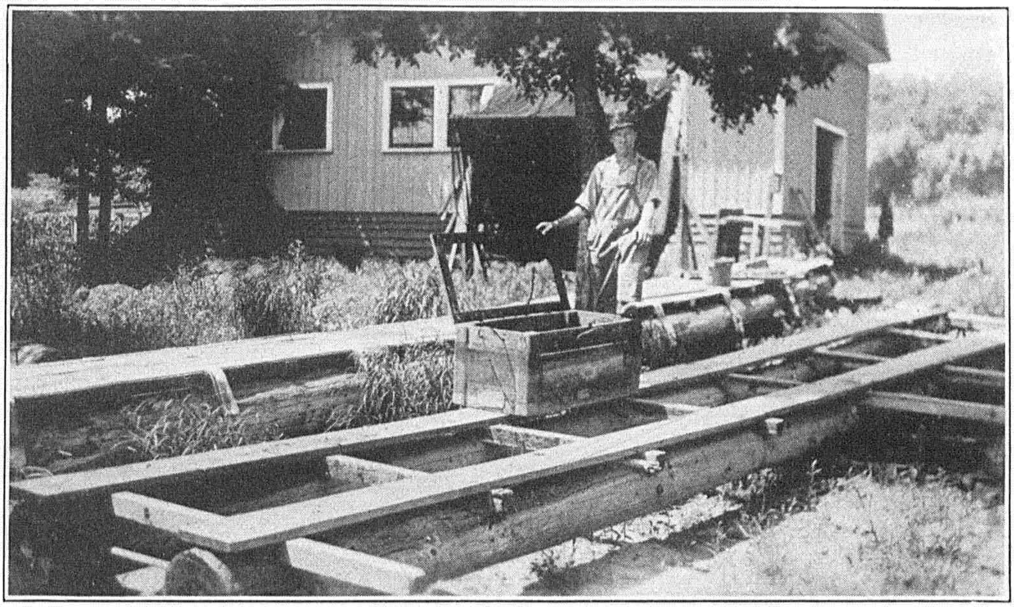


FIG. 58.—Improved float employed in experiments in mussel culture showing one of crates on "deck" opposite its berth.

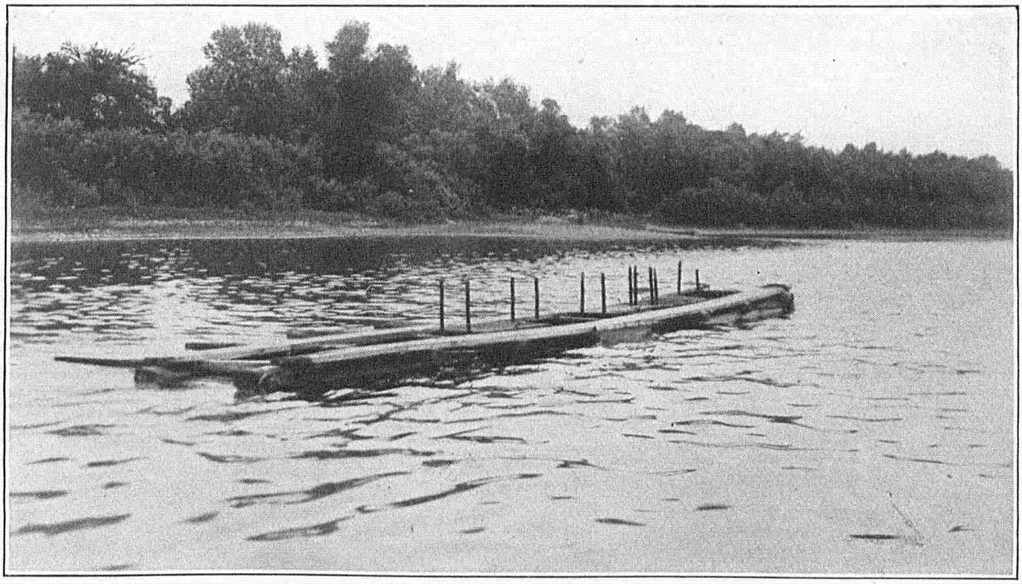


FIG. 59.—Same float as in fig. 58 anchored in the river showing three crates in position supported by adjustable iron hangers which are visible above the float.

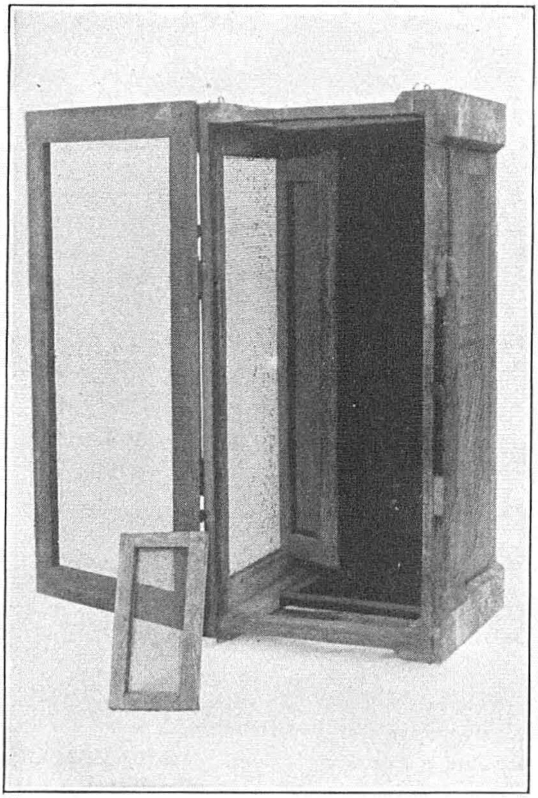


FIG. 60.—A crate of improved pattern showing outer screens of $\frac{1}{4}$-inch mesh and inner detachable screens of copper cloth, one of which is completely removed and the other turned in to show manner of insertion. Infected fish are held in the crates until the parasitic mussels are shed. The copper cloth prevents the escape of the mussels in the early minute stages.

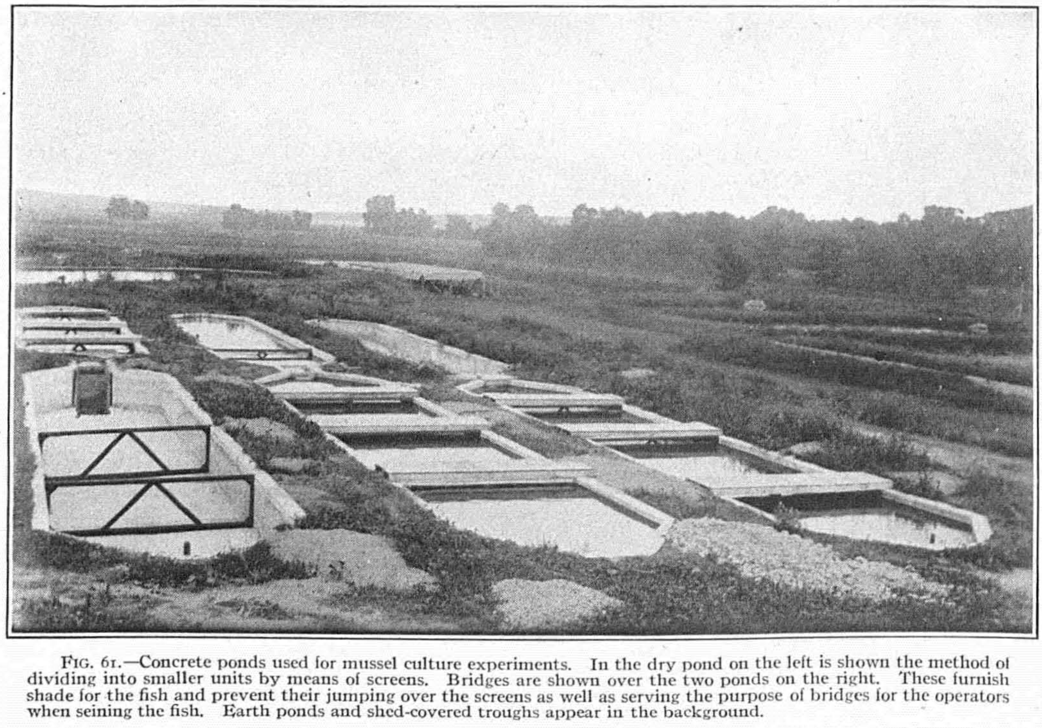


FIG. 61.—Concrete ponds used for mussel culture experiments. In the dry pond on the left is shown the method of dividing into smaller units by means of screens. Bridges are shown over the two ponds on the right. These furnish shade for the fish and prevent their jumping over the screens as well as serving the purpose of bridges for the operators when seining the fish. Earth ponds and shed-covered troughs appear in the background.

from a floating fish car to which were added barrels to give greater buoyancy. Four baskets (fig. 75) of rectangular shape, 1½ by 2¼ feet, were made to fit inside. These consisted of a framework of galvanized iron attached to a bottom tray of the same material, both of which were painted with two or three coats of asphaltum to prevent corrosion. On the frame was stretched copper cloth 100 meshes to the inch. In the baskets were placed the fish infected with mussels. In order to reduce the length of time necessary for retaining the fish in such narrow confines, they were not placed in the crate until a few days before the end of the parasitic period of the mussels and were removed as soon as the mussels were shed. Plants of the following species of mussels were made from time to time: The washboard, *Quadrula heros* (Say); the mucket, *Lampsilis ligamentina* (Lamarck); Lake Pepin or fat mucket, *L. luteola* (Lamarck); the yellow sand-shell, *L. anodontoides* (Lea); and the pimple-back, *Quadrula pustulosa* (Lea).

Modifications of the floating crates were introduced from time to time with a view to improvement of conditions for both fish and mussels and economy of operation. The latest form of float (figs. 58 and 59) adopted is made from two cedar telegraph poles held apart by crossbeams, 4 by 4 inches, at a distance sufficient to suspend lengthwise seven crates having dimensions 3½ by 1½ by 1½ feet. The crossbeams are placed at 4-foot intervals, and to them are bolted strap-iron hangers by means of which the crates are suspended. On the crossbeams over the telegraph poles are nailed 2-inch planks, 10 inches wide, forming a walk on each side the full length of the float. From this walk two operators can conveniently raise the crates in which the infected fish are placed. A float of this form was devised to protect the crates from wave wash and to give greater stability in stormy weather, when a shorter and smaller float would be tossed about.

The crates or baskets (fig. 60) in the improved type are constructed of cypress lumber, being made as light as the demand for strength permits. The bottom or floor is made of matched lumber and tight enough to prevent the escape of the microscopic mussels. The superstructure consists of a framework, on the outside of which is nailed galvanized screen of one-fourth-inch mesh. Fitted inside of the frame and outer screen are the inner screens, which consist of wooden frames to which copper cloth is fastened with copper tacks. The inner screens are removable, held in place by buttons or other locking devices. The removable screens are so provided with overlapping strips as to give a joint sufficiently tight to prevent escape of the small mussels. In the use of removable wire screens the following objects were in view: It facilitated the cleaning of the copper cloth and provided an opportunity to enlarge the mesh of the screens as the mussels increased in size, thus giving them a freer flow of water and economizing the higher-priced fine-meshed copper cloth. The use of wood instead of metal as employed in the first baskets provided distinct and obvious advantages. Metal was objectionable wherever the young mussels might come in contact with it, was less durable, and was more expensive. Metal cloth could not be dispensed with entirely, because other fabrics will not last under water. The increase in size of the crates or baskets was of marked advantage in providing more room for the fish, thus permitting use of greater numbers with less mortality.

The whole assembly of float and crates provided a convenient and economical means of operation greatly improved over the first crates, in which the raising of the much smaller baskets was necessarily done from boats and in comparison was awkward and difficult. The improved float because of its form is more readily towed and handled in the current than the very much smaller floats first constructed and may be easily drawn out of the river by a team of horses when necessary, as for winter quarters.

Other methods were employed in the investigation and, in a way, carried parallel for comparison to test the possibilities of the equipment already installed at the biological laboratory at Fairport. These were aquaria and indoor tanks and troughs, cement ponds, and earth ponds. Each of these was supplied with running water except in the case of special experiments with balanced aquaria. The water for the most part was taken from a reservoir receiving its supply by pump from the Mississippi River. Thus the water was, as a rule, practically unmodified. In some experiments with balanced aquaria filtered river water was used in order to eliminate the predacious animals which prey on the early stages of the mussels. For the same purpose, as well as to reduce the amount of sedimentation in river water, specially devised settling tanks were employed for supplying aquaria.

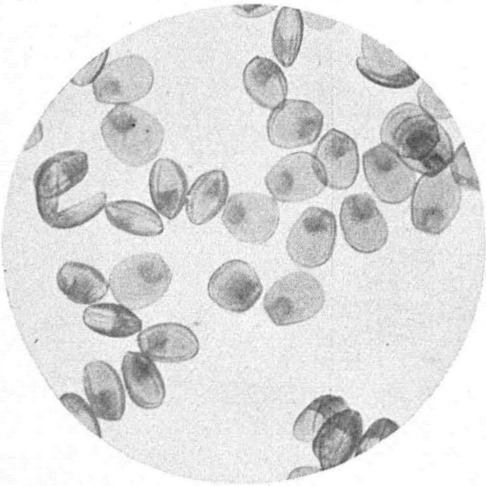
The cement ponds (fig. 61) were of reinforced concrete 50 feet long, 10 feet wide, and averaging 2¼ feet deep, having perpendicular sides and constructed for the temporary retention of fish. An accumulation of mud and a specially prepared bottom of gravel, together with an abundance of water plants, furnished conditions which proved suitable for some of the most delicate species of fish. It was assumed that these conditions were as suitable to the needs of the mussels as they could be made under the circumstances.

The earth ponds were from 41 to 61 feet long and 24 feet wide, varying in depth from 4 inches at the intake pipe to 4 feet at the well. An abundance of water plants furnished food and shade for the fish. The cement and earth ponds as compared with the floating crate do not so readily furnish the means for frequent observations of early stages. In using them it was planned to test their possibilities of rearing clams by a comparison of older juveniles grown in them. Thus the probable disadvantage of frequent disturbance necessary in making observations on younger juveniles would be avoided.

Plants of young mussels were made from infected fish in each of the culture devices mentioned. A modification of the cement pond was used in one instance for the purpose of securing a current comparable in rapidity to that to which the river mussels are accustomed. A flow of 50 gallons per minute was supplied to a trough 16 inches wide by 12 inches deep by 50 feet long, giving a current of 0.1 mile per hour. This is by no means equivalent to the 2 to 3 miles per hour of the Mississippi, but was planned to imitate the conditions of the river more closely than that of the ponds in which the flow is inappreciable.

OBSERVATIONS ON GROWTH OF JUVENILE MUSSELS.

In this investigation studies upon growth have been made with a view to securing data upon general conditions as well as upon the more specific methods of rearing under artificial environments. The species tested were chiefly heavy-shelled river mussels, which include most of those that are considered of commercial value, as distinguished from the thin-shelled pond-dwelling forms. The latter apparently offer no particular difficulties. The most complete results were obtained from a species which selects a habitat somewhat intermediate between these extremes, in that it dwells in lakes and



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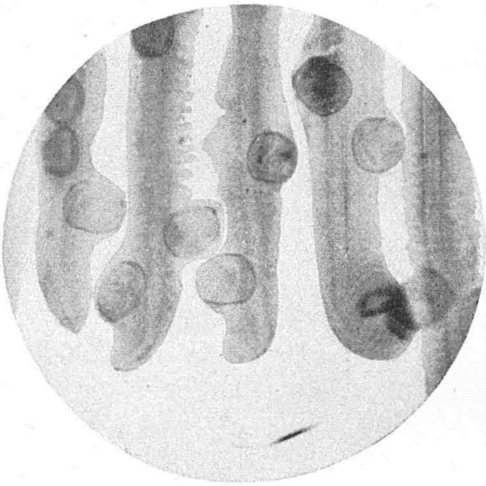

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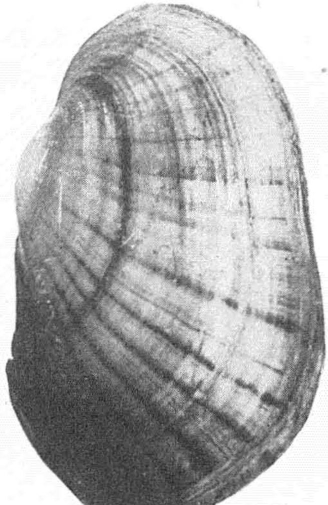

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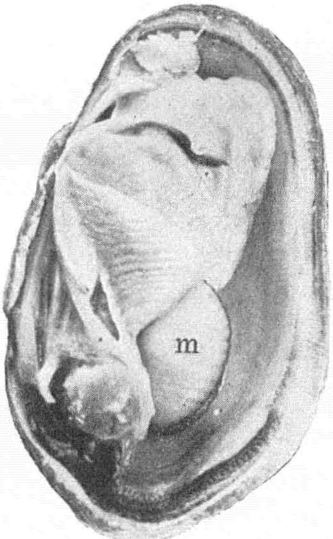

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Lake Pepin mucket, *Lampsilis luteola* (Lamarck), at various stages from young to adult.

Figs. 62 and 63.—An adult gravid female, age about three years. Natural size. The right shell (fig. 63) has been removed to expose the viscera. At *m* is shown the marsupium in which the young are carried from the egg to the glochidial stage. Mussels grown under control in the experiments here described equaled this one in size at the age of first breeding, two years and three months.

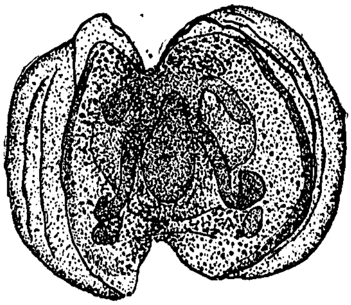
Fig. 64.—Glochidia or parasitic stage in the young as they appear on leaving the parent mussel. One with valves open may be seen at the middle left margin of the field. Photomicrograph, ×27.

Fig. 65.—Gill filaments of a black bass infected with the glochidia of *Lampsilis luteola* 14 days after infection. Photomicrograph, ×27.

Fig. 66.—Left to right: Young mussels of one, two, three, four, five and one-half months of age, respectively. Natural size.

the quieter waters of rivers. This was the Lake Pepin mucket, *Lampsilis luteola* (Lamarck). In this mussel a surprising amount of growth took place during one season. The other species fared less well, in some cases apparently surviving only a short period. Since satisfactory positive results were attained with *L. luteola*, the experiments with this species furnished a basis for comparison of the methods in reference to their influence on growth. As the results with this species may have been largely due to inherent qualities, a short account of its natural history and development seems desirable.

The Lake Pepin or fat mucket, as it is generally called, has a shell of excellent quality and possesses a good reputation as a pearl producer. It is probably the most widely distributed of the fresh-water mussels used commercially. Simpson (1900) gives its distribution as follows: Entire Mississippi drainage southwest to the Brazos River, Tex.; St. Lawrence drainage; entire Dominion of Canada east of the Rocky Mountains. The author has found it under the most varied conditions—from those of the marshy slough of a small creek to the deep waters and wave-beaten beaches of the Great Lakes. These observations would indicate that the form is adaptable to widely varying environment and would, perhaps, explain its thriving condition in this experiment where other species fared less well.



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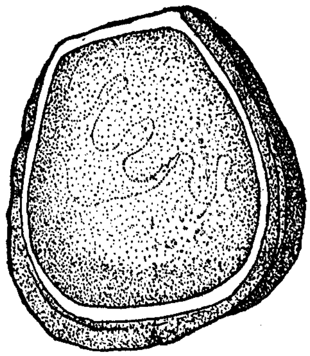

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FIGS. 67 and 68.—A young mussel one to three days after leaving the fish, in outward form like the original glochidium but internally (that is, inside the shell) showing organs developed. Drawn with a camera lucida. × 140. 67.—Ventral view with valves apart, from specimens stained and cleared. 68.—Side view; a narrow growth of the new definitive shell may be seen bordering the glochidial shell.

This species belongs to the bradytictic group called winter breeders. The glochidia are produced in the late summer or fall and are carried through the winter in the distended marsupial gills (see fig. 62) of the female. The glochidia (fig. 64) are favorable for infection, because their comparatively large size makes it easy to follow the progress of infection (fig. 65) and subsequent shedding. Unfortunately, the number of glochidia produced is relatively small.

The gravid mussels for this experiment were obtained in Lake Pepin, Minn., about May 15, 1914, and shipped to Fairport, Iowa, by express. On May 21 ripe glochidia were taken from three of the live mussels for the experiment. Some dozen different species of fish were infected and of these, six proved susceptible and carried the young mussels through their metamorphosis. Before the young mussels began to be shed eight infected largemouth black bass were placed in basket No. 2 of the floating crate. Some very rough weather followed, tossing the crate about in such a way as to make the conditions severe for the fish and killing five of the eight. On June 10, 20 days from the date of infection, most of the young mussels were found to have been shed from the three remaining fish. On the same date shedding was found to have taken place from infected fish placed in the cement ponds and aquaria. The time of shedding for the earth ponds was not observed.

The young mussels were secured at this early stage from the aquaria. At the time of shedding there is apparently no growth of shell beyond that of the original glochidium, but the young mussel (see fig. 67) internally has for the most part the organs of the adult in contrast with the simple structure of the larval glochidium. Growth of the shell begins at once (see figs. 67 and 68), as shown, and in the figure a narrow border of the new shell is already visible.

GROWTH IN FLOATING CRATES.

Two weeks after obtaining the plant of young mussels from the bass, evidence that they were thriving in the crate was obtained. A small sample of sediment from the bottom revealed some half dozen or more. These had already a considerable growth of shell, the largest having an increase in surface of at least three times the size of the original glochidium (see fig. 69).

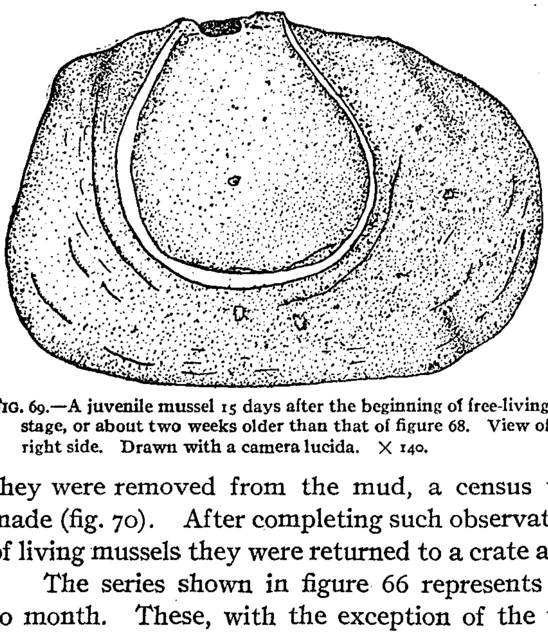

FIG. 69.—A juvenile mussel 15 days after the beginning of free-living stage, or about two weeks older than that of figure 68. View of right side. Drawn with a camera lucida. × 140.

At various intervals throughout the summer and autumn the author readily obtained specimens, making observations on rate of growth and preparing material for studies of development. Figure 66 shows individuals illustrating the amount of growth from month to month. The last examination was made about November 20, when the whole plant in the basket (fig. 75) was photographed under water. Later they were removed from the mud, a census was taken, and more photographs were made (fig. 70). After completing such observations as were feasible upon the whole plant of living mussels they were returned to a crate and placed in a pond to spend the winter.

The series shown in figure 66 represents about the average[1] growth from month to month. These, with the exception of the third, were removed from the basket on the dates given in Table 1, page 69. By inspection it is obvious that the rate of increase in growth as represented by these is not uniform throughout. This is due partly to the fact that in some cases small numbers only were removed at a time. In this way the average size was not secured in each instance. In one case only was a voluntary selection possible, and this was the last, made from several of nearly equal size. The specimen in the series for the second month (fig. 66, second from left) was probably smaller than the average. It will be noted that by months the increase is much more rapid at first, so that the rate is a decreasing one.

[1] These were selected at random in most cases and so probably approximate the average.

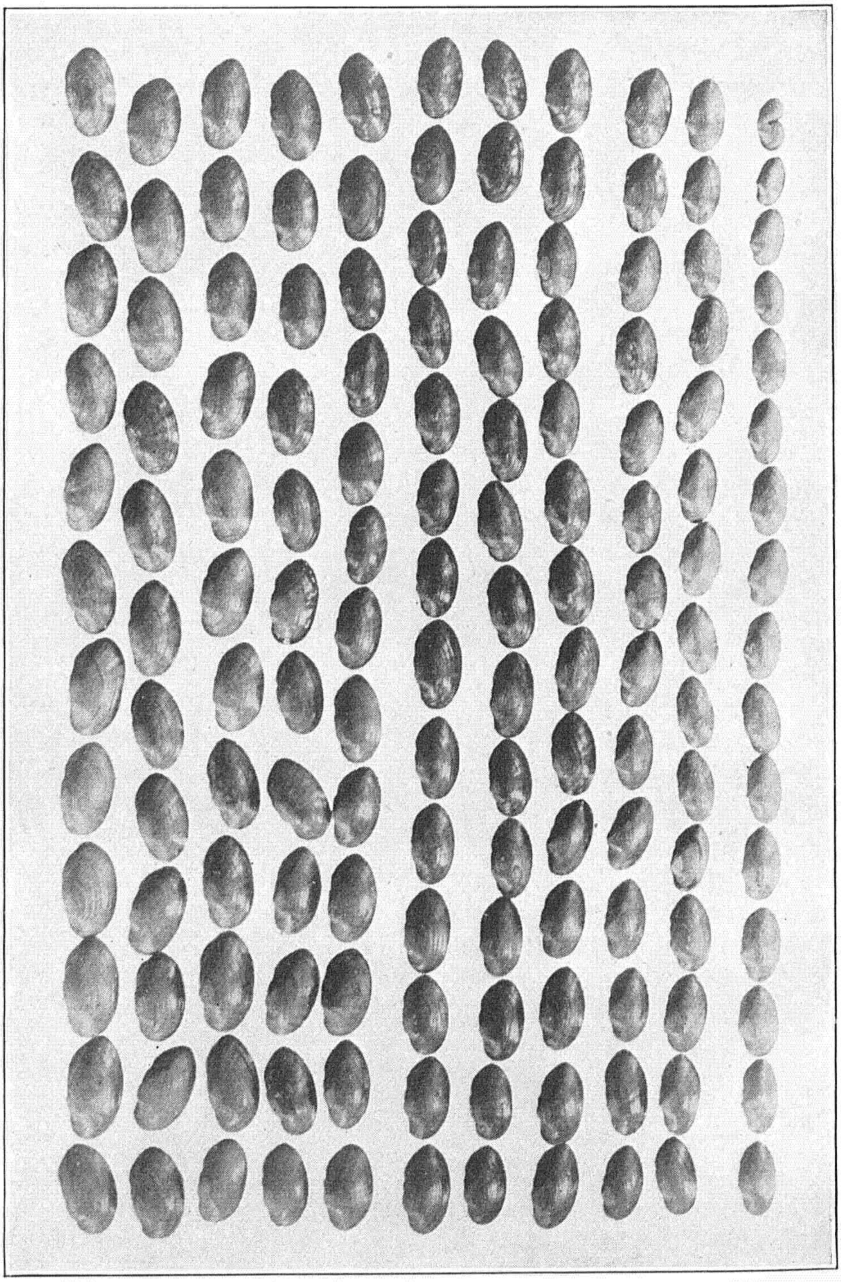

Fig. 70.—The contents of one propagation basket at the end of a season's growth of five and one-half months. The mussels were of microscopic size when shed in the basket by the fish. The arrangement in series shows the amount of variation at this age under the prevailing conditions. Reduced to five-twelfths natural size.

TABLE 1.—INCREASE IN LENGTH OF JUVENILE MUSSELS IN A FLOATING CRATE DURING THE GROWING SEASON OF THE FIRST YEAR, 1914.[1]

Date collected.	Length.	Increase in length.		Date collected.	Length.	Increase in length.	
	Mm.	*Mm.*	*Per cent.*		*Mm.*	*Mm.*	*Per cent.*
June 10	0.25			Sept. 12	22.3	9.3	71.5
July 18	4.2	3.95	1,580.0	Oct. 10	27.2	4.9	21.9
Aug. 17	13	8.8	209.5	Nov. 24	32	4.8	17.6

[1] The mussels measured were taken at random, with the exception of the last one, which was selected as the maximum.

The length of 32 millimeters at the close of the season (1914) is one hundred and twenty-eight times that of the original juvenile at the beginning of free life. This certainly compares favorably with the total length of 3 millimeters reported by Herbers (1913), which was the largest in his culture of juveniles, while the mussels in the experiment of which this paper treats were still alive and vigorous at the end of the season. Figure 70 is a photograph of the contents of a basket at the end of the season reduced to five-twelfths natural size. The mussels range in size from 32 to 15.5 millimeters. The variation is considerable, but it should be noted that less than 27 per cent are under three-fourths of the maximum size. The last mussel in the series, and one of the smallest, is deformed, probably restricted in growth by lodging in a crevice. Two more small mussels were found when the mud was passed through a sieve. Of these one measured 14.1 millimeters and the other the remarkably small size of 6.9 millimeters. The latter was living at the time of removal from the river. These few cases of dwarfing are doubtless due to lodgment in unfavorable locations—under crowded conditions—in the basket.

During the last month, from October 20 to November 20, a record of growth was taken to determine to what extent growth takes place as the water temperatures fall. Measurements of 10 mussels from the basket were taken. After marking and measuring each they were returned to the crate. The results are presented in Table 2, following which are given the water temperature averages, maximum, minimum, and range for the period. It will be seen that the growth for the period was very slight.

TABLE 2.—INCREASE IN LENGTH OF JUVENILE MUSSELS IN A FLOATING CRATE DURING THE LAST MONTH OF THE GROWING SEASON, 1914.

Specimen number.	Length.		Increase in length.	Specimen number.	Length.		Increase in length.
	Oct. 20.	Nov. 20.			Oct. 20.	Nov. 20.	
	Mm.	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*
1	23.3	23.4	0.1	7	25.4	25.8	0.4
2	24.6	24.8	.2	8	23.3	23.6	.3
3	24.2	24.5	.3	9	29.4	29.7	.3
4	25.2	25.5	.3	10	23.5	24.0	.5
5	21.3	21.3	.0				
6	29.0	29.0	.0	Average			.24

WATER TEMPERATURE FOR PERIOD OF MEASURED GROWTH.

	°F.
Average:	
For 11 days, Oct. 20 to 31	54.9
For 10 days, Nov. 1 to 10	50.9
For 10 days, Nov. 11 to 20	43.2
For whole period, Oct. 20 to Nov. 20	49.2
Maximum for whole period, Oct. 20 to Nov. 20	60
Minimum for whole period, Oct. 20 to Nov. 20	32
Range for whole period, Oct. 20 to Nov. 20	28

On consulting the temperature averages the assumption is natural that such growth as occurred took place before the temperature fell.

It is obvious that for the whole period (Oct. 20 to Nov. 20) growth was much less than in the warmer months. Compare the maximum of 0.5 millimeter for the period with the growth of 4.9 millimeters shown in Table 1 (p. 69) for the period from September 12 to October 10. The desire to secure these records resulted in the postponement of the date for removal from the river until a time dangerously late. On the night of November 19 ice floes bore down on the crate. Only by the rarest good fortune was the whole plant saved. The ice instead of destroying the crate or carrying it away landed it on shore, where the mussels were extricated without injury. A count of mussels grown in the basket follows:

Alive in basket Nov. 20	172
Dead in basket Nov. 20	6
Removed from basket June 25 to Oct. 30	45
Total living for season	217

As the original plant from the three surviving bass was an estimated 2,400 juveniles, it would give a survival of something better than 8⅓ per cent. The mortality would be indicated by the difference in the figures of the original plant and the final crop.

Observations upon growth were continued during the second and third summers. The results of measurements taken from month to month on marked mussels are indicated in Table 3. In figure 71 is plotted the increase of growth per month for 18 months, with the graph of the average water temperature. The data are taken from observations on mussel No. 3 in Table 3, as the record for this mussel is the most complete. Absence of growth from November to the middle of April, though not shown in the table, was observed and is supplied in the graph. Lack of observation for May, 1915, is supplied from another brood of the same age giving an approximation to the true figure sufficiently close for our purpose. This would give the following increases in millimeters for each month: May, 1.7; June, 6.1; July, 9.1; August, 7.1; September, 3.9; October, 1.5; May (1916), 1.9. The growing season seems obviously to be correlated with the rising temperature of summer. In a general way, doubtless, it is dependent upon the phytoplankton, and the plankton is controlled to a large degree by the temperature (Kofoid, 1903, p. 572, par. 18).

TABLE 3.—GROWTH OF MUSSELS IN A FLOATING CRATE IN THE SECOND AND THIRD YEARS.

Specimen.			Length in millimeters.										Weight in grams, Oct. 6, 1916.
Number.	Sex.	Mark.	Apr. 19, 1915.	June 10, 1915.	June 22, 1915.	July 22, 1915.	Aug. 21, 1915.	Sept. 25, 1915.	Oct. 26, 1915.	May 31, 1916.	Aug. 15, 1916.	Oct. 6, 1916.	
1	....	I	31.6	....	....	....	....	....	....	....	....	....	....
2	Female	II	30.6	....	36.9	48.5	53.9	57.5	53.8	....	72.0	[1] 71.8	53.5
3	Female	III	27.5	35.3	35.3	44.4	51.5	55.4	56.9	58.8	....	74.6	67.0
4	Male	IV	21.7	....	29.3	39.6	46.9	51.8	52.7	55.5	....	74.9	49.6
5	Female	V	25.1	....	....	47.0	52.4	57.4	....	59.6	....	73.0	57.8
6	....	VI	29.5	....	....	....	....	....	....	....	....	....	....
7	Male	VII	26.4	33.4	....	....	51.5	55.7	55.9	58.2	....	78.8	56.5
8	Female	VIII	21.1	27.7	29.1	....	43.4	....	....	51.6	....	69.6	57.6
9	Female	IX	24.1	30.7	....	41.9	47.2	....	51.1	52.7	....	65.0	44.6
10	Male	X	26.0	....	....	....	51.4	55.8	....	58.6	....	80.0	61.6

[1] No growth indicated here. Decrease perhaps due to breaking of periostracum.

The second summer yielded one individual measuring 62.8 millimeters (2.47 inches) in length, the maximum, and many over 55 millimeters (2.16 inches) in length. From one of these were cut 16-line buttons 2 lines thick (see fig. 72). Although this is not a favorable size for cutting, the fact that the shell in two seasons' growth is almost suitable for commercial use is of significance and far exceeds expectation.

Growth during the third summer, when the adult stage was attained, determined by the first breeding, reached a maximum length of 85 millimeters, weight 63.1 grams, in the male, and a length of 77 millimeters, weight 66.5 grams, in the female (gravid). Length, average male 79.1 millimeters, average female 71.5 millimeters. The growths of the 1915 brood during their second summer compared with that of the 1914 brood for their second summer show a very striking difference. Although the 1915 brood

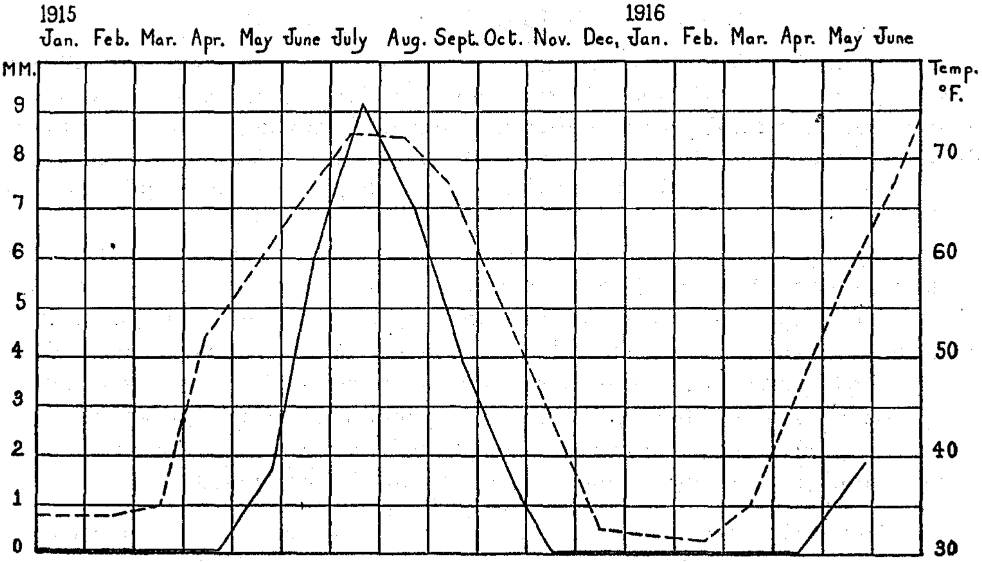

FIG. 71.—Growth of a fresh-water mussel in relation to temperature: ----, mean monthly water temperature (F.) in the Mississippi River at Fairport, Iowa; ——, monthly increase in growth of a fresh-water mussel in its second year, in millimeters. Zero represents the line of no growth and the coordinates represent the increase for each month taken separately. (See p. 70.)

began the second summer very much smaller, averaging 11.6 millimeters in length, compared with 25.7 millimeters for the 1914 brood, at the end of the season the former had increased 475 per cent while the latter had gained only 212 per cent.[2] This disparity in growth brought the brood of 1915 to a size—their second year—equal to that of the 1914 brood at the end of their second year in the face of a large handicap.

This difference may be ascribed to difference in season which is, perhaps, the simplest explanation. The summer of 1916 had higher water temperature, higher water stages, and less wind than usual. Flood stages, generally speaking, have been found unfavorable to plankton production as determined by Kofoid in the Illinois River (Kofoid, 1903). The rapid growth this season occurred on falling stages but at an unusually sustained high level. As this high level was not due to local precipitation, it would seem that the conditions were consistent with (an assumed) high plankton production at the point of observation. The absence of wind as an important cause of turbidity would be favorable to the feeding of mussels.

[2] The small size of the 1915 brood was due to a late planting and partly, doubtless, to a less favorable growing season.

Another explanation of this difference is the possibility of the existence of an inherent controlling factor in growth, whereby an average growth may be obtained by the end of the second year. That is, in the case of a small first year's growth there would be compensative additional growth the second year. This phenomenon is not of uncommon occurrence in organisms. Barney (1922) in studies of growth in terrapins finds "runts" selected in 1913 in 1917 exceeding in growth larger selected individuals of 1913.

A plant of yellow sand-shell, *Lampsilis anodontoides* (Lea), was not as successful in numbers, but yielded three juveniles which survived the summer, and the largest attained a size of 8.3 millimeters in 6 months. The second summer it attained a length of 41 millimeters and a weight of 5.8 grams.[3]

GROWTH IN AQUARIA, TANKS, AND TROUGHS.

A plant of juveniles from two bass, *Micropterus salmoides*, and one calico bass, *Pomoxis sparoides*, was obtained in a rectangular glass aquarium. The young were readily found within a day or two after their escape from the fish, but later than this only shells of the earliest stages could be found. It is possible that the absence of growth in this instance was due to the destruction of the young mussels by enemies to be mentioned later.

Another test of the possibilities of aquaria was made by placing in them rapidly growing mussels taken from the floating crate at a more advanced stage and comparing their growth with the growth of mussels remaining in the crate. The growth in millimeters and the increase is shown in Table 4. While in the aquarium the same individuals were measured each time, the measurements of growth in the crate were not based upon particular mussels, but upon different examples taken as representative of the lot. Observations were made in this way, because the recovery of marked mussels in the crate entailed danger of too much disturbance to the whole plant.

TABLE 4.—COMPARATIVE GROWTHS OF JUVENILE MUSSELS IN AQUARIUM AND IN FLOATING CRATE.

Place of growth.	Length in millimeters.		Increase in millimeters Aug. 17.	Place of growth.	Length in millimeters.		Increase in millimeters Aug. 17.
	July 27.	Aug. 17.			July 27.	Aug. 16.	
Aquarium	6	7	1	Floating crate	(6)	13	7
	5.5	Lost.			(5.5)	12.8	7.3
	3	4.2	1.2		(3)	10.1	7.1

The figures, although only approximate, are sufficiently accurate to represent fairly the great difference in growth that has been shown in many experiments in other ways. The total growth from the beginning of the juvenile stage, June 10 to August 17, is 7 millimeters for the largest of three mussels placed in the aquarium for three weeks, while it is 10.1 for the smallest of three taken from the crate on the same date. This gives a difference of 3.1 millimeters where the influence of the aquarium is exerted only for the relatively short period of three weeks.

[3] Attention is called to the employment of the garpikes, *Lepisosteus osseus* (L.) and *L. platostomus* Raf., as hosts for the mussels in this experiment. These are the only fish found of many tested which will carry the glochidia of this mussel (Howard, 1914b).

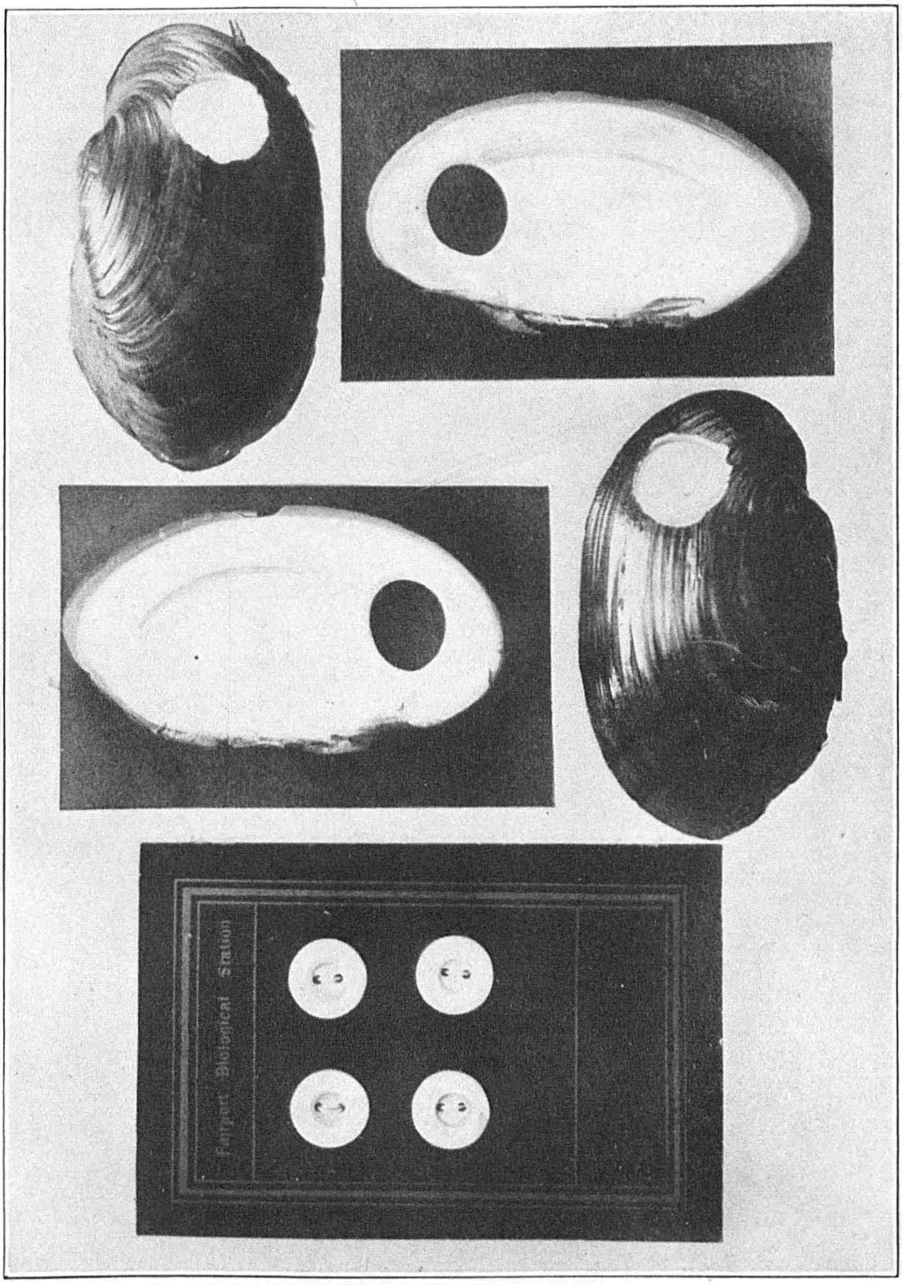

FIG. 72.—Mussels at the age of one year and four months, and buttons cut from them. These mussels were the product of artificial infection and rearing by the crate method. Photographed by J. B. Southall.

Young mussels of various sizes from one-half inch up placed in tanks and aquaria indoors at various times have shown a negligible amount of growth. Likewise, negative results have been secured in plants of young mussels made in the following types of aquaria indoors supplied with flowing river water which was unmodified so far as known: Wooden tanks or troughs, tanks and troughs lined with galvanized iron painted and unpainted, and cement tanks and troughs. Two systems of water supply have been tried. In one the river water was pumped direct, in the other it was pumped first into a reservoir, from which it was distributed by gravity flow. Later results seemed to indicate a difference to be discussed below under cement ponds.

In order to eliminate the destructive turbellarians and other predacious forms that might be introduced with the water, balanced aquaria, large and small, filled with filtered river water were tried. Here, too, the mussels survived for only a short time.

More recent experiments in rearing young mussels in a type of container of comparatively small dimensions have been conducted with considerable success, first by F. H. Reuling (1920) at Fairport and later by the author and others. The conditions were so different from those of the experiments just described that they should throw light on controlling factors in the development of juveniles. Their convenient size made them admirably suited for experimental purposes where a considerable number of units are required. The equipment consisted of galvanized-iron troughs 14 by 8 inches by 8 feet, painted with asphaltum. The troughs were protected from the sun by a shed roof of wood; otherwise they were uninclosed. (See center background of fig. 61.)

The water supply was derived from the surface of a pond containing vegetation. This arrangement yielded water of comparative clarity even when the river supplying the pond was turbid. The point of intake at the surface probably insured a minimum of animal enemies, such as Turbellaria, which might prey on the mussels. Additional precautions were taken against enemies by further straining through ordinary cloth and later close-meshed metal fabric.

Broods of *Lampsilis luteola* and some one-half dozen *L. ligamentina*, the river mucket, were reared in these troughs the first summer. In 1919 successful results were secured with three species approximately as follows: Yellow sand shells, *L. anodontoides*, 2,000; Lake Pepin mucket, *L. luteola*, 3,000; the river mucket, *L. ligamentina*, 500.

The dwarfing effect observed in aquaria and tanks indoors is a condition the causes of which have not been entirely determined. There is reason to suppose that reduced light and excessive precipitation of silt are possible factors, assuming that the water supply is the same as that of the river, ponds, or out-of-door troughs. Any such assumption is unwarranted, however, until comparative determinations of water conditions and contents have been made. Lack of growth suggests that the plankton, supposedly the principal food of the mussels, or other elements are for some reason wanting. The following evidence indicates the nature of some of these constituents which conceivably may be lost in part from water standing in reservoirs.

Detritus, including dead organic matter, forms a considerable proportion of the food of mussels, according to A. F. Shira and Franz Schrader. (Coker, Shira, Clark, and Howard, 1921, pp. 88 and 93.) Wilson and Clark (1912), in the examination of the stomach contents of river mussels, find a proportionally small amount of plankton combined with what is apparently a larger quantity of nonliving organic and inorganic material appearing like the mud in which the mussels are embedded when in their natural habitat. Mussels are supposed by some to act as scavengers in consuming sewage. The evidence indicates, however, that, as a rule, they flourish better in waters of natural purity. (Linnville and Kelly, 1906.) It seems not unlikely that mussels may derive considerable nutriment from substances in solution. Churchill's (1915) experiments on the absorption of fat by mussels seem to support such a view.

Consideration of the finely balanced conditions found necessary for the welfare of other lamellibranchs, including marine clams, to the growth of which considerable study has been given, removes any wonder at negative results with fresh-water mussels that have been subjected to highly artificial environments of aquaria and tanks. Complete success in the use of aquaria and such more or less artificial containers can hardly be expected until the factors of growth and their control are more thoroughly understood.

GROWTH IN CEMENT-LINED PONDS.

The cement ponds (see p. 66 and fig. 61), because of their location, size, and shape, were found very convenient in the experimental work for temporary holding of fish. The perpendicular sides permitted of ready subdivision by screens and easy control of fish, such as removal, transfer, etc. For the planting and culture of juvenile mussels, however, their usefulness is still somewhat a question. Many unsuccessful trials led to the assumption that the cement bottom and sides presented an environment unnatural and unsuited to the life of the mussel; but later results seemed to indicate that by proper control of conditions in them fair results might be obtained.

Variations in bottom were tested, together with changes in depth and flow of water, in order to take into account the special needs of given species so far as known. The kinds of bottom employed were gravel, sand, mud or loam, and the uncovered cement. The gravel, sand, or loam were evenly distributed 1 to 3 inches deep over the cement. In addition to this a greater or less deposit of silt always accumulated from the water, the maximum precipitation occurring at the end where the supply pipe entered.

The plants of juveniles were made from their fish hosts with the following species of mussels: *Lampsilis luteola*, *L. ligamentina*, *Quadrula plicata*, and *Q. pustulosa*. After one plant of *L. luteola* on mud bottom at the end of the growing season in November, 1914, an examination was made to determine the results as to growth. The whole bottom contents of the pond were passed through a sieve of 3-millimeter mesh. Two mussels only were present out of a plant of several thousand. These measured only 11.4 and 15.3 millimeters, respectively, and the appearance of their shells gave evidence of unfavorable conditions. Many tests with the different species were made on a bottom of sand or mud.

Another variation tried was the narrow cement pond in which large plants of the pimple-back mussel, *Quadrula pustulosa*, were made. In these ponds, as has been described (p. 66), a current of water over gravel and sand was kept up during the growing season. There was no opportunity for fish to disturb them, as the host fish (channel cat, *Ictalurus punctatus*) were removed as soon as the mussels had been shed from their gills.

Absolutely negative results were obtained from these experiments, as no trace of mussels could be found in screenings from a series of sieves in which the minimum mesh was 2 millimeters. (There is no doubt that the presence of any mussels approaching normal growth of two seasons would have been revealed by this search.) In these ponds normal aeration of the water and sunlight were more certainly provided for than in tanks and aquaria indoors.

In contrast with these results, largely negative, was a plant of *Quadrula pustulosa*, in which the outcome was more satisfactory. In one pond, in its first year used—i. e., the first year the cement was submerged (1913)—infected fish were placed in the lowest division—i. e., nearest the outlet and farthest away from the inlet pipe. This division was reserved for channel catfish for the purpose of simplifying the history of this section in case any results were obtained. The pond as a whole was employed as a stock pond. A continuous supply of water was kept up summer and winter with a view to giving any mussels that might be obtained opportunity to reach a size that could readily be found.

During four years the water was drawn down only a few times. On these occasions the lowering of the water was not allowed to an extent that would be injurious to any mussels that might have started. Only a cursory examination was made for mussels that might have reached a size to be readily detected. Purposely the treatment of this pond was varied from that accorded to the other ponds which, one or two years after plants had been made, were subjected to close inspection by sieving of the bottom soil. Had the same regimen been followed in this case the young mussels would certainly have been found even the first year, and it was an odd chance that the mussels prospered in this one pond where the "let-alone policy" was carried out. As this policy was different from that accorded to all ponds only in respect to the second to fourth years of growth it had no particular bearing upon the question as to how a set was obtained the first year. In seeking an answer to this question we may find a clue by considering wherein the conditions differed from the other ponds.

In respect to two features, or rather a combination of two (possibly more, of course), the conditions here seem to have been unique for this type of pond. In the first place the division in which the catfish were held was practically free of bottom soil, there being an exceedingly thin layer only, if any, on the cement. In the second place, this division was farthest removed from the intake pipe, around which there was considerable subaquatic vegetation, with the result that the water reaching the lower end of the pond was comparatively free of silt which had been unloaded in the upper division. It is pretty certain that juveniles of many species in the earliest stage can not thrive where silt is precipitating rapidly, and it is quite probable that certain species of Naiades, like some marine pelecypods, require a clean bottom and possibly a hard substratum. It is somewhat difficult to avoid silt precipitation in ponds supplied with water pumped from a turbid river. In this case the form of the pond, the vegetation, and the position of the mussels presumably brought about the result.

Another probable factor in the successful "set" was the "newness" of the water supply system and the consequent nonestablishment of predacious species which are found under usual pond conditions. Rhabdocœls are abundant in the ponds but not in the river water. Since the reservoir which supplies the ponds was filled first only the previous fall and this pond was filled for the first time a few days before the plant was made, it seems likely that rhabdocœls and similar enemies had not yet become established. The number of successful sets observed in the case of newly established ponds (see earth ponds) leads to the conclusion that this factor of "newness"[4] may be very important.

In Table 5 below are given the measurements of 10 of these shells, including the largest and smallest. There is given the increase per year as indicated by the winter rest line:

TABLE 5.—GROWTH OF 10 MUSSELS QUADRULA PUSTULOSA, DURING FOUR YEARS IN A CONCRETE-LINED POND.

Specimen number.	Yearly growth in millimeters.				Total length in millimeters.	Specimen number.	Yearly growth in millimeters.				Total length in millimeters.
	1913	1914	1915	1916			1913	1914	1915	1916	
1	4.3	6.2	6.2	5.3	22	7	4	6.5	5.5	4.5	20.5
2	4.6	7.2	6.8	5.6	24.2	8	4.8	6.9	5	4	20.7
3	5	6.1	5.8	5.7	22.6	9	4.4	5.3	4.4	2.3	16.4
4	4.8	3.6	6.4	3.2	18	10	3.7	4.6	5	2.3	15.6
5	4.3	3.8	5	4.5	17.6						
6	4.5	6.1	5	4.7	20.3	Average	4.44	5.63	5.51	4.21	19.79

The largest mussel of this series reared in a pond is considerably smaller than a mussel of about the same age grown in the river, as shown by the following figures: Pond grown, length, 24 millimeters; weight, 1.9 grams. River grown, length, 28 millimeters; weight, 4.6 grams. The retarding effect of the artificial conditions is obvious enough in this comparison, where the advantage of selection is all in favor of the pond-grown shell and in which the river-grown shell is a few months younger.

In the summer following the discovery of this "set" of juveniles experiments were carried out to determine if the results could be repeated. The conditions as to bottom and clarification of water and source of water supply were made to coincide as closely as possible with those of the successful "set." In one respect only as far as known was there a difference, namely, in regard to the factor of "newness" or absence of pond conditions. The water was taken from the same reservoir which, having been in use four years, had in a measure acquired the characteristics of a standing body of water. This difference was realized, but it seemed best to make use of the established system of supply as long as its suitableness was not disproved. Three species of mussels were used and several plants made with each. These species were *Lampsilis ligamentina*, *L. anodontoides*, and *L. luteola*. The results were negative except with *L. luteola*, which, as indicated elsewhere, is not a typical river mussel and has yielded successful sets in almost all instances under the conditions prevailing in the ponds at the Fairport laboratory. These results would seem to indicate at least that the conditions provided were not decisive factors in the one successful set of *Quadrula pustulosa*, and that possibly the one factor in question, namely, the water supply, is the one which was responsible for success or failure.

A review of the results attained in this type of pond, with its successful plants among the failures, holds out some hope still for the solution of the problems of rearing the true river mussels. The line of procedure indicated would seem to be the provision of a water supply direct from the river and a rigid exclusion of established pond condi-

[4] The condition of the water supply before typical pond conditions have time to develop.

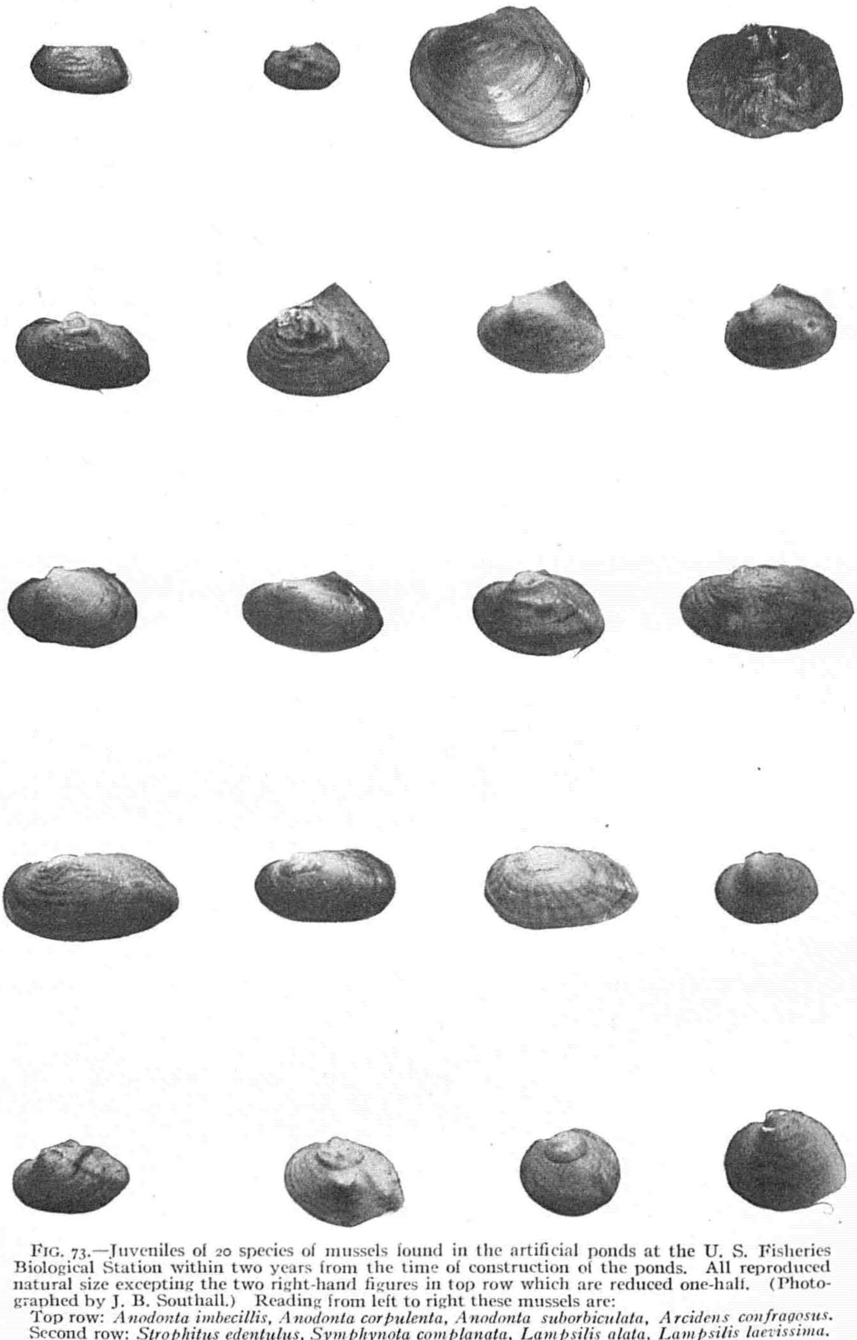

FIG. 73.—Juveniles of 20 species of mussels found in the artificial ponds at the U. S. Fisheries Biological Station within two years from the time of construction of the ponds. All reproduced natural size excepting the two right-hand figures in top row which are reduced one-half. (Photographed by J. B. Southall.) Reading from left to right these mussels are:
Top row: *Anodonta imbecillis*, *Anodonta corpulenta*, *Anodonta suborbiculata*, *Arcidens confragosus*.
Second row: *Strophitus edentulus*, *Symphynota complanata*, *Lampsilis alata*, *Lampsilis laevissima*.
Third row: *Lampsilis capax*, *Lampsilis gracilis*, *Lampsilis ventricosa*, *Lampsilis luteola*.
Fourth row: *Lampsilis subrostrata*, *Lampsilis parva*, *Lampsilis ligamentina*, *Obovaria ellipsis*.
Fifth row: *Plagiola donaciformis*, *Obliquaria reflexa*, *Quadrula plicata*, *Quadrula undata*.

tions. It should be possible to maintain such conditions by thoroughly cleaning the walls and bottom each season and, so far as possible, excluding pond plants and animals during the critical period when the young mussels are escaping from their hosts.[5]

GROWTH IN EARTH PONDS.

A large plant of *Lampsilis luteola* was made in an earth pond in 1914 from crappie of two species, *Pomoxis annularis* and *P. sparoides*, and the sunfish, *Lepomis pallidus*. The following spring an examination of the bottom yielded some eight mussels, the largest 24 millimeters in length, the smallest 12. The growth was not as great as that in the floating crate, but compared favorably. The number surviving, however, compared with the thousands introduced into the ponds by means of the fish, was disproportionately small.

In lowering the water level of the pond there were found a few sheepshead, *Aplodinotus grunniens*, whose presence was quite unexpected and contrary to the plan of the experiment. As this is a mussel-eating fish, its presence might explain the disparity in numbers of the young mussels. Fortunately, a smilar plant was made the same season by the fish-cultural staff at the suggestion of the director. Since the pond was larger and the total number which was recovered was greater, it will better represent the results by the pond method.

A number of black bass were infected with *Lampsilis luteola* in the fall of 1913. In the spring they were placed in one of the large earth ponds, 0.843 acre in extent, used for propagation. The following November (1914), when the pond was drawn, some 60 mussels were picked up from the bottom. In the spring of 1915 more were recovered, making a total of 150. These were examined and measured. They had attained about the same growth as the mussels in the floating crate. The largest measured 35 millimeters in length, the smallest 15.5.[6] The greater length would be explainable as due to the longer growth period; having been on the fish during the winter, they would in all probability have completed their parasitic development some time before June 10, the date on which the plant in the floating crate was made. As compared with the small pond, the size doubtless contributed to the maintenance of more favorable conditions. We have in such a body of water conditions closely approaching the habitat of *L. luteola* in nature. Whether the distinctively river-growing mussels would thrive in such a pond in the absence of a current has not yet been satisfactorily determined. However, the fact that, in spite of many failures with some of these species, a few of these (represented in fig. 73) have been found in the ponds, for the most part of unintentional or sporadic occurrence (see Coker, Shira, Clark, and Howard, 1921, p. 165), leads one to believe that favorable results might be obtained by a proper control of conditions.

GROWTH IN PENS.

Recently a device was employed by Roy S. Corwin (1920) at Lake City, Minn., which gave very satisfactory results with the Lake Pepin mucket. A box 10 by 10 feet square and about 8 inches high was surmounted by chicken wire and the whole

[5] Experiments planned to conform as closely as equipment permitted to the conditions proposed were carried through the season of 1919. Precipitation of silt occurred in large quantity, which doubtless accounts for failure to secure a plant of river mussels. A plant of lake mussels (*L. luteola*) was obtained.

[6] Measurements of these mussels after a second summer's growth, Dec. 1, 1915, give for the largest a length of 65.6 millimeters. From two of these were cut 16-line buttons 2 lines thick. (See footnote, p. 71.)

sunk in a protected part of Lake Pepin. In the pen thus made it was possible to retain a considerable number of fish carrying heavy infections. At the end of the season the wooden bottom was floated to the surface, and an examination revealed a total of 11,000 small mussels as reported. This is to date the greatest quantity production of mussels yet attained in an inclosure. This method has several obvious good features for situations in which it may be employed. It approaches natural conditions more closely than the other methods described. The suitable depth for both fish and mussels is more readily obtained than in a crate, as well as more ample range in other directions. It seems doubtful if it can be used in a river where the current would remove the young mussels or the silt deposit cover them too rapidly.

This season (1920) a test of the device is being made in the growing of river mussels in the Fox River, where the mucket mussel (*Lampsilis ligamentina*) is abundant and apparently thriving, since young mussels are readily found. The water of this stream is clear so large a part of the time that a protected location devoid of current should prove suitable. It is difficult to see how such a pen could be employed in a turbid river like the Mississippi, since at points devoid of current the precipitation of silt would bury the young mussels. The habitat of juvenile mussels in the Mississippi has been found to be a current-swept gravel bottom, always clean despite the almost constant presence of mud-laden waters.

STRUCTURE AND DEVELOPMENT OF JUVENILE MUSSELS.

The rearing of these mussels through the juvenile stage presented for the first time the opportunity to determine the structure at almost any age and processes of development during this period in the life history of fresh-water mussels. The investigations by Herbers (1913) and Harms (1909) have recounted in detail the development during that period for the Anodontas, Margaritanas, and Unios. In these cases, however, the juveniles were obtained for the most part free in nature, and therefore their age could not be given with certainty. As no detailed account has been published for the development of the large and valuable group of mussels included under the Lampsilinæ, the description of complete development in these would be a distinct contribution to our knowledge of mussels. However, because of other features demanding more attention at the present time, the intention of this paper is to mention only a few prominent points in the development, reserving the detailed account for another publication.

Upon beginning free life the shell of the young mussel, as has been stated above, is that of the larva. When closed, therefore, no striking difference between the young mussel and the glochidium is noticeable. Like the glochidium, it is for the most part colorless and transparent. If, however, the young mussel is alive it soon extends its foot, and in its use quickly demonstrates it to be an organ well developed for the purposes of locomotion. The foot is somewhat cleft at the apex, so as to give a bilobed appearance, and is clothed with cilia, all of which are in rapid motion during extension. On smooth surfaces like glass it has the power of adhesion, a property apparently not held in the adult, at least not to the same extent. By means of this organ the young mussel is able to move about rapidly. These peculiarities in the foot of the early juvenile are soon lost, and during the first month the foot assumes the characteristic form of this organ in the adult.

The gills are in the form of papillæ, of which at this stage there are three or four on each side of the foot, the longest being anterior, since it is the oldest or first developed (see figs. 67 and 68). They are long, slender processes slightly recurved at the ends. These increase in number with age and later become united to form the continuous lamellæ of the inner gill. The outer gills become visible between the first and second month or at a length of between 3 and 5 millimeters. Schierholz's (1888) determination of the time as the second and third year for Anodonta and third and fourth for Unio has been shown by Herbers (1913) to be incorrect for Anodonta, and will probably be found to be rather late for Unio.

Other prominent features in the youngest juveniles are the liver and the adductor muscles. The liver, because of its dark color, becomes quite prominent before the young mussel leaves the fish. It furnishes in this manner a ready index for the degree of development when examined alive. The adductor muscles also become conspicuous, but in another way. Because of their form and an index of refraction higher than that of the surrounding tissues they appear as bright spots. The stomach and intestines seem to become functional at once, the latter at first with a few turns comes gradually to the tortuous condition in the adult. The heart and kidney can not readily be made out in whole mounts. Herbers (1913) by sectioning finds their development pretty well advanced in *Anodonta celensis* at a length of 2.59 millimeters, corresponding to the second month in *Lampsilis luteola.*

The mantle is a direct derivative of the same organ in the glochidium. The coming of free life marks a change in its function. Where in the glochidial and parasitic periods (in this species) no increase of shell occurs, in the juvenile stage a phenomenal growth takes place. Beginning as a delicate microscopic membrane lining the glochidial shell, it increases with the growth of the mussel until, as we have seen, it is increased in size thousands of times in a single summer and eventually produces the heavy shell, the protective armor of the grown mussel.

The shell of juveniles up to the second month has two features that are characteristic of this early period. In consistency it is like horn, being transparent and less hard than later, when it becomes calcareous. The surface is uneven owing to a series of regular and relatively high undulations, knobs, etc., which are characteristic for each species (fig. 73). These are designated as "umbonal sculptures" by conchologists in describing the adult mussel, in which they are not infrequently found well preserved.

A structure to which special attention is called is the byssus, an organ that is characteristic of the juvenile stage in certain groups of fresh-water mussels. It consists of a hyaline thread produced by the byssus gland located on the ventral and posterior median edge of the foot. The first instance of it observed in the present culture was at an age of about 38 days, when the smallest of the mussels collected had a length of 4 millimeters (other cultures 1.9 millimeters). In this same species in nature the author has seen it present at a size of 2.8 millimeters. In juveniles of *Quadrula heros*, at an age of a few days, there is apparent a tough mucous-like secretion that serves to anchor the young mussel. Near the end of the growing season byssi were found on mussels of over 1 inch in length. The strength and caliber of the threads are appropriate to the size of the mussel. When the mussels were removed from the water at a temperature near that of freezing on November 20, attachment by byssi was not noted. However, the circumstances of their removal from the river rather than the change in temperature may have caused them to become detached. An examination in March of the following spring revealed the byssus present in most of the individuals, and it was present until June 10, after which date it could no longer be found. The disappearance at this time near the middle of the season's growth requires some explanation. It comes at the beginning of the period of most rapid growth, which is, perhaps, a decided physiological change, although very gradual, coming as it does after two months of spring growth. The observations to be recounted of a byssus in adult mussels would lead one to expect the persistence of the byssus under favorable conditions. On August 14, 1914, the author found an adult *Plagiola donaciformis* on a byssus, and later E. A. Martin showed the author a still larger individual. The byssi in these cases were strong enough to support the weight of the mussels. In this species (*Plagiola donaciformis*), then, we find the byssus habit not confined to the juvenile stage.

The development of the reproductive glands in fresh-water mussels was clearly made out by Herbers (1913) in Anodontas and Unios. He was able to distinguish early stages of the glands in Anodontas of 5.7 millimeters length. The maturity of these organs would mark the adult stage. In collecting various species of mussels in the field one occasionally discovers remarkably small individuals breeding. As these are so uncommon they are undoubtedly examples of precocity and exceptional.

The author has not found gravid individuals of *Lampsilis luteola* under what was apparently the third year. In the cultures here described sexual differentiation in secondary characters appeared the second summer. Modifications of the gills to form the marsupia appeared in the female, together with the corresponding fullness of the shell over that organ. The males were marked by the more pointed posterior portion of the shell. In the middle of August of the third summer the first gravid mussels were found. This, the first observed date of breeding, was 2 years, 2 months, and 24 days from the date of implantation of the glochidium. All females as far as examined were found to be gravid, which indicates that breeding is general at this age. The glochidia were mature in some individuals on August 14 and near maturity in others, which from the date of last observation would fix the time of ovulation as July.

Mature glochidia from these mussels were taken and an implantation obtained on a number of fish. The first free juveniles after metamorphosis were obtained in 10 days, others remained as late as the 18th day, a rather long period of shedding. The juveniles obtained represent the second generation of mussels, but the life cycle was completed when glochidia were obtained, as that was the stage with which the experiment began.

HABITS AND HABITAT OF JUVENILE MUSSELS.

The juvenile or postparasitic period begins with the release of the young mussels from encystment on the host. Because of the small size of mussels at this stage information regarding their habits and environment must depend largely upon studies under conditions of control or experiment. Obviously, it is entirely impracticable to count on finding them thus early in nature. The watching of the process of separation from the host has been found practicable only by making cuttings of infected gills from living fish and by examinations under the microscope. The first sign of the change is a repeated opening and closing of the shells. This is followed by extension of the foot, the movements of which become gradually more vigorous until this remarkably motile organ sweeps an arc in the plane of the valves included by the three sides of the mantle cavity (the anterior, posterior, and ventral opening of the shell).

The cases observed by the author took several hours, but under the conditions of observation the difficulties are greater than when normal in the living host. There seems to be an adhesion of the shell to the host's excised tissues that is due, very likely, to coagulation. In some cases the process was so prolonged that, before escape was effected, considerable decomposition of the host tissue was apparent. The juveniles, therefore, exhibited a remarkable resistance to the products of decay toxic to most animals.

The free juvenile under conditions of observation appears at times very active. In moving from place to place the foot is extended a distance fully equal to the length of the shell, becomes fast to the glass or some object, then contracts, bringing up the remainder of the animal. This is repeated again and again, thus accomplishing a kind of creeping motion which carries the small organism across the field of the microscope in a suprisingly rapid manner. The presence of cilia all in rapid motion upon the foot and edges of the mantle add to the effect of vigorous vitality.

It seems probable that the young mussels do not move about much if they find a suitable bottom. Time and again the author has looked for them on trays set on the bottom of the aquarium to catch them as they fall from the hosts, but all in vain before washing off the sediment. When this accumulated sediment in which they were lying was removed, they could be seen, and after being left for a few minutes without disturbance they would extend the foot and begin the migration reactions mentioned above. Often one finds considerable débris adhering to their shells. In one species delicate hair-like processes were observed. A covering of bottom sediment doubtless serves as a shield from enemies.

The mortality at this age is very high as may be seen by the number of empty shells and the scarcity of live mussels a few days after the beginning of free life. Their chief enemies, so far as noted under cultural conditions, are very small rhabdocœls, turbellarians that are extremely abundant during the summer in the water as it comes from the reservoir. These swarm over the bottom of the aquaria, and examples may readily be found through the transparent body walls of which may be seen the mussels they have eaten. These have been observed in both the glochidial and early juvenile stages.

The species of Turbellaria as determined by Caroline Stringer were *Microstomum* sp., *Stenostomum leucops*, and *S. tenuicauda.* Specimens of the Microstomum were preserved with the young mussels still inclosed in their relatively capacious intestines. Another enemy which it has been possible "to arrest with the goods still on him" is a small chætopod, apparently Chætogaster. Neither of these worms is more than 0.4 millimeter wide, so that after the mussel attains three weeks' growth it must be safe from their ravages.

The food of the very young juveniles seems to be similar to that of the adult; i. e., at least in part, microscopic plants and animalcules taken in through the incurrent siphonal aperture. In small juveniles one can watch these as they enter. The author once observed a considerable deposit of excreta containing the skeletal remains of such forms as diatoms. This débris was lying in a heap outside beneath the excurrent siphonal opening.

The floating crate method furnished an unusual opportunity for the study of living juveniles after the first two weeks, but as it was the first successful trial, for fear of disturbing the plant, the occasions for raising of the baskets were reduced to a minimum. Such incidental notes as were taken while tending the cultures may be of interest, inasmuch as so few observations have been made upon the habits and habitat of the juvenile Naiad.

In relating observations upon the habits of the culture attention is directed to the conditions prevailing during the experiment. The arrangement of the crate and baskets is described under Methods, page 64. (See also figs. 74 and 75.) The crate, being placed in the river channel, received a current of 2 to 3 miles per hour. In the individual baskets when at the surface no current could be detected. The fineness of the mesh was chiefly responsible for this. Much of the time, however, owing to a slight sinking of the crate, water to the depth of an inch flowed over the top. Thus the mussels, although probably never in a continuous current comparable to that in the river, received a constant renewal of the water supply. A gathering of the mussels at the sides of the basket was very marked. This might be construed to indicate that they found there conditions more favorable than at other points. Doubtless at the bottom of the basket the freshest supply would be at the outer edges. During a greater part of the summer flood conditions prevailed in the river, so that the content of suspended silt was very high. The checking of the current on reaching the baskets resulted in the deposit of this silt at the rate of over 1 inch per week. This is considerable when the conditions are considered. Thinking this might bury the young mussels, the silt was removed weekly by washing through the sides of the basket. Later this regimen was abandoned, being considered too violent and an unnecessary disturbance for the minute mussels. At the end of the season in November the silt in the bottom had accumulated to a depth of 3 inches. This sedimentation, however, covered a long period, most of which was not in time of high water.

The first collection of *Lampsiles luteola* from the crate numbered 7 at an age of 15 days. Three of these were built into the mosaic tube of a caddisfly larva, and of these three, two were still alive. The larva finding a scarcity of sand grains and similar building material had evidently made use of the mussels. The predacious worms mentioned above as so abundant and destructive of mussels were not found in the crates. They are apparently a bottom species, and thus the position of the crate on the surface forestalls their ravages. One of the most conspicuous species associated here with the mussels was the larvæ of the Ephemerid mayflies. As they are vegetarian they could be destructive of young mussels only in a competitive way, but ordinarily in crate culture they would not develop in time to be troublesome. The presence of these and like insect forms is doubtless due to the development of eggs deposited by the adult insects in the crate itself. Some other forms observed were numerous Hydra and Polyzoa, together with the free-swimming forms which make up the plankton of the main river.

The byssus was first observed in mussels of 38 days. The attachment was to such objects as could be found in the mud at the bottom of the baskets, some on the filaments of Cladophora and other algæ growing in the basket. One was found attached to the tarsus of a dead spider. The byssus increased in diameter and length with the growth of the mussels. When the latter were large enough to be readily seen, it was surprising

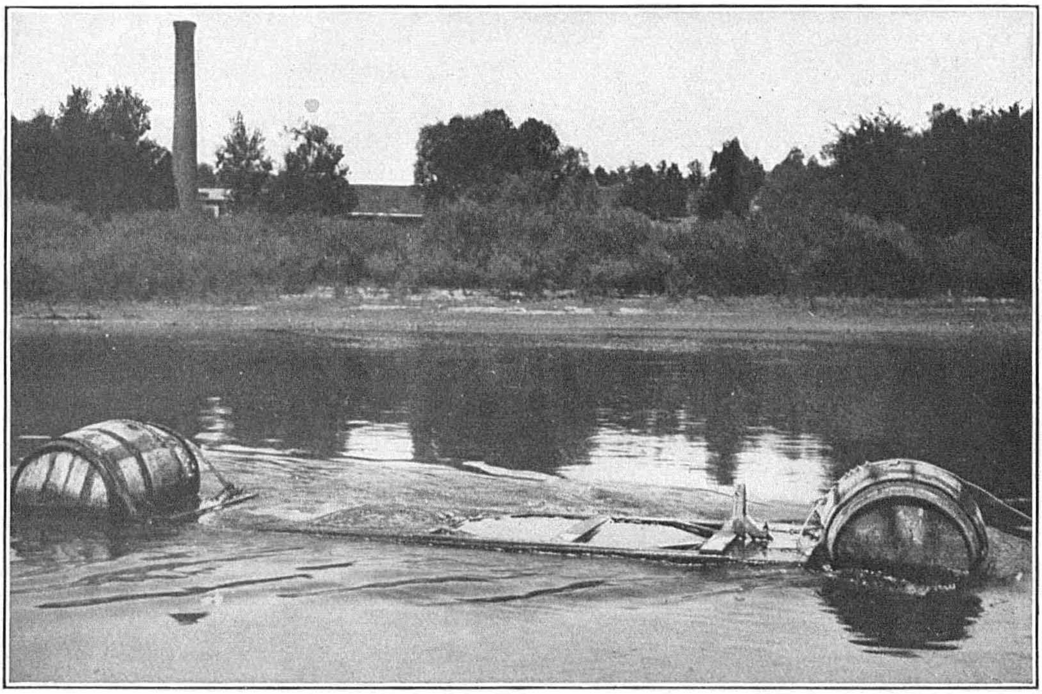

FIG. 74.—A floating crate containing four baskets (cf. fig. 75) in which were placed the fish infected with mussel glochidia. The first successful attempt to rear mussels was made in this device.

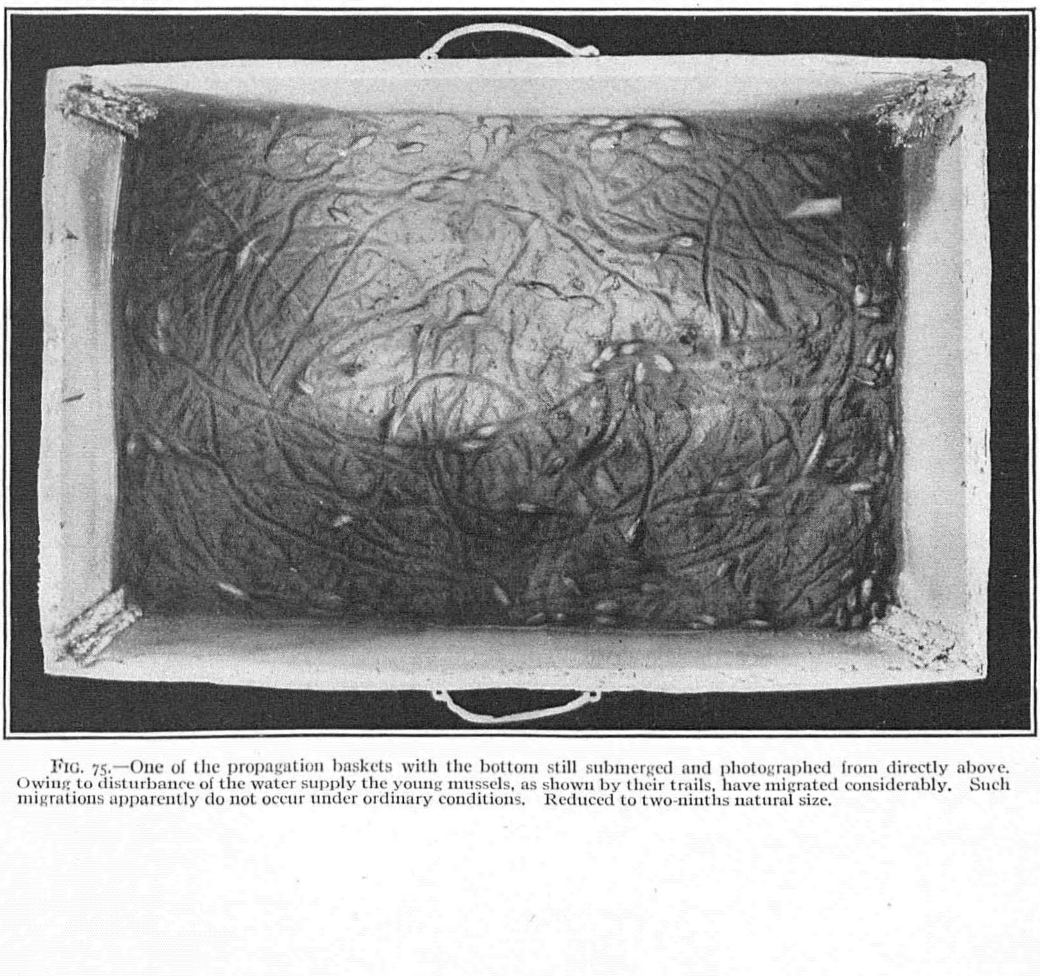

FIG. 75.—One of the propagation baskets with the bottom still submerged and photographed from directly above. Owing to disturbance of the water supply the young mussels, as shown by their trails, have migrated considerably. Such migrations apparently do not occur under ordinary conditions. Reduced to two-ninths natural size.

to find that they, like adult mussels, were usually buried in the mud, a small portion only of the posterior end of the shell reaching the surface. In fact, the only exception observed was in a case of interference with the water supply coming to the mussels, a discussion of which will be taken up later. No evidence of migration, by tracks or other signs, was seen. It would seem, therefore, that for this species when on a mud bottom the byssus would serve chiefly as an anchor for emergencies and would not frequently be called into service (cf. Isely, 1911). A change of position in the mud was noted when, owing to the presence of a small catfish that had escaped from another basket, the mussels burrowed deeper.

At the time of removing the mussels from the river for the winter the basket containing the brood of *Lampsilis luteola* was placed in a tank and the fresh supply of water cut down; then the mussels began to migrate, as can be seen by their tracks in the photograph (fig. 75). When the water was entirely drawn off, those on the surface fell over and closed their shells.

Altogether by observations for such brief periods the author did not note a varied number of locomotor reactions. The fact is, mussels when thriving and undisturbed seem to be comparatively inactive. Experimentally, doubtless, there would be a varied number of reactions depending upon the variety of stimuli applied. At present in our campaign to preserve the mussels and to increase their numbers we are particularly interested in the reactions manifested under natural conditions. We have some evidence of adaptations to depth of water and migration determined by river stages. There are indications also that some breeding reactions are influenced by light, others by temperature, chemical action, etc. The reactions of mussels when caught on sand bars by receding water vary with the species. The hieroglyphics of their wanderings under these conditions are sometimes very elaborate.

The discovery that the parasitism of mussels is limited in some species to one or a few species of hosts suggests the possibility of specific reactions in these by means of which the infection of the host is insured. (Howard, 1914a, Conditions of Infection in Nature, p. 39). This particular phase of their habits did not come within the range of this investigation, but it is suggested that in these ecological relations of parasitism the student of animal behavior may find that the ordinarily inactive fresh-water mussel will furnish a varied and interesting subject for study.

DISCUSSION AND APPLICATION OF RESULTS.

In considering the results of the foregoing experiments attention is directed particularly to those which seem applicable immediately to the campaign for mussel conservation.

Prof. J. L. Kellogg (1910) points out that there can be practically no conservation without culture or cultivation. Extinction has been the unvaried fate of useful forms, plant or animal, where the natural supply has been depended upon. In the more primitive human societies all food is obtained from the public domain, but civilization, with increase of population, has survived by assigning individual property rights from the public domain, thus encouraging and making cultivation possible. To give an example in a field closely allied to that of fresh-water mussels, this principle has been strikingly illustrated in the history of the oyster and clam fisheries. Those States, as Rhode Island and Connecticut, which framed laws encouraging the culture of oysters increased immensely their production, while a constant decrease was observed where the natural reefs were depended upon without sufficient encouragement to cultivation (Massachusetts Commissioners of Fish and Game, 1907).

This may be an extreme view, but it has been often true. It may be said, on the other hand, that although game protection (of fish, birds, and mammals) has been so frequently only a name in America, there are cases known to all where wild species have thrived under efficient protection combined with restocking in cases of depletion. Past efforts in the conservation of mussels have been largely confined to this limited type of protection. The work has consisted in "artificial propagation" (definition of which follows) and a certain amount of protection by law instituting open and closed seasons to fishing. The closing of certain streams for a number of years, thus creating preserves, has been advocated. Further assistance to nature in recovering from the effects of depletion is suggested in a system of culture, including protection and planting like that employed in restocking with fish.

The experiments here described furnished practically the first positive data contributing to the development of a system for the culture of fresh-water mussels. It seems worth while to consider whether cultural methods, which the present investigations indicate to be quite feasible, might add anything to the methods now in use. In using the term culture we distinguish from propagation.

ARTIFICIAL PROPAGATION.

Artificial propagation as it has been applied to mussels is a method which, as indicated above, has been employed by the Bureau of Fisheries some eight years past. The larval mussels are brought in contact with and allowed to infect the host fish, which are then released to spread the mussels under the usual conditions prevailing in nature.

In the effort to secure increased production of mussels this artificial infection has the following advantage: Whereas in nature the number of mussels which succeed in finding lodgment upon a fish is, as a rule, comparatively small, by artificially bringing parasite and host together the fish is made to carry a much greater number than would otherwise succeed in finding a host. Thus, the number of mussels reaching the juvenile stage is increased.

The place of shedding of the young mussels from the fish is to a large extent doubtless a matter of chance. As among marine clams probably those only survive which fall on, or subsequently reach, a favorable bottom. These considerations are largely responsible for the present investigations in the effort to supplement artificial propagation.

THE CULTURAL METHOD.

The cultural method as suggested by the present experiments would consist in carrying protection through the second critical period in the life of the young mussel and in planting in favorable localities the mussels obtained.

PROTECTION.

In almost all successful attempts at rearing animals or plants protection in critical stages is the important factor. An example from fish culture is the raising of trout. In agriculture the plant or animal is placed under the best environment attainable and protected from destructive forces of all kinds at all stages until used. If finally consumed for human use, provision is made to insure the perpetuation of the stock. In nature the dominant animals are the mammals which apply the principle of protection in the care of their young. Likewise among plants, those lines that have adopted this economy have attained dominance.

By the "artificial propagation method" the young mussel is carried through one critical event (infection) only. Liberation from the host and the early juvenile stage are equally if not more critical. Evidence showing this has been given above, and corroborative of this is the following testimony of Prof. Kellogg (1910) regarding the corresponding stage in the soft clam:

> Probably not even the swimming stage is more critical for Mya than this period of creeping which is of longer duration. It is exposed to numerous enemies and has little defense against them, for its transparent shell is still very thin and brittle.

Lefevre and Curtis (1912, p. 192) say regarding this stage of fresh-water mussels:

> It is to be supposed that only a very small proportion of individuals thus liberated would succeed in reaching maturity, as they would be exposed to the same destructive agencies as are encountered under natural conditions.

The results attained in the present investigation seem to indicate that a culture carried at least through the early juvenile stage and possibly to the adult stage would be economically practicable. In the floating crate method and the ponds [7] we seem to have found methods of protection. The proportion of survivals (8 plus per cent) in the crates is apparently greater than from those raised in the ponds (according to the best records we have) and doubtless can be greatly improved upon. Compared with the number under analogous conditions in nature it is tremendous. For example, Prof. Möbius (1877) finds that a young oyster has $\frac{1}{1045000}$ of a chance to survive and reach maturity. The same is true among practically all forms in which the young are early exposed to the vicissitudes of a free life. In the culture of sea clams the operator is dependent for planting upon such seed clams as are obtainable from a purely natural and thus somewhat uncertain supply. There is this decided advantage in operations with fresh-water mussels, that the necessary glochidia can be obtained with practical certainty as long as adult mussels last.

Protection at other than the two critical periods mentioned would be included in a complete system of culture. During the parasitic period it would consist in the proper care of the host fish. It may be noted that the fish when infected demands reasonable care, as the attaching glochidia cause a certain amount of laceration of the gills which subjects the fish to possible infection from fish mold (saprolegnia) and doubtless to some exposure from bacterial invasion.[8]

Culture for the adult mussels consists in providing the best environment for growth as well as economical means of protection and recovery. Experience has shown that other things being equal more rapid growth and development of heavier shell occurs in flowing water than where a current is lacking. (For other factors, see "Habitat," p. 94, Coker, Shira, Clark, and Howard, 1921.)

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[7] The recent results described under troughs and pens have yielded even larger percentages.

[8] *Bacterium columnaris* Davis has caused considerable mortality in experimental work at Fairport.

PLANTING.

The planting of mussels in nature by dropping from the host fish, although conceivably controlled to a certain extent by natural factors favorable to the mussel (Howard, 1914a, p. 39), is doubtless for the most part a haphazard process. Those which fall on unfavorable bottom must perish, and there is every reason to believe that successful mussel beds are the results of a precise combination of conditions at a given place. The investigations on sea clams and oysters show that myriads of the young develop to a given stage only to die if they are not on a suitable bottom. Great accumulations of these young clams on unsuitable ground may be saved by transplanting. When so employed in cultural operations, they are designated as seed clams.

In the case of fresh-water mussels an artificial planting likewise would doubtless be more economical of mussels—at least than the planting in nature by fish allowed to go at large. In restocking either privately controlled or publicly owned waters the general procedure that suggests itself is to rear the young mussels to an age of 2 or 3 months or more and then to release them on bottoms that are known to be favorable.

COMMERCIAL POSSIBILITIES.

If the natural supply is not maintained by the means described and the price of shells continues to advance, there will possibly come a time when the rearing of mussels by a complete system of culture will become commercially profitable for individuals and privately owned corporations, whereas now carried out only by Government agencies.[9]

A few experiments have been made to test the palatability of fresh-water mussels. Incomplete and inexhaustive as these tests have been they have yielded encouraging if not completely satisfactory results. Reports of edible species have been received. The use of the mussel for food in addition to the present use of the shell alone would aid greatly in making the culture of mussels commercially profitable. The successful culture of the marine mother-of-pearl shell (*Margaratifera* var. *maxatlantica*) has been described by Dr. C. H. Townsend (1916). Señor Gaston J. Vives, on Espiritu Santo Island, in the Gulf of California, reared these shells on a scale commercially profitable.

The development of an industry of this nature in the culture of fresh-water mussels might be dependent upon the acquirement of property rights on river bottoms suitable for rearing mussels. Precedents for such allotments of water-covered areas are familiar in the leases for oyster beds on our sea coasts. However, the experiments thus far carried out indicate that the culture of mussels may differ to this extent from that commonly employed in America [10] for edible oysters, in that mussels can more conveniently be grown in crates or containers of some sort rather than on open bottom. This is true at least because of the potential migratory nature of the mussel as compared with the sessile habit of the oyster; i. e., it is necessary in the former case to provide for a possible loss of a plant by migration. However, that the recovery of fresh-water mussels may be comparatively easy under some conditions is the testimony of Prof. Isely (1914). He

[9] The possible alternative is the practical extermination of the mussel through excessive fishing either for the mussel itself or its host fish, or both. There have been well-known examples in history of complete extermination of useful species.

[10] In the more intensive cultivation of oysters and clams in Europe containers called ponds, which are in the nature of sluiceways through which flowing water is conducted, have been extensively employed.

was successful in finding a very large percentage of marked mussels months and even over a year after planting. It will be noted that his work was done in small rivers where collection was possible by wading during low water.

Solution of some of the problems still unsolved can doubtless be more directly and economically reached by further investigations of the life history and habitat of mussels and especially of the early juvenile stage. A few of the recent studies along these lines not mentioned in the foregoing pages follow: Allen (1914, 1921) has made a study of the food of lake and river dwelling species. Baker (1916, 1918) has made extensive ecological investigations in Oneida Lake. The author has had the opportunity of making an ecological survey of a portion of the Mississippi River, where mussels are abundant. A report is in preparation putting forth the results of this study of conditions controlling the development of mussel beds and the growth of mussels under such an environment. In general, much more detailed information is required concerning the various elements in an environment favorable to the mussel (see Coker, Shira, Clark, and Howard, 1921), including water content, as substances in solution and in suspension, both food and gases; temperature variations; depth and flow; amount of light; and kind of bottom.

That the conditions favorable to juveniles sometimes differ from those for adults has been indicated. If this is the case, as it is well known to be for many animals, a more complete knowledge of the requirements of the critical postparasitic stage in mussels will certainly contribute to their culture. Perhaps the most pressing problem is the securing of a complete knowledge of their enemies and means of combating these. There are still some commercial species for which the appropriate host is yet undetermined, and in most cases where the host has been determined practically nothing of the manner of infection and like ecological relations is known. The solution of these problems is difficult because dependent upon the observation of phenomena occurring in a medium different from our own. In the case of river mussels this medium owing to turbidity is not readily penetrated by sight. In spite of such difficulties, however, we must agree with Lefevre and Curtis (1912) that among invertebrate animals the Unionidæ, for the variety in economic and scientific interest of the problems they present, are scarcely excelled.

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