An Historical Analysis of Mussel Propagation and Culture:
Research Performed at the Fairport Biological Station

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Clear Creek Historical Research
Ames, Iowa
James Pritchard, Ph.D., Principal Investigator
December 21, 2001

Common Name	Other names	Current scientific name	Previous scientific name
Washboard		*Megalonaias nervosa*	*Quadrula heros*
Winged Mapleleaf		*Quadrula fragosa*	
Monkeyface	Maple-leaf shell	*Quadrula metanevra*	
Wartyback		*Quadrula nodulata*	
Pimpleback		*Quadrula pustulosa*	
Threeridge	Blue-point	*Amblema plicata*	*Quadrula plicata*
Ebonyshell		*Fusconaia ebena*	*Quadrula ebena*
Wabash Pigtoe	Pig-toe	*Fusconaia flava*	*Quadrula trigona*
Round Pigtoe		*Pleurobema sintoxia*	*Quadrula solida*
Paper pondshell		*Utterbackia imbecillis*	*Anodonta imbecillis*
Giant floater		*Pyganodon grandis*	*Anodonta cataracta, Anodonta grandis, Anodonta corpulenta*
Creeper		*Strophitus undulatus*	*Strophitus edentulus*
Flutedshell		*Lasmigona costata*	*Symphynota costata*
Mucket	River mucket	*Actinonaias ligamentina*	*Lampsilis ligamentina, Actinonaias carinata*
Butterfly		*Ellipsaria lineolata*	*Plagiola securis*
Hickorynut		*Obovaria olivaria*	*Obovaria ellipsis*
Black sandshell	Black sand-shell	*Ligumia recta*	*Lampsilis recta*
Pondmussel		*Ligumia subrostrata*	*Lampsilis subrostrata*
Yellow sandshell	Yellow sand-shell, Slough sand-shell	*Lampsilis teres*	*Lampsilis anodontoides, Lampsilis fallaciosa*
Fatmucket	Grass mucket, Lake Pepin mucket	*Lampsilis siliquoidea*	*Lampsilis luteola*
Plain pocketbook		*Lampsilis cardium*	*Lampsilis ventricosa*
Higgins eye	Higgins sandshell	*Lampsilis higginsii*	*Lampsilis higginsi*
Shovelnose sturgeon	Sturgeon	*Scaphrhyncus platorhynchus*	
Short-nosed gar		*Lepisosteus platostomus*	
Freshwater drum	Sheepshead	*Aplodinotus grunniens*	
Skipjack herring		*Alosa chrysochloris*	*Pomolobus chrysochloris*
Sauger		*Stizostedion canadense*	
White Bass		*Morone chrysops*	*Roccus chrysops*
Bluegill	Blue-gill sunfish	*Lepomis macrochirus*	*Lepomis pallidus*
Orangespotted sunfish	Red-spotted sunfish	*Lepomis humilis*	
White crappie	Crappie	*Pomoxis annularis*	
Black crappie		*Pomoxis nigromaculatus*	*Pomoxis sparoides*
Green sunfish	Blue-spotted sunfish	*Lepomis cyanellus*	*Apomotis cyanellus*

Table 1. Common and Scientific Names of Mussels and Fish

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Table of Contents:

Fig. 1. Fairport Biological Station, 1920. From the left, the temporary lab, the tankhouse, the boathouse, shed, and main laboratory. Courtesy Iowa Dept. of Natural Resources, Fairport Fish Hatchery.

Acknowledgments

The author thanks the U.S. Army Corps of Engineers for supporting this project. I am grateful for support and advice from Dr. John Downing, limnologist at Iowa State University. Sincere appreciation is due all the folks who provided important clues that forwarded this treasure hunt, including historian Phil Scarpino, Pam Thiel (USFWS), Kevin Cummings (Illinois Natural History Survey), Bob Howells (Texas Parks and Wildlife Department), Jeff Janvrin (Wisconsin DNR), Dick Neves (Virginia Tech), David H. Stansbery (Ohio State University), Marian Havlik (Malacological Consultants), Sue Bruenderman, (Missouri Dept. of Conservation), and David Heath (Wisconsin DNR). Malacologists including Rafael Araujo, Bill Lellis, Steve Fraley, and Bob Summerfelt helped out with information on test-tube mussels. I express thanks to the many fine folks who took an interest in the history of mussels, including Scott Gritters, Kevin Hanson, Ken Snyder, Warren Johnson, Gary Wege, Kurt Welke, historian Mark Madison, Al Buchanan, and Diane Debinski. I found the Illinois Natural History Survey's Mollusk Collection website helpful in learning about the natural history of mussels as I researched the history of the scientists who worked at the Fairport Biological Laboratory.

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Some of the photographs in this report appear courtesy of the Musser Public Library, which houses the Oscar Grossheim Collection. The photo of Ellis inspecting the bottom samples was provided through the courtesy of Cornelia Motley and Philip Scarpino. The majority of the photographs originally appeared in the *Bulletin of the United States Bureau of Fisheries.* B.G. Isom and R.G. Hudson's 1982 article is reprinted here with the kind permission of *The Nautilus,* associated with the Bailey-Matthews Shell Museum in Sanibel, Florida.

I thank Mark A. Cornish, biologist at the U.S. Army Corps of Engineers, for information reflected in the table of common and scientific names of mussels. I assume responsibility for any errors in the table, which I checked against Turgeon, et al., *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks.* Technical assistance in working with the photographic images and computer programs came from Walter Gilbert, Brenda Van Beek, Liz Weber, Patrick Brown, Christa Gerdes, Alan Vetter, and Adam Pfister. Finally, thanks are extended to the anonymous reviewers that helped improve this report.

James Pritchard
Ames, Iowa
December, 2001

Introduction

The Button Industry and its Hope for Mussel Propagation

As local legend has it, J. F. Boepple cut his foot while swimming in a river, reached down, pulled up a mussel and had a brainstorm. In reality, he had abandoned his established button-cutting business and immigrated from Germany around 1886, having heard about the rich clamming to be had west and south of a city named Chicago. Locals at first seemed unimpressed by Boepple, who claimed "mein buddons vill make you rich!" Within a few years, button manufacture using the shells of freshwater mussels grew by leaps and bounds. Mussel harvesting on the Mississippi began in earnest as early as 1889, and certainly by 1892. The industrial scale of the enterprise, revealed in Iowa photographer Oscar Grossheim's contemporary images, was prodigious. Manufacturers soon sought the most efficient use of raw materials possible, but those measures did not slow the harvest of mussels. When scientist Winterton C. Curtis visited Muscatine in 1907, he reported that "these fellows are doing everything they can to make the most of their material." Competition from foreign markets tempted American manufacturers to emphasize higher quality buttons that made less efficient use of material. Technological innovations, such as the automatic button cutting machine, intensified the pace of exploitation. By 1900, nearly 50 percent of buttons manufactured in the U.S. came from freshwater mussels.[1]

Fig. 2. Mountains of shells rose up alongside the Mississippi as clammers made a living harvesting mussels to supply the button industry. From the Oscar Grossheim Collection, courtesy Musser Public Library, Muscatine, Iowa.

Intense harvesting pressure caused noticeable drops in mussel populations in as few as three years, and by 1899 the impact was generally acknowledged. In a scene repeated all over the Midwest, a single mussel bed (measuring less than .75 square kilometer) near New Boston, Illinois, that had produced more than 9,000 metric tons of shells from 1894 to 1897, was exhausted and abandoned by 1899. Older and larger mussels became a smaller proportion of harvest, and by 1914, less valuable shells (less than five centimeters long) comprised 60 percent of the catch. Maintaining the same level of button production required more of the smaller-sized mussels (about 3,200 10 cm *Fusconaia ebena* shells weighed 900 kg, whereas about 20,000 5 cm shells weighed 900 kg). The rate of depletion only increased over time as the mussel beds were efficiently and repeatedly

scoured by crowfoot bar, dip net, and dredge. In 1898, Dr. Hugh M. Smith (later Director of the U.S. Bureau of Fisheries) published his investigation of the mussel fishery and the pearl button industry on the Mississippi. He described the process of harvesting mussels from beds in the river, emptying the shells, drilling rounds out of the shells, and transforming those rough disks into finished buttons. Smith adamantly warned that some action would have to be taken to conserve the resource, or certain commercial species would be wiped out. Industrialists who owned the button factories and the many workers who harvested the mussels, drilled the shells, and finally shaped and packaged the buttons all had an interest in preserving the mussel harvest.[2]

As Arthur F. McEvoy points out in his book *The Fisherman's Problem: Ecology and Law in the California Fisheries 1850-1980,* stresses on a fishery "manifested themselves in friction between different participants in the industry and . . . between industry and government. By 1911, tension was high in Muscatine as the button workers went out on strike, prompting local officials to call in the army. As for Boepple, by 1907 he experienced "straightened circumstances." W.C. Curtis wrote that Boepple was "in no way suited for the competition and necessities for executive ability which exist to-day." In his earlier prosperity, Boepple had contributed his time and money "to furthering the permanent interest of the entire industry," and had also shown a "real scientific interest in his fight against the wasteful methods of collecting and using raw materiel . . . ." Curtis vigorously supported hiring Boepple for consultation and assistance with mussel surveys.[3]

The button industry reached its maximum production in 1916, when the U.S. produced more than 40,000,000 gross buttons that were valued at more than $175,000,000 (1998 $US). Around 1925, the industry began to decline. Various causes contributed, including labor issues and competition with foreign markets, but not least among the sources of trouble for the button industry was the decline of mussel harvests.

A Biological Laboratory for the Midwest

Worries over declining mussel harvests prompted the establishment of the U.S. Bureau of Fisheries' Biological Station at Fairport, Iowa. Three groups cooperated to create the laboratory: leaders from the button manufacturers, government officials (most notably associated with the U.S. Bureau of Fisheries), and zoologists at the University of Missouri. Considerable overlap existed between the scientists and government, as the Bureau of Fisheries employed well-qualified scientists on a full and part-time basis. The activities of all three groups, separately and in concert, helped create the laboratory.

The Fairport Station opened in 1914 with the strong support of the captains of the pearl button industry located in Muscatine, Iowa. Leaders of manufacturing enterprises generally believed (as did fisheries officials) that if the scientists could rear young mussels in quantity and release them into the beds, higher harvest levels would be maintained. Thus they envisioned a sort of put, grow, and take mussel fishery, in much the same way that the U.S. Bureau of Fisheries conceived of fish propagation and rearing.

The U.S. Bureau of Fisheries was an important institution for Progressive era conservation. At the same time that Gifford Pinchot sought to use scientific principles to rationalize forest resource use, so a conservation-oriented government sought to rationalize and improve fisheries. The ideas of eliminating waste, putting resources on planned schedules of harvest and renewal, and the use of resources for the public good proved compelling rationales during Teddy Roosevelt's presidential administration. Finally, scientists working for the Bureau (more so than academic ecologists often emphasized in the histories we read) also provided a primary motivating force in conceptualizing and building the biological station at Fairport. The development of practical applications involved scientific questions that required scientific expertise.[4]

Three major efforts to propagate mussels

Some of the original techniques for the propagation of fresh-water mussels were pioneered in conjunction with the creation of Fairport Laboratory by Winterton C. Curtis and George Lefevre, from 1908 to about 1914. This first phase gave hope for success in the lab and for industry. The first director of the Fairport Laboratory, Robert E. Coker, further developed those techniques through the late 1920s. Generally speaking, scientists under Coker's direction during this second phase seemed to have success with propagation both in the river and in land-side troughs, tanks, and ponds. By 1920, Fairport scientists claimed to have infected six million fish with 478,705,000 glochidia, and by 1923, they successfully reared half a million mussels in troughs. In 1922, Coker declared that the Lake Pepin Mucket *(Lampsilis luteola)* "can be reared in quantities, under conditions of control." During a third period centering in the 1930s, Max Mapes Ellis claimed success for his more artificial methods of propagating freshwater mussels. Despite these continuing claims of progress, mussel propagation was a tricky business at best, and conveying the successes of the laboratory into the field presented new challenges.[5]

Part of the difficulty in attaining success was the button industry's desire that mussels be produced in prodigious quantity. The major bottleneck for mussel reproduction in the river, scientists believed, was the juvenile (glochidia) stage. If humans could propagate glochidia in great numbers, the founders of the station believed, the number of young mussels would increase and the problems of the industries that relied on mussels would be over. Overcoming this limitation in the stream of production and use became the scientific and technological question, as well as an obsession for physiologist Max Mapes Ellis.

Two things are immediately striking about the idea of propagating mussels from 1908 to 1941. First, button manufacturers, as well as scientists and the Bureau of Fisheries, adopted an industrial model in thinking about river resources. If humans harvested the mussels, it was a technical matter to supply nature with the raw material to ensure future bountiful harvests. Given the tenor of the times, with its firm faith in progress and the power of technology, it made sense. Yet the industrial model also limited thinking about what sort of problems needed to be addressed. It was the zoologists who transformed understanding of the river. Second, the scientists who worked on mussel propagation came to understand the problem in broader terms than originally conceived. They all began by considering the technical problems of improving effective infection rates of glochidia and the survival rates of juvenile mussels in captivity. Lefevre, Curtis, Coker and Ellis went on to consider changes in Mississippi river structure and ecology, as well as the effects of pollution on mussel populations. During the formative years of American plant and animal ecology, these scientists found a compelling case study in the Mississippi River.

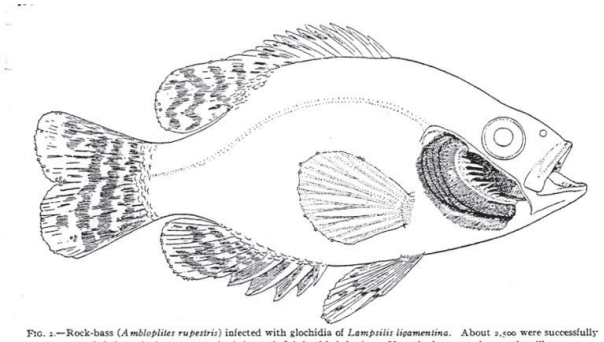

FIG. 2.—Rock-bass (*Ambloplites rupestris*) infected with glochidia of *Lampsilis lipamentina*. About 2,500 were successfully carried through the metamorphosis by each fish in this infection. Note the large number on the gills.

Fig. 3. Rock Bass showing gill and fin infection. From Lefevre & Curtis, "Studies" (1910).

Timeline

1904 George Lefevre seeks U.S. Bureau of Fisheries (USBF) funding for his mussel work
1907 Winterton Curtis visits button industry folks in Muscatine Iowa (June)
1908 Funds appropriated by Congress for construction at Fairport
Major surveys of mussels in river systems underway
1910 Lefevre and Curtis publish "Reproduction and Parasitism" in *J. Experimental Zoology*
Lefevre and Curtis publish "Studies on the . . . Artificial Propagation"
Robert E. Coker appointed Director of the Fairport Biological Station
1914 Dedication of laboratory building at Fairport (August 4)
1914 Arthur Day Howard's "Experiments in Propagation" published
1915 Thaddeus Surber publishes "Notes on the Natural Hosts"
Coker appointed director of USBF Division of Scientific Inquiry
1917 Laboratory building destroyed by fire (December 20)
1919 First trials with sectional closures of Lake Pepin
1921 New Fairport laboratory building dedicated
1922 Coker, Shira, Clark & Howard publish "Natural History and Propagation"
1925 Max Ellis begins working on mussels in association with Fairport
1926 Ellis publishes claim regarding nutritive solution in *Science*
1927 Ellis visits European laboratories
1930 Pollution effects are obvious, siltation in Mississippi River a noted problem
USBF emphasizes "Ellis method"
1932 Pollution studies underway, Ellis supervises "Investigations in Interior Waters"
Raceways built at Fort Worth Station, Ellis begins to move his work to Texas
1934 Funds for mussel culture at Fairport dry up
1940 U.S. Bureau of Fisheries reorganized as U.S. Fish and Wildlife Service
1942 USFWS cuts off funds for Ellis's mussel propagation

Lefevre and Curtis

Early work on artificial propagation of fresh-water mussels on the Mississippi River was performed by George Lefevre and Winterton C. Curtis, professors of zoology at the University of Missouri. R.E. Coker later called their work "extensive and admirable." Lefevre and Curtis cited prior work on the life cycles of mussels & glochidia, including Leeuwenhoek, Poupart (1706), Rathke (1797), Pfeiffer (1821), Jacobson (1828), De Blainville (1828), Carus (1832), De Quatrefages (1836), Leydig (1866), Flemming (1875), Braun (1878), Schmidt (1885), Schierholz (1878 & 1888), Lillie (1895), Latter (1891, 1904), and Harms (1907 & 1909). Glochidia had been observed as early as 1695 in the gills of European mussels, and was thought to be the larval mussel form, but so little was known that in 1797 a writer suggested the glochidia were actually parasites on mussels, and gave them the name Glochidium parasiticum. Even a special committee of the Paris Academy of Sciences in 1828 did not dismiss this Glochidium theory. In 1832, Carus observed eggs passing from the ovary into the mussel gill pouches, and the mechanism became clear, although the

name glochidia stuck. In 1866, Leydig discovered glochidia embedded on the fins of fish, and thus the essential fact of mussels' parasitic stage was revealed. Braun (1878), Schmidt (1885), Schierholz (1878-78) and Harms (1907-09) took that clue and studied mussel life stages and the course of parasitism from glochidium to the miniature adult. These last four scientists "obtained their material in great abundance by the artificial infection of fish" with glochidia. These previous studies laid out the basics of mussel reproduction, but in 1907 mysteries remained, for example, exactly which species of host fish were required for each sort of glochidia.[6]

It's important to note the close connection between the Department of Zoology at the University of Missouri and the Marine Biological Laboratory (MBL) at Woods Hole, Massachusetts, and therefore the close ties between Lefevre and Curtis, developments in embryology, and the operations of the U.S. Bureau of Fisheries. What's important is that the work and the people at Woods Hole were leading the way in the development of experimental biology in America. William Keith Brooks, an important figure in embryology, had urged Winterton Curtis to study "something important" for his dissertation, such as mollusks. Curtis began his connection with the MBL as a student in the invertebrate zoology course. In 1897 he became an assistant collector, in 1898 an investigator at MBL, in 1899-1903 a member of the Invertebrate Staff, and from 1908 to 1911 he was appointed an instructor in charge, continuing to spend summers there after 1911. So by 1899, Curtis was already experimenting with propagating mussels, infecting carp with *Anodonta* and *Symphynota.* He performed that and later work associated with the Mississippi River specimens at the amply equipped laboratory at Woods Hole, where he rubbed shoulders on a daily basis with leading scientists who were introducing the rigor of experiment to biological studies. When Curtis was appointed to the zoology faculty at the University of Missouri in 1901, some wondered why it was necessary to hire a Yankee. Before the mussel investigation on the Mississippi, he wrote on planarians and marine cestodes.[7]

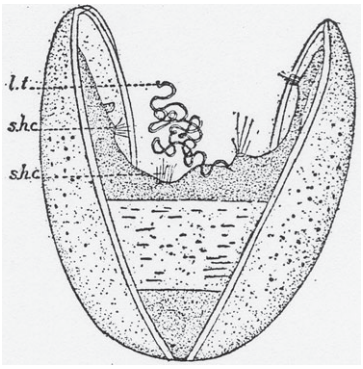

Fig. 4. Glochidia of *Quadrula Heros* with larval thread. From Coker et al., (1922), p. 143.

Lefevre was appointed a professor of zoology at the University of Missouri in 1899, served as chair of the Zoology Department from 1899 until his death in 1923, served on the MBL Board of Trustees from 1909, and was Secretary to MBL staff from 1913. Curtis called Lefevre "a princely entertainer," and his affable nature (Lefevre said "agreement is no criterion of friendship") served him well as he connected with people up and down the Mississippi during the mussel research.[8]

In August of 1904, George Lefevre got the whole thing started when he addressed a letter to Barton W. Evermann at the U.S. Bureau of Fisheries. Lefevre wrote of his "intention next year to begin an extended series of observation and experiments on the growth, general ecology and propagation of the fresh water mussels of Missouri," and asked if the Bureau would financially support such work, beginning with the construction of tanks. Clearly aware of issues beyond the laboratory, Lefevre wrote "it would seem possible to materially influence the supply of those species that are of special economic value." Evermann responded with enthusiasm, and invited Lefevre to propose a plan. In November of 1905, Lefevre reported that the investigation was "well underway, and we are pushing the work as energetically as possible. We expect soon to infect fish in large numbers and liberate them in favorable localities where the results can be kept under observation." In practice, it took years to achieve that goal. It's suggestive that the five articles Lefevre requested

from the libraries of the nation's capital were all written in German–fresh water mussels were still largely unknown to American scientists.[9]

By January of 1906, Lefevre was writing to button manufacturers advertising not a study, but a "scientific investigation" of the embryology of freshwater mussels in the Mississippi River Valley, with an eye to propagate them in new localities and restoring them to places where they had been exterminated. In short, he was seeking specimens directly from the sources of industrial supply. A tentative plan dated April 20, 1907, called for examining the geographic distribution of mussels, their habits (including what today we'd call ecology and population biology), and experiments in artificial propagation to be carried out in the lab at Columbia, Missouri. In June, 1907, Curtis visited Muscatine, with a list of 24 questions in hand. He interviewed at least fourteen manufacturers and individuals, gathering all sorts of basic information including prices (doubled in seven years), and people's opinion on why the mussel fishery had declined (most thought overfishing the cause). He noted that manufacturers tried to use harvested shells in the most efficient manner possible, one of them saying "we would fight our men all the time over that," and telling Curtis that it was regular practice to pay the cutters extra money for expert and careful work that yielded the greatest possible number of button blanks from each shell. Indeed, "efficiency" was the watchword of this era.[10]

From September through November 1907, they carried out preliminary experiments with infection. Sources of mussels were carefully labeled by lot number, and each experiment (or batch, trial) was documented with a card. For example, in one experiment they infected seven small bass with glochidia of "species A," leaving the fish in a dish with glochida for one-half hour. *Quadrula fragosa,* unfortunately, doesn't show up in the surviving lab data. In 1907, they did refer to *Quadrula metanevra* (Monkeyface) as the "maple leaf shell." So there may be some confusion for us here. Additional references to the maple leaf shell include a letter from the D.W. MacWillie of the Wisconsin Pearl Button Co to Professor Curtis in November of 1917. He wrote that the shells Curtis had sent had arrived, identifying them as maple leaf shells, "not quite as good as the [ebonyshells] on account of the prominent ridges," but they worked up very nicely to a bright luster and were not very brittle. Ebonyshells, previously listed as *Quadrula ebenus* (Lea, 1831), were a preferred species for button manufacture, and today are known as *Fusconaia ebena*.[11]

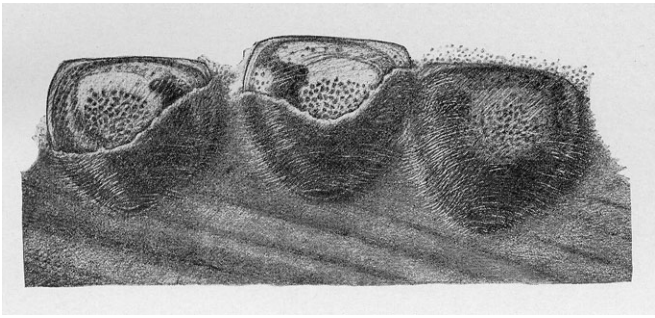

Fig. 5. Glochidia on host fish showing stages of encystment. From Lefevre and Curtis "Studies," (1910), plate 10.

In 1908, Lefevre and Curtis focused their attention on the *Unionidae* of the Mississippi River system, carrying out a field season that summer on the upper Mississippi. Their plan for 1908 was ambitious–to survey not only the upper Mississippi but also the Iowa River, Minnesota River, the Grand river in Michigan, the Yellow River in Indiana, the Wabash River, Deer Creek and Wildcat Creek in Indiana, and the Miami River in Ohio. It's not clear whether they fully carried out their impressive plans for infecting host fish and releasing glochidia. They utilized a small building with tanks in La Crosse, Wisconsin, owned by the Bureau of Fisheries, and also worked aboard the steamship *Curlew,* a vessel used in the Bureau's fish rescue operations. The first thing they did was gather specimens for examination. Lefevre and Curtis investigated the stages of mussel reproduction in the *Unionidae,* particularly the parasitic stage, reporting their results in 1910. Their work

gathered basic information about mussels and their life cycle, for example the general timing of spawning, length of gravid period, exact mechanism of fertilization, conglutination of the embryos, structure of the marsupium, structure of the glochidia, and the mechanisms of their parasitism.[12]

Fig. 6. Crew members working with Lefeve and Curtis dredging in a slough near La Crosse as they survey mussel beds in the Midwest. Fig. 68 in Lefevre and Curtis, "Studies" (1910).

They spent a lot of time figuring out the spawning period of mussels. Surviving laboratory records demonstrate that they were out on the river near La Crosse collecting mussels every few days, especially from May to August, noting the number of each species collected on which day, and in what reproductive state–male or female, gravid, with early or late embryos, or bearing glochidia (see sample breeding record in addenda). Although they examined many species, no data sheet now exists for *Quadrula fragosa.* For *Quadrula metanevra* they found 68 not gravid (mostly July 9-August 11), 18 early embryo, 8 late embryo, and 4 with glochidia. We mention *metanevra* because while they listed *fragosa* in at least one place, they also referred to *metanevra* as the Maple Leaf shell. Commercial shellers would sometimes lump the entire genus *Quadrula* together as "mapleleafs," because they couldn't tell them apart. For *Quadrula ebena,* a particularly desirable commercial species, over the season they examined 167 not gravid, 206 with early and 95 with late embryos, and 23 with glochidia. During 1907 and 1908, they inspected 4,641 specimens of 34 species to compile their breeding record data. These data sheets show they found few *L. higginsii:* one not gravid on July 10, another on the 19th and two not gravid on the 22nd, and one with early embryos on August 3, 1908. Of *L. higginsii* Lea, Curtis noted that the marsupium is at the posterior portion of the outer gill, that the glochidia have never been observed, named four locations where they had found *L. higginsii* including Winona and Homer. The only breeding record was one female on August 3, 1908, which contained embryos in late cleavage state. *Quadrula fragosa* is not found in these data sheets, but *Quadrula metanevra* was found: 68 not gravid (mostly July 9-August 11), 18 early embryo, 8 late embryos and four with glochidia, all near La Crosse.[13]

They noted something particular to all species of *Quadrula* they collected–every one "that came into our hands exhibited to a greater or less degree the habit of aborting embryos and glochida, when taken out of the river." This accounted for the fact that gravid mussels had not been observed for some species. They found it necessary to examine specimens of *Quadrula* immediately to determine the condition of the marsupium.[14]

Lefevre and Curtis noted that the glochidia of *Lampsilis* and *Quadrula,* like six other genera, were hookless, becoming attached to the gill filaments. They argued that the larval thread was not a

conspicuous feature of all glochidia, at least not in North America. They pointed out the "inexcusable error" in texts claiming that glochidia (upon release from the marsupium) swam about by clapping together their valves. To the contrary, "as is now well known," glochidia were "entirely

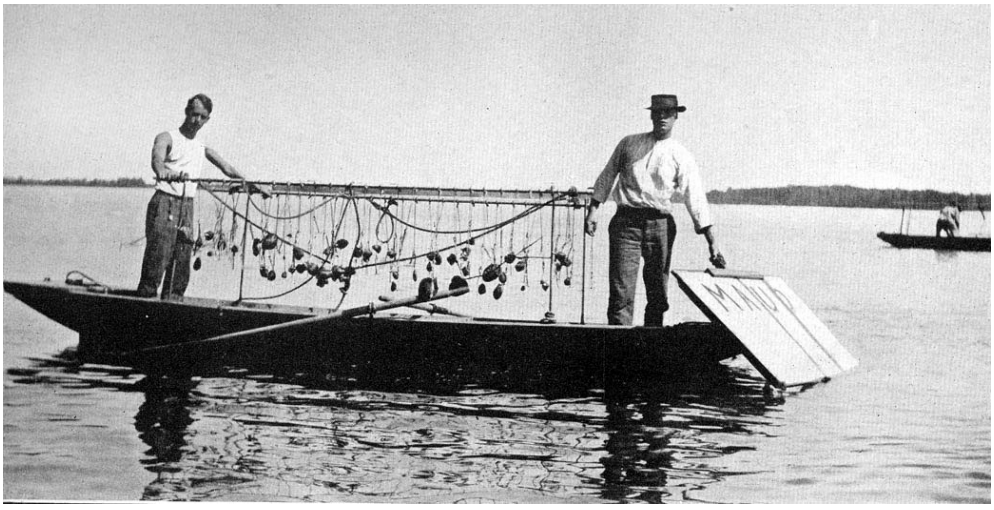

Fig. 7. The crowfoot bar was employed by scientists as well as clammers. Scientists gathered specimens themselves, but also procured mussels from fishermen. From Lefevre and Curtis, "Studies" (1910), fig. 69.

incapable of locomotion and remain in the spot where they happen to fall."[15]

Given the later work of Ellis, their observations regarding fish blood seem worthy of note. O.H. Latter had observed that the tail of a Stickleback thrust into a tank threw the glochidia into "the wildest agitation" for a few seconds. Lefevre and Curtis tested glochidia "both with fins and gills of different fishes, and, provided that a bleeding surface is not brought in contact with the water containing the glochidia, absolutely no response . . . takes place." The glochidia in their tests were "thrown into rapid and violent contractions, alternating with relaxations," snapping for ten to fifty seconds. When hookless glochidia were taken up by host fish and lodged in gill-filaments, "abrasions of the delicate epithelium . . . always occur and produce more or less extensive hemorrhage from the blood capillaries." It seemed evident that blood exuded at this moment must "be efficacious in bringing about a firm and permanent attachment to the filaments." Interestingly, diluted sea-water and solutions (0.5 to 1.0 per cent of NaCl, K4Cl, Kcl and NH4Cl had the same effect as the fish blood.[16]

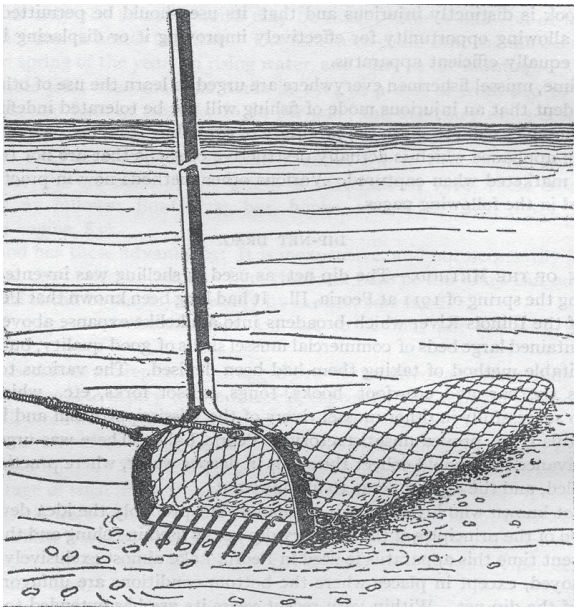

Fig. 8. Dipnet used to collect mussels. From Coker, "Mussel industries" in *Bulletin* (1917-18), fig. 4.

From the beginning, it appears Lefevre and Curtis got involved in the business of fish rescue. Collecting fish from sloughs near La Crosse, Wisconsin, handling over 25,000 fish and noting

natural infections of one to twenty glochidia per fish. Demonstrating the preliminary nature of research into mussels, the "only infections which we have ever observed in nature" were *Anodonta grandis,* infecting six different species of fish.

Lefevre and Curtis looked to "points in the life history where wholesale destruction of the individuals is most likely to occur." Nature, they surmised, was entirely too wasteful. Glochidia, simply dispersed about on the river bottom, involved too much chance, few of them finding a place on a host fish. This wasteful habit of nature yielded a bottleneck in production. Luckily, "Nature is prodigal with the supply of glochidia." Lefevre and Curtis judged that fish could carry many more glochidia than usually found in nature; one fish in the lab might be induced to carry as many glochidia as one thousand fish in their natural state. Taking those two points, "the point of attack for artificial propagation is clear. The fish must be made to carry more glochidia."[17]

Small Fish, Shallow Dishes

Lefevre and Curtis experimented with fish fewer than 6 inches in length, because they were easy to catch and to keep (see "The Parasitism" in addenda). Hookless glochidia also stood a better chance to attach to the fins of smaller fish. They followed in the footsteps of artificial propagation "as practiced since the work of" German scientists W. Harms, M. Braun (1878) and F. Schmidt (1885). They placed fish in small receptacles, or shallow dishes just deep enough to cover the fish, into which they added glochidia washed "from the gills of the clams." The motion of active fish like the rock bass *(Ambloplites rupestris)* and the large-mouthed black bass *(Micropterus salmoides)* kept the water "so well agitated" that the glochidia remained in suspension, yielding "tolerably constant results." Active fish such as rock bass stirred up the glochidia more, whereas quieter fish like the crappie *(Pomoxis annularis)* needed someone stirring up the water to promote infection. Shallow water helped because it kept the fish near the bottom, touching or stirring up the glochidia on their own. Fin infections could be carried out with sluggish fish like the German carp *(Cyprinus carpio),* and the darters *(Ethoeostoma coerleum spectabile)* that habitually rested on the bottom received glochidia on fin and gill yet seemed to be able to throw them off as well.[18]

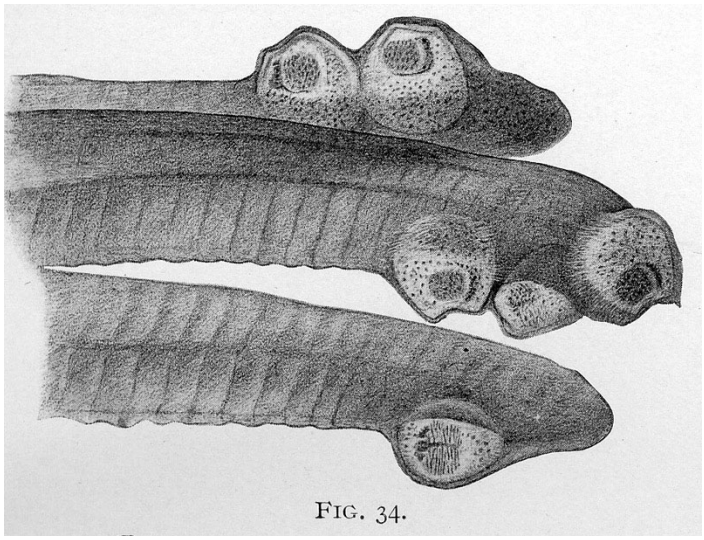

Fig. 9. Gill filaments of the rock bass infected with glochidia of *Lampsilis ligamentina.* From Lefevre and Curtis, "Studies" (1910), fig. 34.

Lefevre and Curtis were very much interested in the precise mechanisms of glochidia attachment, and studied attachment to both gills and fins. For infections with hooked glochidia, they used mostly *Anodonta cataracta* imported from Falmouth, Massachusetts, infected into German carp. They also tried other host fish for the hooked glochidia of *Symphynota complanata* and *S. costata.* Yet the hookless glochidia of species of commercial interest occupied their main attention. Species of *Lampsilis (ligamentinus, rectus, anodontoides, ventricosus, subrostratus,* and *luteolus)* were used mostly, and then a smaller number performed with a few species of *Quadrula* and one species of *Unio* (see sample record of infection experiment and Table 1, in addenda). They

used a wider variety of host fish compared to the hooked glochidia work. The hookless glochidia of *Lampsilis*, they noted, had been used successfully for infecting blue-gill sunfish *(Lepomis pallidus),* yellow perch *(Perca flavescens),* crappie, large-mouth black bass, rock bass, red-spotted sunfish *(Lepomis humilis),* and the green sunfish *(Apomotis cyanellus).* In a 1908 account of their work seeking to enhance laboratory infections, they mentioned "stimulation by weak solutions of sodium oxalate, sodium chloride, and other salts" as they hoped that "a rhythmic contraction of the adductor muscle in the hookless glochidia can be brought about by chemical means."[19]

The scientists used small numbers of fish in the lab but believed their methods could be used with larger numbers of fish. In 1907, Lefevre and Curtis took 25,000 fish under 6 inches at the Bureau's substation in La Crosse Wisconsin, infecting 12,000 blue-gill sunfish, 3,700 yellow perch, 7,000 catfish, 2,000 crappie, 150 rock bass, 150 carp, and 100 roach *(Abramis crysoleucas).* They infected most of those fish with glochidia of *Lampsilis ligamentina*. Smaller numbers of fish were infected with *L. anodontoides* and *L. recta.*

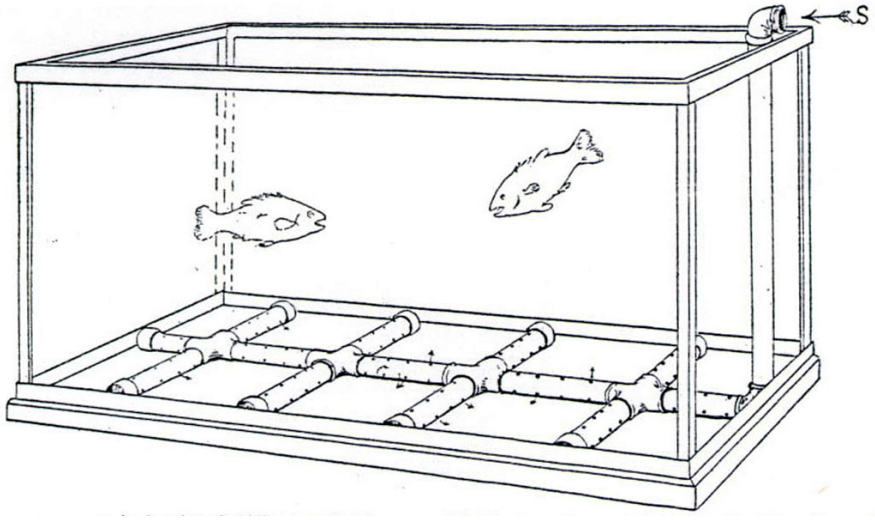

Fig. 10. Laboratory apparatus for keeping glochidia in suspension during infection. From Lefevre and Curtis, "Studies" (1910).

They had the best results from placing "100 to 200 fish in a common galvanized iron washtub about two-thirds full of water." Using the glochidia from two or three specimens of *Lampsilis,* they stirred the water by hand when it seemed necessary, getting "tolerably constant results." They claimed it was possible to use the same tub several times without changing the water or adding glochidia. They tried using a method similar to their lab technique, lowering the water level to 4 inches with the same number of fish, finding this "quite inadequate" and so returned the fish to the tubs to infect them. This experience seems to argue against their lesson learned in the lab, but here they were dealing with batches of 200 fish instead of a few.[20]

The Problem of Over-infection

Despite their enthusiasm for the number of glochidia fish might be forced to carry with the assistance of human device, Lefevre and Curtis warned against over-infecting fish, a problem that presented costs in fish mortality. Over-infection, they wrote, is "easily accomplished and easily fatal," but the limit wasn't clear because different species of fish varied in their ability to carry numbers of glochidia. Fins infected by glochidia showed swelling that prevented normal function. Gills showed similar problems. In one of their more successful experiments matching rock bass with *Lampsilis ligamentina,* Lefevre and Curtis noted that 4 inch fish carried around 2,500 glochidia, an average of more than two for each gill filament, yet they evinced surprisingly little mortality. They suggested that for every seven glochidia that had attached to the end of a gill-filament, one had attached on the side of the filament, and "thus the greater part of very filament was left unchanged

and in full functional condition." Much higher mortality was found in infections such as *L. ligamentina* on large-mouthed black bass where many glochidia attached themselves to the sides of gill filaments, even though the number of infecting glochidia was much less.[21]

Infected fish from a demonstration project were kept six weeks, and then some were released into the west channel of the Mississippi River at La Crosse. The scientists shipped some of the remaining fish to Columbia, Missouri, for laboratory examination, noting results were "probably as favorable as could have been expected under the circumstances."[22]

Lefevre and Curtis tried again in December 1908, infecting 6,200 large-mouth black bass and 3,800 crappie with glochidia of *Lampsilis ligamentina* (and fewer numbers with *L. anodontoides, recta,* and *ventricosa)* in the Bureau's station in Manchester, Iowa. Dosing the tanks with the same numbers of glochidia they had tried in Wisconsin, they discovered the large-mouth rock bass suffered 55 percent mortality during the next 30 days. By the third day of infection, gill hypertrophy was visible to the eye, "clearly the cause of death." They recommended 1,000 glochidia per fish rather than the 2,000-2,500 used in this trial. The crappie did not fare well either, and the scientists considered it unfit for this use. Surviving fish were released in the Maquoketa River near Manchester, Iowa.[23]

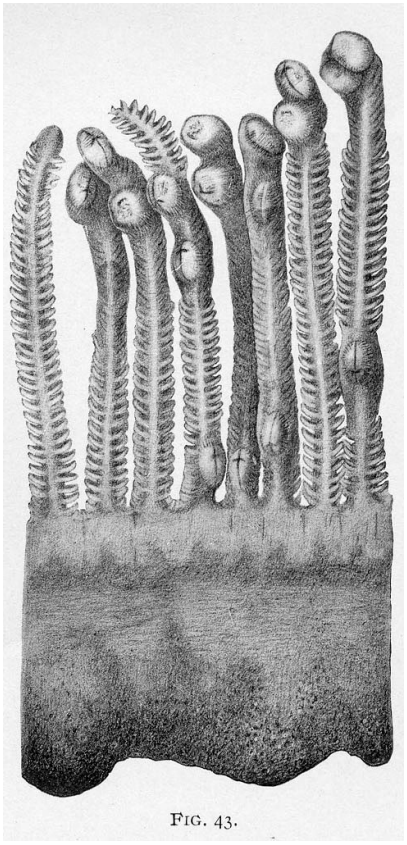
FIG. 43.

Fig. 11. Black bass gill infected "above the optimum" with L. ligamentina. Fig. 43 in Lefevre and Curtis, "Studies" (1910).

Field Trials

From surviving lab records, it's clear that Lefevre and Curtis placed young mussels obtained from their infection experiments into cages and hence into the river, from June 29 to August 10, 1908. Mussels were measured before at least eleven of these cages were placed in the West Channel near La Crosse and secured to bridge pilings. In November, 1910, Coker found 2 of the 11 cages. One cage had been buried in mud, perhaps shortly after the planting, for the mussels showed little growth. Six living mussels were found in the other cage, namely 3 *Lampsilis ventricosa,* one *Obovaria ellipsis,* one *Quadrula solida,* and one *Anodonta imbecillis.* These mussels had grown from 172 to 233 per cent in length and height, and from 770 to 880 per cent in weight.[24]

Lefevre and Curtis were excited by their discovery of a single live individual of *Lampsilis ventricosa,* found in the sand of a tank in Columbia Missouri, where the scientists had placed black bass infected with glochidia from *Lampsilis ligamentina, L. ventricosa,* and *L. recta* at Manchester, Iowa. They claimed it was the "first fresh-water mussel actually reared artificially from the glochidium." It was still alive two years later in June, 1911, but had grown to only 41 x 30 mm. Tap water from deep wells supplied its tank, which contained "little that a mussel could utilize as food," accounting for its slow growth. This mussel "added further luster to its fame" by dying on the 4th of July, 1911.[25]

Although their work focused on scientific study, Lefevre and Curtis also kept in mind the importance of practical demonstrations that might indicate the possibility of working with larger numbers of fish and glochidia. On January 28, 1908, the Manchester (Iowa) Station released fish

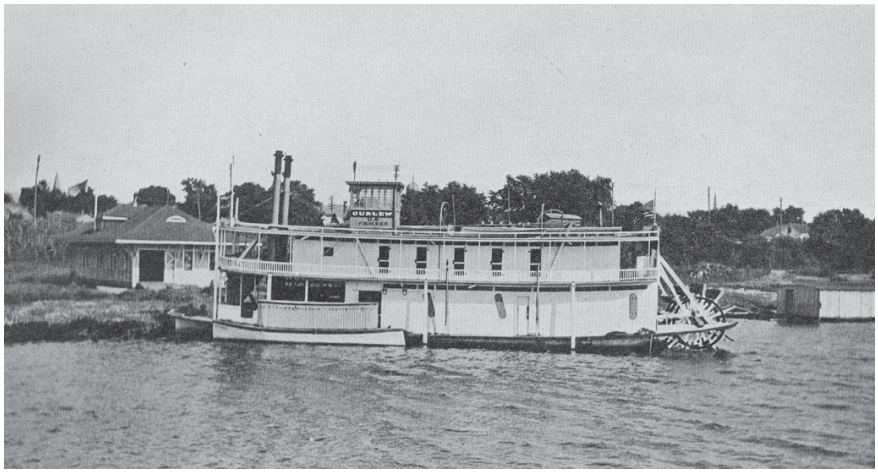

Fig. 12. "Station of the Bureau of Fisheries at North La Crosse, Wisconsin, and steamer Curlew, summer of 1908." Fig. 69 in Lefevre and Curtis, "Studies" (1910).

into the West Channel of the Mississippi River opposite La Crosse, two months after infection. Pushing the scientists to release fish, Commissioner Hugh Smith wrote to Lefevre, inquiring after the fish and asking if they were to be released after the scientists were done with their mussel infection experiments. It's a bit unclear whether Smith was more worried about the fish that had been rescued, or the mussels. Lefevre's response mentions releasing fish infected at Manchester into the river between two dams (in 1908, he may have been referring to the Maquoketa River between Manchester and Delhi, or perhaps to wing dams on the Mississippi). Lefevre also cautioned that the current run of experiments put mussels in cages with the intention of measuring their development, not to breed and release. An intentional program of propagation and release was still in its infancy. In 1908 when Lefevre and Curtis used the term "plant," they sometimes meant placing their propagated mussels into the river environment under the scientists' control. They also used the term "plant" in discussing the infection and release of host fish carrying glochidia. By December 1908, they were planning to release infected fish in the Maquoketa River in Iowa. On December 19, 1908, Commissioner Smith clarified his expectation that fish sent to Lefevre for inoculation would be "planted in the waters where they will thrive and produce results in addition to serving as hosts for the glochidia."[26]

In 1909, Lefevre and Curtis planned a field season that would investigate the White River of Missouri and Arkansas. There is evidence that W.I. Utterback, who became a well-known malacologist, was assisting with the field work by the summer of 1911.

Metamorphosis without Parasitism in *Strophitus.*

One of the Unionidae, the genus *Strophitus* Rafinesque was found to metamorphose without a parasitic period. The embryos and glochidia were known to be embedded in short cylindrical cords that were discharged the exhalent siphon. Lefevre and Curtis were lucky enough to observe a single *Stophitus edentulus* discharging its cords in February of 1911. Young mussels that developed within the cords and stayed there until the cords disintegrated survived, those that somehow got out too early did not survive. The survivors displayed all the structures that young mussels dropping off their host fish possessed.

At the suggestion of a student, L.E. Thatcher, Lefevre and Curtis tried to rear the larvae through the metamorphosis with an artificial nutritive medium. Although they encountered no success, they continued experimenting. Fish blood was used in most experimental trials, as it seemed to provide "the most favorable nutritive conditions." They took glochidia of *Lampsilis ligamentina* and *L. subrostrata* from the marsupium, washing them several times in distilled water to

remove bacteria. Glochidia were dropped into a drop of fish blood on a glass slide, then sealed under glass and Vaseline. If not infected by bacteria or infusoria, the glochidia lived for a few days, but then perished without sign of development. They tried other nutritive media, including blood of the frog and Necturus, and extracts of fish's tissues, bouillon and "other nutritive media," but without success. Lefevre and Curtis speculated that insufficient aeration was the problem. These experiments are of interest because Max Ellis later continued them and claimed success.[27]

Self-assessment

Lefevre and Curtis thought that their technique might be expanded to larger production methods. It was simply a matter of finding the most suitable fish and discovering methods to handle them in quantity. They felt a crucial item would be a device to create uniform distribution of glochidia in the water for the entire exposure period. They tried a propeller rotated slowly by hand in the bottom of a tub, which didn't work very well. They also tried a promising system of iron pipes with many holes that forced jets of water out at the tank bottom, swirling the glochidia upwards.

Fig. 13. "Interior of station at North La Cross, equipped as a laboratory."
Fig. 66 in Lefevre and Curtis, "Studies" (1910).

Lefevre and Curtis argued three things were important: "the uniform suspension of the glochidia," the reaction of the glochidia when they touched the host, and the reaction of the fish's tissues after attachment. They suggested working with small numbers first, examining sample fish with a microscope until it became clear the desired level of infection had been reached. They gave some numbers for infection time, such as rock bass exposed for 30-40 minutes had 2,000 to 2,500 on the gills of each fish; large-mouth black bass exposed 15-20 minutes showed 500-1,000 on gills; crappie exposed 20-30 minutes had 200-400 on gills, yellow perch exposed 20 minutes had 400-600 on gills, German carp (using Anodonta) exposed 30-40 minutes had 200-500 on fins. The parasitic period, they noted, depended on temperature, with shorter maturation periods given a higher temperature. In their trials, they measured parasitic periods from 12 to 25 days, although at lower temperatures they recorded a 74 day maturation period for *S. costata.*

Lefevre and Curtis had commercial applications very much in mind. On August 6, 1907, they presented their "Statement of the Principal Facts in the Life History of Our Freshwater Mussels

and of the Means Proposed for Increasing the Supply" to the National Association of Pearl Button Manufacturers' meeting in Chicago, Illinois. In their 1908 field season, Lefevre and Curtis had placed 163 small mussels of eight genera within wire cages (put into the river & tied to a bridge) in an attempt to find out their growth rates. The upshot was that "commercial mussels may reach a marketable size in three years from the time they leave the fish." Noting that *Lampsilis* reached marketable size faster than species of *Quadrula,* they speculated that even slow-growing mussels such as *Quadrula ebena* (20-30 years to maturation) might be hurried along toward useful size if science could just discover the necessary conditions to render the maximum rate of growth.[28]

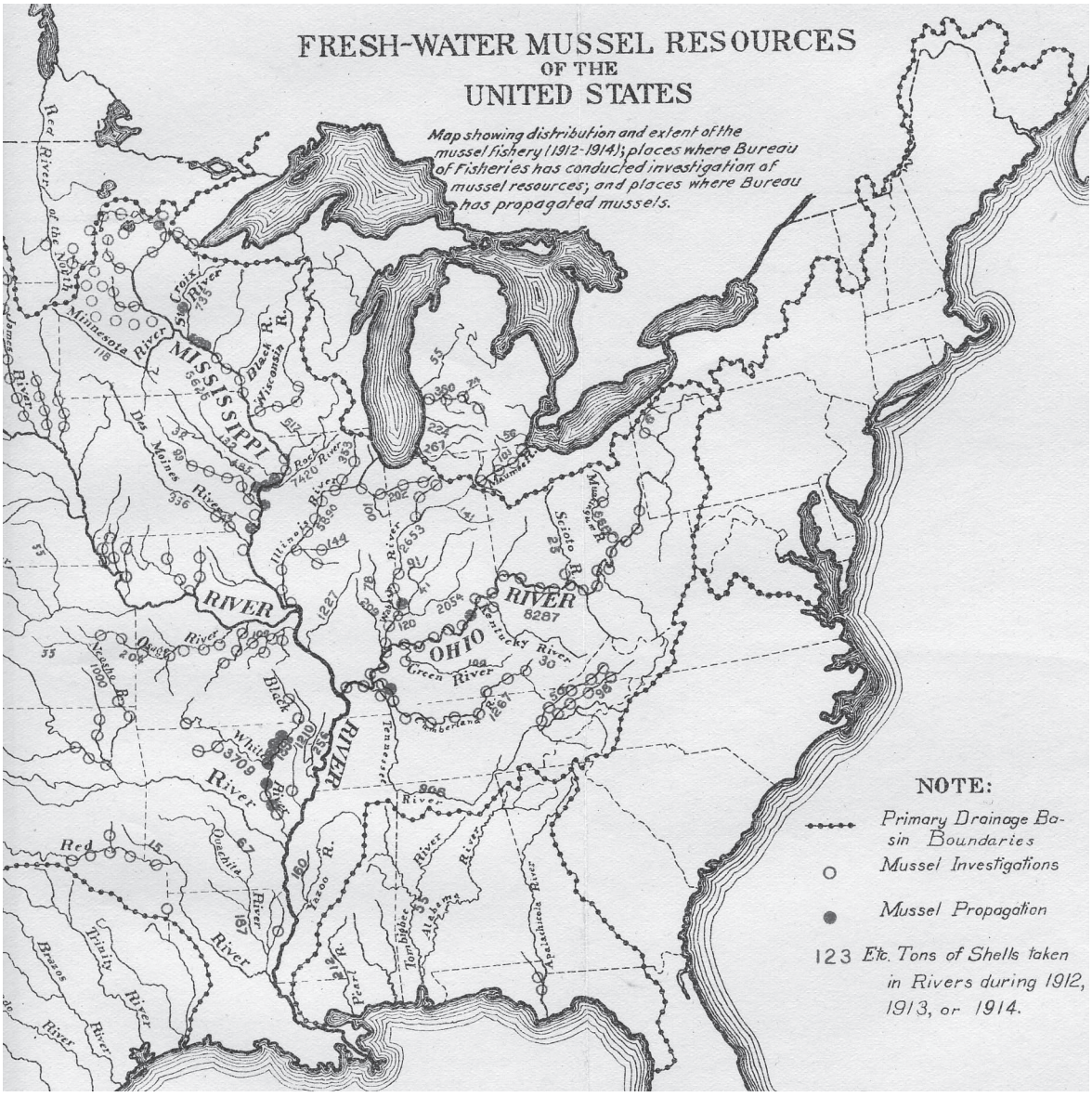

Fig. 14. By 1914, surveys had revealed a great deal about mussel resources.
From R.E. Coker, "Fresh-Water Mussels and Mussel Industries" (1921).

A map from 1914 titled the "Fresh-Water Mussel Resource of the United States" demonstrates the activities of Lefevre and Curtis from 1906 through 1914. The map, perhaps more than other surviving sources, gives a sense of the extent of their work. Circles show places in seventeen states where they may have sampled mussel populations. Dark circles show where they propagated

mussels. Fourteen locations were on the Mississippi River, six on the White and Black Rivers of Arkansas, and one each on the Cumberland, the Ohio, the Wabash and the St. Croix Rivers. The wide distribution of propagation sites probably means they were infecting fish in the field, rather than infecting the fish in a lab and then transporting the fish to the field locations, but then again that might have been possible. A separate large map found in the National Archives and drawn by the Corps of Engineers between 1911 and 1914 depicts 54 dams on the Ohio River from Pittsburgh to its mouth. It's not clear whether the dams were planned or actual. An overlay shows how biologists had mapped 219 "clam beds" on the Ohio River.[29]

Problems with raising mussels in laboratory conditions

Lefevre and Curtis glumly noted that "we have not succeeded in keeping the young mussel alive in the laboratory for a longer period than six weeks." At first the young mussels would be quite active, creeping about the dish, but then disappointment always ensued. Harms had raised the young mussels to about six weeks, yet they were then destroyed by small Crustacea. The stages immediately following parasitism up to development to about 20 mm. were "less known than any others. . . . Indeed, no one has yet succeeded in following individual specimens for more than a few weeks beyond the beginning of life on the bottom."[30]

Lefevre and Curtis tried without luck to infect German carp, minnow *(Notropis cayga* and *N. lutrensis),* and darters *(Etheostoma coeruleum spectabile)* with hookless glochidia of the genus *Lampsilis.*

They noted that "the whole problem of the food of mussels is as yet untouched." No one, evidently, had yet done work on the micro-organisms that mussels might eat, nor did anyone know whether different species utilized different forms of food. They suggested studies to determine "the possibility of artificially rearing cultures of the unicellular organisms" mussels might use as food. Lefevre and Curtis kept specimens of *Symphynota costata* and *Anodonta cataracta* alive in "small dishes containing green plants" for one to two weeks after they dropped from host fish, while *Lampsilis ligamentina* and *subrostrata* stayed alive for six weeks. After the first week, little or no growth was observed, even though the mussels were active. They surmised that "lack of a suitable food supply" was the problem.

On the other hand, they felt that adult mussels (to be used as sources of glochidia) "thrive very well in confinement, in small ponds and laboratory tanks, and that without any special attention to a food supply." They kept specimens alive for months in tanks with sand bottoms and "tap water" (probably from a well), frequently from fall to summer. "It should therefore be an easy matter to keep mussels for breeding purposes in ponds with natural bottoms in any quantity desired, and, if the ponds are fed with river water, a natural food supply should be present in abundance." Different species of *Quadrula* had become gravid in Fairport laboratory tanks, after confinement of weeks and even months. Lefevre and Curtis also noted that not much was known about parasites and diseases of mussels.[31]

Despite these problems, they saw the artificial propagation of mussels as a technical problem that could be solved. They found twelve farm ponds near Columbia, Mo., that contained mussels, evidently having dropped off of fish that had been stocked in the ponds. "If a small body of water can be so fully stocked by the scant infection of glochidia obtained by fish in nature, we should be able to introduce mussels like these into a pond far more effectively by the use of fish which had been artificially infected," they wrote. It would be a matter of providing a reliable supply of host fish, finding the best season for infection (late spring and summer), keeping a supply of mussels, and rearing and distributing the young mussels.[32]

Lefevre and Curtis on Conservation

Early on, Lefevre and Curtis outlined basic possibilities for mussel conservation that twenty years later became hotly contested in state legislatures. In the spring of 1907, they suggested artificial propagation, regulation of the fisheries, transplanting mussels to extend their natural range, closed seasons, and other fishery restrictions aimed at conserving small mussels and those ready to spawn. In the spring and summer of 1909, Lefevre and Curtis organized a field party to investigate conditions on the White River and its tributaries in Missouri and Arkansas. They noted that since the construction of "government dams," the slow water and muddy bottom permitted the use of clam bars that harvested mussels more efficiently. Charging the pearlers with "wanton destruction," Lefevre and Curtis wrote: "All things point to almost extinction of the fresh water mussel in the near future." In 1910, Lefevre and Curtis argued the "utter futility of laws which would establish a closed season of the year" because "the entire year is the breeding time of the Unionidae." At any point in the year, some species were bearing embryos or glochidia. Legislation to "close a river or large section of a river for a period of five years or more" would be the best solution because during the closed season beds could be replenished by natural and artificial means. Even artificial propagation on a large scale would be ineffective, they warned, "for unless some means can be devised for saving he young mussels it is difficult to see how much headway could be made against the destruction of the supply.[33]

It's not clear why, but Lefevre and Curtis moved on to other things after 1914. The mussel investigation on the Mississippi had occupied a prominent place for the zoology department from 1906 to 1914, but it seems that with the creation of the Fairport Biological Station, the impetus passed to the station and its first director, R.E. Coker. Curtis wrote that an illness and "time spent to questionable advantage" on his book *Science and Human Affairs* from 1912 to 1922 occupied his time, as did his fascination with the Scopes "monkey trial" and his support for the teaching of evolution in public schools. In the 1920s and 1930s he again used planarians to look at effects of radiation on regeneration, and served on the Committee on Radiation of the National Research Council. George Lefevre, unfortunately, died of pneumonia after a brief illness on January 24, 1923, at the age of 53, leaving his spouse and a five year old son. He had taught and led the zoology department for 24 years. Lefevre had written on mussels, genetics, cytology, and *Tunicata* (sea squirts). College Dean Guy Noyes and Winterton Curtis helped to carry his coffin.[34]

The promising experimental work of Lefevre and Curtis led directly to the creation of the Fairport lab. As the contemporary *History of Muscatine County* put it, "the experimental results were very satisfactory to the investigating scientists, hence the hatchery station at Fairport and the growth of flattering hopes in the breasts of the pearl button manufacturers and the thousands of men, women and children dependent upon the industry for a livelihood."[35]

Fairport Biological Laboratory

In 1908, Congress appropriated funds for the construction of a biological station at Fairport. This was the result of considerable lobbying by officials of the Bureau of Fisheries, the button manufacturers, the cooperation of zoologists, and the support of local congressmen. Barton K. Evermann, an ichthyologist, Bureau official, fish culturalist and by 1915 director of the California Academy of Sciences, personally helped select the site and arrange details, as did Lefevre. The property (about 60 acres) was evidently purchased and donated to the government by the National Association of Button Manufacturers. Construction of buildings began in 1909 and the dedication was held on August 4, 1914, with Robert E. Coker appointed the first director.[36]

Fig. 15. Fairport laboratory staff on the porch of the Temporary Lab, 1914. It was used until the main lab building was finished. Courtesy of the Fairport Fish Hatchery, Iowa Department of Natural Resources.

Fig. 16. Temporary Lab at Fairport. Courtesy Fairport Fish Hatchery, Iowa Department of Natural Resources.

Investigation of mussel problems began in the summer of 1910, mussel propagation started "on a practical scale" in 1912, the lab building was constructed in 1912-13, and the station was "opened for general investigations" on June 15, 1914 (see floor plan and Coker's 1914 account of propagation in addenda). In the true spirit of science and reflecting the close connections between the Bureau and academic scientists at places like the Marine Biological Station at Woods Hole, by 1917 the Fairport Biological Laboratory on the Mississippi attracted not only Dr. A.D. Howard's work on propagating mussels, but also Professor C.B. Wilson, working on dragonflies and damselflies in relation to fish culture, Professor Emmeline Moore, studying aquatic plants in relation to fish culture, five other scientists engaged in projects related to fish or fish culture, not to mention four scientific assistants and Dr. Leslie B. Arey, "a table occupant not in Bureau's service" studying retinal pigment. By 1920, emphasis on fish culture activities had grown. Fairport studied the "conditions necessary to make individual ponds as productive as possible for market fish, experi-

mented with catfish and buffalofish propagation with an eye to increasing food supplies, and experiments related to "the growing of game fishes in ponds." In 1920, R.E. Coker clearly argued that the Fairport Station served public interests by engaging in both mussel and fish culture activities and research. In 1927, Fairport sent several shipments of *L. luteola* (fat muckets) to Japan to restock depleted mussel beds. Out of 2,500 mussels, even with careful temperature regulation and procedures to lessen the shock, only 556 survived the entire process (c. 16-22%). By 1928, the station also assisted in "development of the fish resources of the Upper Mississippi Wild-Life and Fish Refuge."[37]

The physical facilities at Fairport provided the necessary elements for experiments in propagation. Much of the Superintendent's job involved the details of maintaining the physical facilities. By 1914, 17 earthen ponds were constructed, and by 1920 there were as many as 36 separate ponds; of those, 14 were small concrete ponds, and 22 were earthen ponds from one-tenth of an acre to about an acre in size. The main water supply came out of the Mississippi river via a pipe that fed the ponds and tank house. During fiscal year 1927, the pump house impelled 108, 616,000 gallons of unfiltered water and 1,484,805 gallons of filtered water to supply the needs of the station. Reservoirs placed above the ponds received water from the pump house, and then a gravity system was used to feed the various ponds. The pump was evidently powered by coal, in 1927 costing the Station $1,137 for 240 tons. The station also possessed some button making machinery, used to test different sized shells, to test the products of mussel culture work at different ages, and to work on more efficient blank cutting techniques.[38]

From 1908 to 1922, personnel at Fairport a) discovered that each species of glochidia restricted itself to one or a few particular host fish, b) reared young mussels from the stage of infection, and c) showed glochidia were true parasites, growing while attached to fish. Finally, Lefevre and Curtis observed that *Strophitus edentulus* seemed to undergo metamorphosis without a host, and later scientific assistant A.D. Howard observed that *Anodonta imbecillis* (paper pondshell) developed without the parasitic stage. These last discoveries held considerable fascination but did not bear the hoped-for fruit.[39]

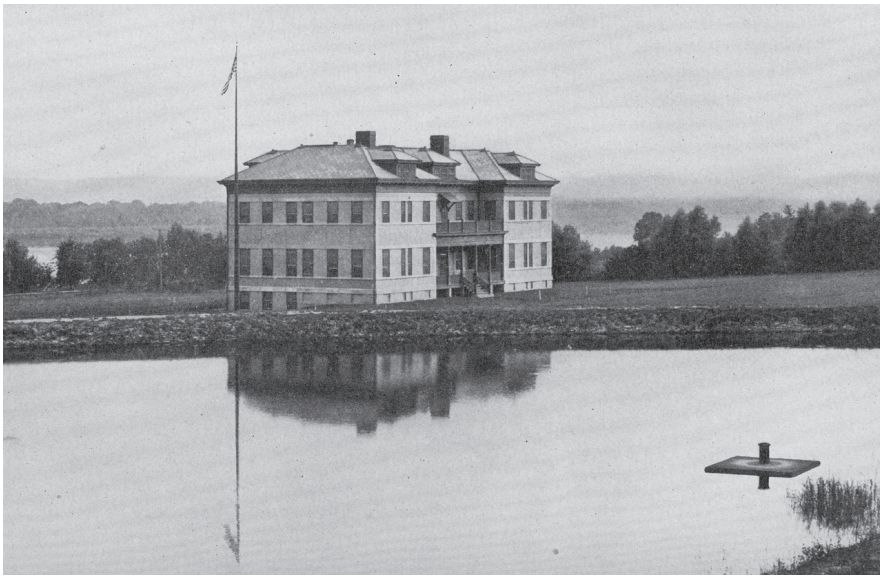

Fig. 17. The main laboratory building at Fairport Station (1914) represented a significant investment for inland fisheries. From Coker, "The Fairport Fisheries Biological Station" (1914).

Early on, station personnel experienced great difficulty rearing the young mussels after they dropped from the fish. Coker et al., writing in 1920, wrote that for practical purposes "all attempts . . . failed." Lefevre and Curtis (1912) reared a single live mussel that grew to 41 by 30 mm. In 1914, Howard reared more than 200 Lake Pepin muckets *(L. luteola)* when he kept the infected fish in a "small floating basket" in the river, mussels reaching

3.2 cm. during the first season, many raised to maturity and a second generation raised when Howard successfully infected fish with the glochidia of the first generation. In 1914, station director Shira used "watch glasses and balanced aquaria" to rear a few mussels *(L. luteola)* from infection to a size of .44 cm. in 291 days. Coker initiated an experiment at the station in 1913, raising young mussels *(L. luteola)* in a pond to 3.5 cm. in the first season. At the age of four years some of these mussels had reached commercial size.[40]

Rescuing Fish and Infecting Fish

Each year as the Mississippi River flooded, thousands of fish were left stranded in pools of water isolated from the river, doomed to die as the pools evaporated. This was viewed as a terrible waste, and so in 1876 at the instigation of Iowa Fish Commissioner B.F. Shaw, the states began to spend a great deal of time and energy rescuing the fish and returning them to the main river channel. Missouri started fish rescue work in 1881, Wisconsin followed in 1893, and in 1889 the U.S. Fish Commission undertook operations at Quincy, Illinois. In 1922, around the high point of operations, at least 20 stations participated in the work. It was very physical work, and employed substantial crews seasonally.

The entire enterprise of infecting host fish became tied to the practice of fish rescue. The business of raising "pond fish" or "warm water fish" was overseen by the Division of Fish Culture. The scientists associated with mussel propagation and culture did not give much attention to fish propagation. Their main concern was which species would readily take an infection of glochidia. Quite a bit of the mussel infection work associated with Fairport Biological Laboratory was carried out in the field by crews operating out of fish rescue stations at Homer and La Crosse.[41]

Fig. 18. Seining black bass in overflowed lands near La Crosse, to be infected with glochidia. Fig. 67 in Lefevre and Curtis "Studies" (1910).

When Lefevre and Curtis began work on the Mississippi, they needed fish to practice infecting, and the Bureau of Fisheries station at Manchester provided those fish at the direction of the Commissioner. In 1908, Lefevre and Curtis had a problem finding or seining enough host fish because of high water on the river. When Lefevre suggested he could use the Bureau's ship *Curlew* as a floating laboratory for mussel infection, however, Manchester Station Superintendent Henderson protested that it would interfere with the "usual work." Evidently, the *Curlew* was used not only in transporting fish to or from the station, but also for fish rescue work. Both Lefevre and Henderson defended their intended use of the *Curlew,* each believing that the "usual work" or mussel propagation needed to take precedence in the *Curlew's* schedule. It took Commissioner

Smith himself to step between them and smooth out arrangements so that the fish rescue program was pressed into service for the new mussel propagation program[42].

It is evident that by 1913 the two programs were cooperating. In 1914, Bureau personnel "planted" 227,536,814 glochidia, meaning they infected fish with that many (estimated) glochidia. From 1913 to 1914, they increased their infections by 50 per cent. Carrying those glochidia in 1914 were 167,819 fish liberated into rivers and lakes, and of those, 66,645 had been rescued from overflowed lands. Fish were released into the Mississippi River near Fairport and near La Crosse, Wisconsin, in Lake Pepin, Minnesota, in the Black and White Rivers in Arkansas, and in the Wabash River, Indiana. Smaller experimental plants were made in the Grand River, Michigan, Lake Pokegama, Minnesota, and in the Maumee River, Indiana. In 1916, seven commercial mussel species were used to infect fish and plant in the Mississippi near Fairport and in Lake Pepin, the Wabash, and the Black and White Rivers in Arkansas. Those species were (in descending number of plants) *Lampsilis ligamentina,* (Mucket), *Lampsilis luteola* (Lake Pepin mucket), *Lampsilis recta* (Black sand-shell), and smaller numbers of *Plagiola securis* (Butterfly), *L. ventricosa* (Pocketbook), *L. anodontoides* (Yellow sand-shell), and *Quadrula plicata* (Blue-point). By 1920, Commissioner Hugh Smith had molded the two programs to fit together hand-in-glove. The operations at Fairport and the other stations was seen to serve "two national purposes; it will maintain the valuable food and game fishes of the Mississippi River and will, at the same time, preserve the national resources in clams."[43]

Costs of the fish rescue and infection operations were carefully tallied. In 1919, the cost of infecting the fish that went forth to produce a ton (they guessed) of marketable shells was $5.65, which was very attractive given that a ton of shells sold for $35 the ton. Coker suggested that the mussel propagation work was paid for simply by the value of the fish taken from backwaters and returned to the main channel. Smith pointed out the fact that it was considerably cheaper to rescue the fish than it was to raise them from scratch in pond hatcheries. Given all the scientific work that bemoaned the wastefulness of nature, it's fair to assume that nobody believed that all the glochidia used in infections survived to become adult mussels. In fact, the 1921 annual report discussed how pike perch infected with the Lake Pepin mucket in an enclosure in the lake "yielded an average of 833 juvenile mussels per fish." If they bore the "usual infection" of 3,000 glochidia on each fish, then the yield was 27.4 per cent, "a much higher percentage than has ever been assumed to result from practical operations in artificial propagation of mussels."[44]

In 1927, seven stations at Homer, Minnesota, La Crosse, Wisconsin, Lynxville, Wisconsin, Marquette, Iowa, Bellevue, Iowa, Rock Island, Illinois, and Simmesport, Louisiana, reported rescue operations that returned over 88 million fish to flowing waters or utilized for the purpose of stocking ponds. By 1928, the combined program of rescue and mussel infection was reporting high numbers of potential juvenile releases. This appears to have been the major business of the Homer Station. La Crosse reported they had infected fish with 104.8 million glochidia of *L. luteola* (grass mucket), and Genoa reported 130.9 million glochidia were off to re-populate the mussel beds of the Mississippi River. In fiscal year 1927, eleven stations were involved in mussel infection work, infecting fish with the glochidia of *L. luteola* (grass mucket, 642 million), *L. ligamentina* (river mucket, 329 million), and *L. ventricosa* (4.9 million). Those stations were located at Winona and Homer, Minnesota (Homer performed the most infections), La Crosse, Genoa, Ferryville and Lynxville, Wisconsin, Marquette, Guttenberg, Buena Vista, and Bellevue, Iowa, and Andalusia, Illinois. By fiscal year 1928, sixteen stations were involved, with additional activities near Minnieska, Chimney Rock, Wabasha, Dakota, and West Newton, Minnesota, as well as Alma, Wisconsin.[45]

By 1927, the rescue of fish and their infection with glochidia was a smoothly-running operation. Report forms titled "Collection and infection of fishes during month of (date)/ Biological

Station, Fairport, Iowa," were printed. There must have been hundreds or thousands of these, but today only eight remain preserved in the archives of the D.C. Booth Historic Fish Hatchery (see data sheet for infection work in addenda). Personnel would fill in the forms indicating which substation the work was associated with, where the fish were collected and rescued, the species of fish, how many and what species of glochidia had been utilized in each infection, and where the fish were liberated. Anywhere from 2,000 to 600,000 fish might be estimated, the higher numbers pertaining to fry or fingerlings. A standard sort of method for estimating fish numbers was used. The number of fish that might fit in a certain sized container was counted only once. A given volume of water was placed in the container, and fish (carefully counted) were added until the water reached a second given level. From then on, given the same size of fish (and perhaps species as well), all field workers had to do was fill the container with water and fish according to the procedure, and there was the count. We can imagine some similar method of guessing the number of glochidia was used. The forms allowed field crews to make clear what portion of rescued fish had been infected. For example, one crew out of Lake City, Minnesota, visited 19 locations around Lake Pepin, gathering eight different species of fish, which they infected in (evidently) 19 different batches with 18 million glochidia of *L. luteola.* Over 5.8 million fish were infected during fiscal year 1928.[46]

In 1922, the Bureau noted that because of the vast number of fish handled, some fish received minor injuries that permitted infections by bacteria and "fungus," often killing them. They solved this problem by "immersing the fish in a solution of copper sulphate after the encystment of the glochidia," that were not injured by the procedure.[47]

Surber

In 1915, the Bureau of Fisheries published work on host fish by Thaddeus Surber, assistant at the U.S. Biological Laboratory at Fairport. His work was significant because scientists were unsure about what fish species served as the hosts during the parasitic stage of many mussel species in the Mississippi River. The first step was to examine fish for their natural infections, and therefore it was essential to be able to identify glochidia. Surber described and drew fifteen species of fresh-water glochidia. The answers to the larger questions were not immediately obvious—it took Surber three years of experiments to discover the specific host (skipjack, *P. chrysochloris*) of the commercially important *Quadrula ebena.*

The second object in Surber's work lay in developing a human-designed system of propagation that might improve on nature's system of repopulating the world with mussels. In 1912, Surber examined 2,815 fish of 38 species taken from the river, finding that only 46 fish of 11 species were naturally infected. Surely, the logic went, humans could improve on that dismal record. The "advantages of artificial infection can be readily imagined", he wrote, "when the small percentage found infected in a state of nature is considered. . . . . all man has to do is find the specific host of a given species, procure that host, and load it to the limit, which may exceed the optimum infection of Lefevre and Curtis in some cases."[48]

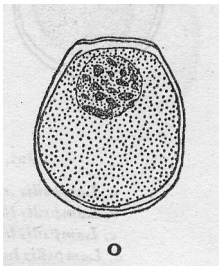

Fig. 19. Drawing of *L. higginsii* glochidia. After Surber, 1915, from Coker et al., fig. 9.

Surber divided fish into two categories, those that were regular hosts to maturing glochidia, and those that were accidental or occasional hosts. He thought the sauger *(Stizostedion canadense)* might belong to the group of regular hosts, but only one specimen of *L. Higginsi* did not provide conclusive evidence. Other species of *Lampsilis* were found encysted on freshwater drum *(Aplodinotus grunniens),* white bass *(Roccus chrysops),* and to lesser degrees on white crappie *(P. annularis),* shovelnose sturgeon

(Scaphrhyncus platorhynchus), and blue sunfish *(Lepomis pallidus).*

Regarding the Higgins sand-shell *(Lampsilis higginsi),* Surber wrote that the "only fish so far taken which unquestionably holds this glochidium" ws a specimen of *Stizostedion canadense* (sauger) that was found with about 600 glochidia. Other specimens of *Stizostedion canadense* were found to be infected with four other species of glochidia. He also noted that he found *L. higginsi* specimens bearing glochidia in May and September. *Quadrula fragosa* is not mentioned by Surber, but the *Quadrulas* were found encysted mostly on skipjack herring *(Pomolobus chrysochloris),* and in lesser quantities on white crappie *(Pomoxis annularis),* bluegill *(Lepomis pallidus),* blue-spotted sunfish *(Apomotis cyanellus),* sauger *(Stizostedion canadense),* and black crappie (*Pomoxis sparoides*).[49]

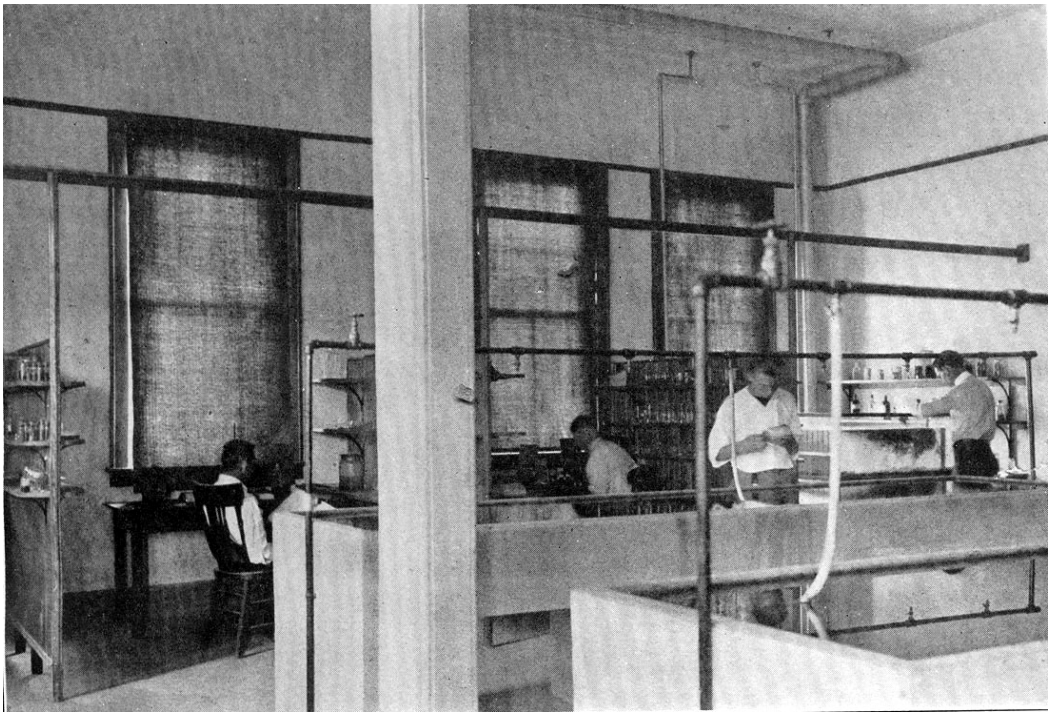

Fig. 20. Lab space in the main building at Fairport Biological Station.
Plate 78 in Coker, "Fairport Fisheries Biological Station" (1914).

Some sort of trouble emerged between Surber and his supervisors. In 1913, the Fairport director wrote to the Commissioner of Fisheries, complaining that "Mr. Surber's general behavior is infurious (sic) to the station, as well as wasteful of the time of the Director." The director also wrote that the "intention was that Surber's connection to the station was only temporary." It seems that Surber requested a transfer, but withdrew the application. Later, Surber lived in Homer, Minnesota and performed work associated with the Bureau of Fisheries station there.[50]

Howard & the Floating Crates

In 1914, the Bureau of Fisheries published the work of Arthur Day Howard, the "scientific assistant" whose expressed task was to propagate the mussels at Fairport. Building on the 1912 work of Lefevre and Curtis, Howard's main concern was the culture of young mussels after their parasitic stage, yet we get the sense that Howard and the other members of Fairport's staff participated in several of the various facets of the station's work (see Howard's Tables 1-4 in addenda). Howard worked with the Warty-back *(Quadrula nodulata),* pimple-back *(Q. pustulata),* Maple-leaf

(Q. lachrymosa), Monkey-face *(Q. metanevra),* Ebonyshell *(Q. ebena,* today *Fusconaia ebenus),* Round pigtoe *(Q. solida,* closely related to *Q. ebena),* Pig-toe *(Q. trigona),* Blue-point *(Q. plicata),* and Washboard *(Q. heros)* mussels. Howard used the usual collection methods employed by the "clammers," and noted special problems with the short-period breeding of the Quadrulas. He also noted that *Anodonta imbecillis* developed or could develop without a host fish.[51]

Fig. 21. "Lifting one of the baskets from the crate for examination and cleaning." From plate 19 in Coker et al. (1922).

Undoubtedly working alongside Surber, Howard collected fish in the river to determine which species of glochidia became attached in the natural scheme of things. Then he took the same fish specimen, artificially adding the same species of glochidia "to determine the possibilities of artificial propagation." Howard took glochidia directly from the marsupial pouch of a mussel, placing them in a receptacle with the fish. He noted that after the glochidia passed through the gills of the fish (or became attached to the fins) "there is a reaction of the tissue in the nature of a hypertrophy of the external epithelium which produces a cyst enveloping the glochidium."[52]

Howard tried various culture methods, building floating crates, indoor aquaria, troughs indoors and out, and utilizing the station's ponds. In each culture device, he planted young mussels from infected fish. The best results came from earth ponds and from crates suspended in the river, and poor results came from using cement ponds and various equipment indoors. Although the water system at Fairport made possible the control of water supply, it had its limits. In a cement pond, he tried to establish a 50 gallon per minute flow, and got a current of .1 mph, but was unable to attain the 2-3 mph flow of the river. In 1922, Howard published his results in the *Bulletin of the Bureau of Fisheries.* He noted the steady but slow

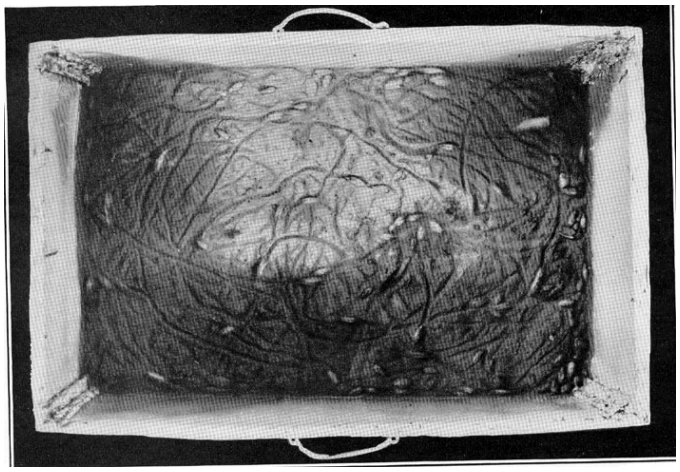

Fig. 22. A propagation basket used with floating crate above. The mussels were agitated by inspection, leaving tracks in the sand.
Fig. 75 in Howard (1921-22).

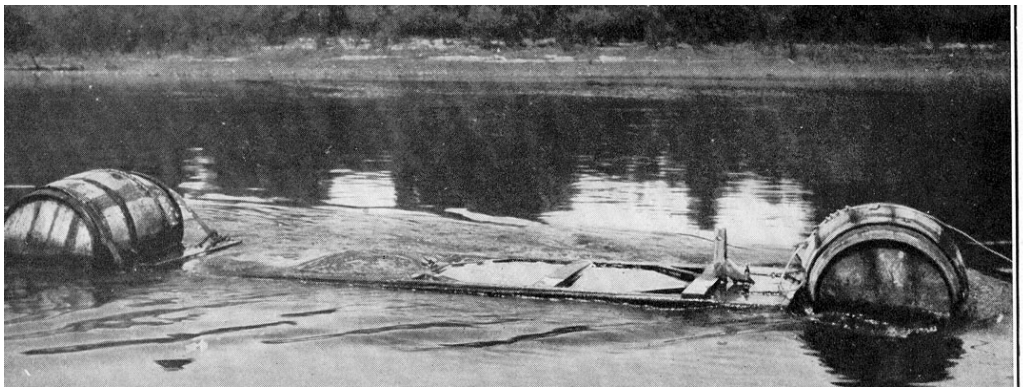

Fig. 23. Howard's "floating crate containing four baskets" holding fish infected with glochidia. "The first successful attempt to rear mussels," wrote Howard, "was made in this device." Fig. 74 in Howard (1921-22).

progress in keeping captive mussels alive; in 1885-1888, Schmidt and Schierholz had mussels live to four or five weeks, Harms in 1907 had mussels live to seven weeks, and in 1913 Herbers kept mussels alive for two months, and Lefevre and Curtis found a mussel alive two years after it was planted (in a pond or a cage so they could locate it again).[53]

Howard noticed a dwarfing effect in aquaria and indoor tanks. He did not know if it was silt, or reduced light, or a lack of plankton that made his captive mussels smaller than mussels in the wild. This helps us understand why Howard made particular mention of his thoughts on natural versus artificial propagation, speculating that "there must be some vital deficiency under artificial conditions . . . ." He sought a method of propagation "which would depart from the natural habitat only so far as the necessity of mechanical control demanded." In trying to imitate nature, Howard manufactured "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 (sic) mussels."[54]

Howard manufactured crates or baskets that were suspended at the river's surface in small rafts so that the major control exerted was holding the mussels in one place (retrievable) but water temperature and chemistry, etc., would be as close to natural conditions as could be achieved. The first raft was made from "a floating fish car" with attached barrels, to which four baskets measuring 1.5 by 2.25 feet were attached. Howard continually improved the raft or "float," making it larger and more stable in the current, and replacing the original

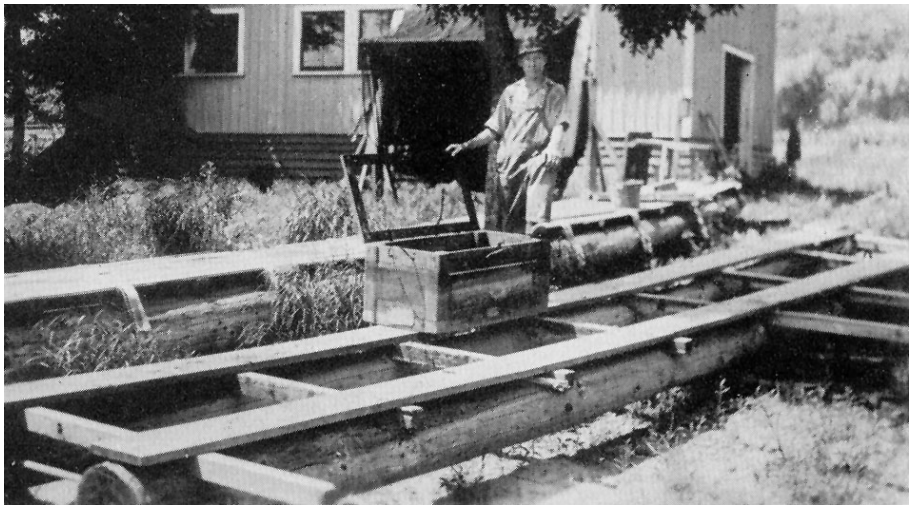

Fig. 24. Howard's improved float, with one of the crates removed for viewing. Fig. 58 in Howard (1921-22).

metal on the baskets with wood frames, which was less expensive and did not harm the mussels. On the improved model, seven crates (3.5 x 1.5 x 1.5 feet) with frameworks of cedar lumber were suspended by strap-iron hangers between two cedar phone poles separated by four foot cross beams and topped with 10 x 2" planks to walk on. Operators could raise the crates easily, whereas with the earlier model the work had to be carried out from a small boat, an unstable and inconvenient arrangement. Each crate had an outer screen with 1/4 inch galvanized mesh, and fixed to the interior surface of the frame were detachable screens of copper cloth with a fine mesh (100 to the inch). These were easy to clean and water flow could be increased to the mussels by replacing a larger sized mesh screen as the mussels grew in size. At the surface, Howard presumed, the young mussels wouldn't encounter their enemies found at the river bottom. Additionally, he thought, the mussels would be spared the harm wrought by excessive silt deposition. Infected fish were placed in the

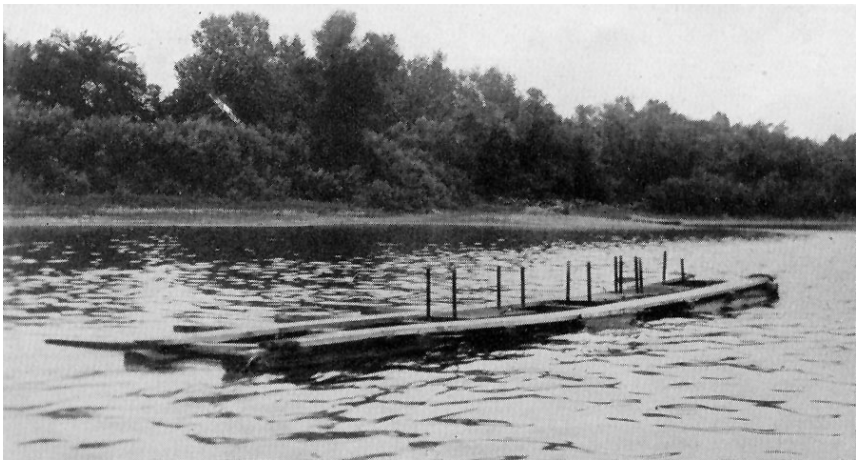

Fig. 25. Howard's improved float in the Mississippi River. It supported three crates with the iron hangers vivible above the float. Fig. 59 in Howard (1921-22).

baskets "a few days before the end of the parasitic period of the mussels and were removed as soon as the mussels were shed."[55]

The main experiment with the floating crates began in May of 1914, when fat muckets *(L. luteola)* from Lake Pepin were express shipped to Fairport. On May 21, Howard took ripe glochidia from 3 of the 5 live mussels. He attempted to infect 12 species of fish, and 6 proved susceptible. Howard placed eight infected largemouth black bass in "basket No. 2 of the floating crate," anchored in the river just offshore from the station. On June 10 (20 days after infection), most of the young mussels had been shed (infected fish placed in cement ponds and aquaria during this particular experiment shed their matured glochidia on the same day). By November 24, the average size of these mussels was 32 mm., approximately 128 times larger than the tiny juveniles that dropped from their host fish. While the original "plant" from the three surviving bass was 2,400 juveniles, Howard found that 217 mussels lived

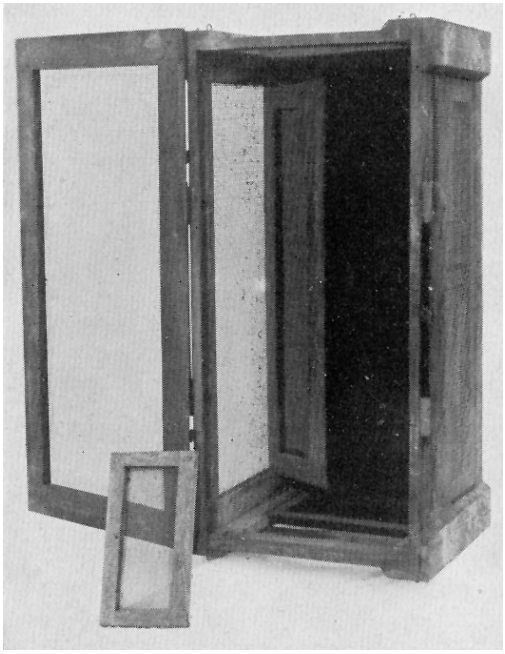

Fig. 26. One of several crates from the improved float. Fig. 60 in Howard (1921-22).

through the season, giving them a survival rate of a bit more than 8%.[56]

Nature provided all sorts of challenges to science, some of them more dramatic than others. During the early winter of 1914, Howard almost lost his floating crate, along with his important experiment in mussel culture. On the night of November 19, "ice floes bore down on the crate" (70) and "only by the rarest good fortune was the whole plant saved. The ice instead of destroying the crate . . . landed it on shore, where the mussels were extricated without injury."[57]

During the summers of 1915 and 1916, Howard continued his work. Carefully measuring mussels on many occasions over a three year period led him to surmise that a mussel's growth was much faster when water temperatures were warm. The growing season was obviously correlated with the warming temperatures of summer, he noted, undoubtedly because the plankton were controlled by temperature, with the mussels dependent on the plankton.[58]

Howard tried other methods of mussel culture as well, measuring the growth of mussels in aquaria, tanks, and troughs. He constructed indoor tanks and troughs, using running water in all but one or two aquaria. Among other things, Howard tried baskets of galvanized iron (painted with asphaltum to prevent corrosion) in lab tanks. In a rectangular glass aquarium, a plant of juveniles was obtained from two bass *(Micropterus salmoides)* and one calico bass *(Pomoxis sparoides).* These mussels grew slowly, measuring around 4.2 mm. by August 10th, whereas average mussels in the floating crate measured over 10 mm. by the same date. In just three weeks, a mussel placed in the floating crate outpaced an identical specimen placed into the aquarium by a full 3.1 mm.[59]

Howard claimed that mussels one-half inch and larger placed in tanks and indoor aquaria showed little growth. He also got "negative results" while testing indoors aquaria supplied with flowing river water, whether they were made of wood, painted and unpainted metal, or cement tanks and troughs. He tried filtered river water in balanced aquaria, in an effort to avoid "destructive turbellarians and other predacious forms." But the mussels only survived a short time in the indoors equipment.[60]

Fairport's ponds were put to use in Howard's experiments. The cement ponds were 50 x 10 x 2.25 feet deep containing specially prepared gravel. They were especially useful for holding fish used in the experiments, because they could be easily subdivided. They didn't seem to work well for mussel culture, however, perhaps because "the cement bottom and sides presented an environment unnatural and unsuited to the life of the mussel." "Many unsuccessful trials" were followed by more careful experiments that seemed to promise "fair" results. Fairport staff tried gravel, sand, mud or loam, spread out evenly 1 to 3 inches deep over the cement bottoms. Silt would also be deposited from the flowing river water, deepest at the end where the water supply pipe was located.[61]

In concrete ponds with vertical sides, seines were used to remove fish after they shed the young mussels. In 1914, they tried plants of *Lampsilis luteola, L. ligamentina, Quadrula plicata,* and *Q. pustulosa.* From a plant of thousands of *L. luteola* on a mud bottom, only two mussels of 11 and 15 millimeters were found using a 3-millimeter mesh to strain all the mud. They tried large plants of the pimple-back mussel, *Quadrula pustulosa,* in a narrow cement pond with a current of water flowing over gravel and sand. Even though the aeration of water and sunlight were better than indoor tanks, sieving the pond's contents after the second season with a 2-millimeter mesh failed to reveal any surviving mussels.[62]

Better luck was had with a plant of *Quadrula pustulosa* on channel catfish in a new concrete pond. In 1913 the infected fish were released in the lowest division of the pond, away from the inlet and near the outflow. A flow of water was maintained in the pond all year, and no inspections were conducted until after the 4th growing season. The ten specimens recovered averaged growth to 19.79 millimeters. Again the "retarding effect of the artificial conditions is obvious" as the largest pond-

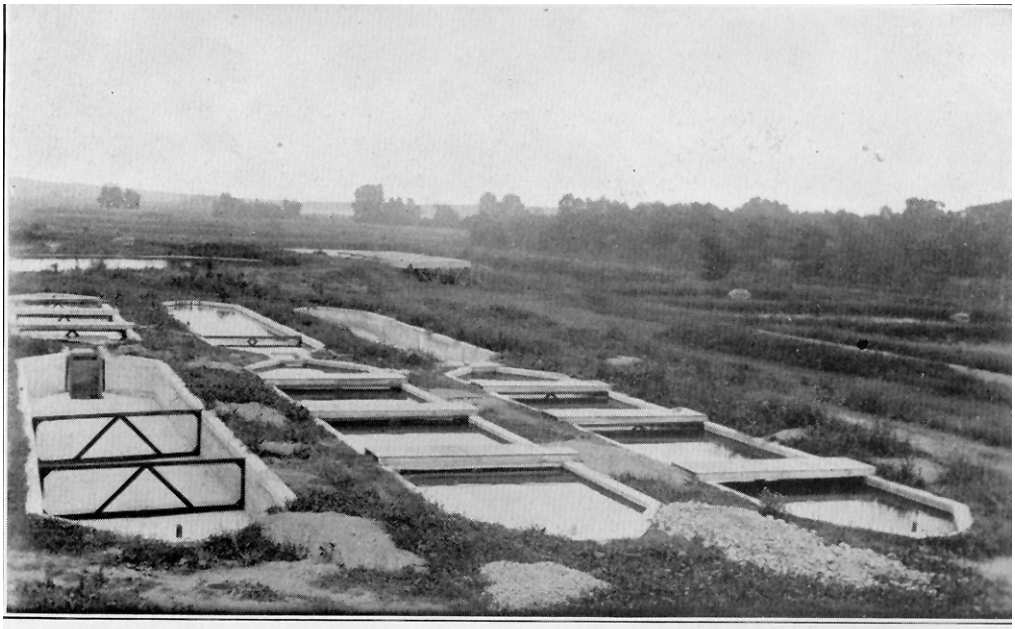

FIG. 61.—Concrete ponds used for mussel culture experiments. In the dry pond on the left is shown the method of dividing into smaller units by means of screens. Bridges are shown over the two ponds on the right. These furnish shade for the fish and prevent their jumping over the screens as well as serving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

Fig. 27. The cement ponds where some mussel experiments were conducted. At left center, just to the right of a pond, note the shed roof covering the outdoor troughs. Fig. 61 in Howard (1921-22).

grown mussel measured 24 mm. and weighed 1.9 grams, whereas an equal-aged river grown mussel measured 28 mm. and weighed 4.6 grams. This cement pond was more successful than the others, perhaps because the lower division where the catfish had been held was "practically free of bottom soil." Second, subaquatic vegetation had congregated at the intake end of the pond, so silt accumulated in that upper division. Third, because the water system (the pond itself) was new, predacious species such as rhabdocoels had not become established. Attempts to replicate the first "set" (successful plant) and similar experiences with earth ponds led Howard to suggest that the "newness" of the water supply, "before typical pond conditions have time to develop," could be very important. He advocated providing water directly from the river "and a rigid exclusion of established pond conditions," maintaining good conditions "by thoroughly cleaning the walls and bottom each season [and exclude] pond plants and animals during the critical period when the young mussels are escaping from their hosts."[63]

The earth ponds measured 41 to 61 feet by 24 feet by four inches deep at the intake to four feet deep at the well, with care taken to put in many water plants. A large plant of *Lampsilis luteola* was carried out in 1914 from two species of crappie *(Pomoxis annularis* and *P. sparoides)* and the sunfish *(Lepomis pallidus)*. The next spring eight mussels were recovered, ranging from 12 to 24 millimeters. Part of the reason for the small success was the unexpected presence of a few sheepshead, *Aplodinotus grunniens,* a mussel eating fish. A plant of *L. luteola* in 1913 in one of the large earth ponds (0.843 acre) yielded (over two years) 150 mussels measuring 15.5 to 35 millimeters in length. The growth of mussels in earth ponds, wrote Howard, compared quite favorably to growth in the floating crate.

Howard evidently raised small broods of Yellow sandshells (2,000), Lake Pepin mucket (3,000) and the River mucket *(L. ligamentina)* (500). By 1922, he was rearing *L. luteola* and *L. ligamentina* "in troughs" (see section below on the use of troughs). While some mussels did survive most of the plants in the various culture devices, Howard was clearly aware that these were small numbers, compared to the thousands of juveniles he had placed in these artificial habitats.

Howard on Conservation

In 1922, Arthur Day Howard cited J.L. Kellogg (*Shell Fish Industries* published by Henry Holt around 1910) who said conservation would not work without culture or cultivation [of commercially exploited species]. Like others, Howard saw extinction as the likely result if people relied on only a natural supply. Nature, wrote Howard, was a "haphazard" process. He thought that people could improve on nature: "an artificial planting likewise would doubtless be more economical of mussels." Howard believed that fish could be made to carry a greater number of parasites than normally found in nature, and that the number of mussels reaching juvenile stage could be increased by human intervention.[64]

Robert E. Coker

Dr. Robert E. Coker served as the first director of the station (1910-1915), and directed the Division of Scientific Inquiry in the U.S. Bureau of Fisheries (1915-1922). He acted as a knowledgeable and vocal advocate for the mussels during a period of considerable development of river transportation and hydroelectric facilities. In a very short period of time, he began to see a larger picture beyond the technical problem of propagating mussels. He wrote not only about mussel rearing techniques, but also about the button industry, conservation of mussels, river conditions and pollution.

Fig. 28. Dr. Robert E. Coker, c. 1930. Courtesy Southern Historical Manuscripts Collection, University of North Carolina.

From 1902-04, he served as a "custodian" of the U.S. Fisheries Biological Station at Beaufort, North Carolina, from 1906-08 he was a special investigator for fisheries with the Peruvian government, and in 1909 he was a scientific assistant for the U.S. Bureau of Fisheries. He married Jennie Louise Coit in 1910, and from 1910 to 1915 he was Director of the U.S. Fisheries Biological Station at Fairport. Their first son, Robert Jr., was born in 1911 in their home in Muscatine. From 1911 to 1916, Coker served as vice-president of the Ecological Society of America. From 1915 to 1922, Coker was placed in charge of the Bureau of Fisheries' Division of Scientific Inquiry in Washington, D.C. From 1922 to 1923, he also served as director of the U.S. Fisheries Biological Station at Woods Hole, Massachusetts, and in 1923 he moved to the University of North Carolina in Chapel Hill where he worked as a professor of Zoology. From 1927 to 1935, he was a teacher and the director of the Allegany School of Natural History, associated with the Buffalo

Museum of Natural Science and the New York State Museum of Natural History. In 1947, he retired at the age of seventy-one, and in the same year his book *This Great and Wide Sea* was published, a reflection of his growing interest in marine life. Coker served as the president of no fewer than four scientific societies— the Ecological Society of America (1937), the Limnological Society of America (1938), the American Society of Zoologists (1941), and the American Biological Society (1939). He died in 1967.[65]

In 1914, the Bureau of Fisheries published Coker's investigation of the effects of the first major dam on the Mississippi, the Keokuk dam, built for power generation. Coker sought to quantify, prove or disprove the rumors and anecdotal reports that fewer fish of certain species were seen above the dam. Because mussels utilize a parasitic stage on fish, their distribution up and down the river system might be affected by a limitation on their host fish's mobility. Coker wrote to S.A. Forbes, director of the Illinois Natural History Survey, inquiring whether any change had been "noted in the fish runs in the Illinois River."[66]

In 1914, Coker put forth his ideas on conservation in Bureau of Fisheries Document No. 793, "The Protection of Fresh-Water Mussels." He noted that infant mussels should not be taken, and that "it would be desirable to leave portions of the rivers entirely undisturbed by the operations of shelling during periods of some years." He wrote "A proper solution as fair as possible to all will be found in a plan of rotation which will give rest periods to different portions of a river in succession." He suggested that conservation of the mussel beds would not be easy: "ultimate benefits can scarcely be obtained without some temporary sacrifice, although it should be aimed to make the immediate loss felt as little as possible. It is the unwillingness of individuals to make individual sacrifices, independently, for the good of the mussel beds that makes legislation of any kind necessary."[67]

The fire

The laboratory building at Fairport housed the work of Surbur, Howard and Coker, but soon disaster struck. At 2:30 a.m. on December 20, 1917, W.S. Carter was awakened by smoke, as was Apprentice Fish Culturalist Mr. Schroeder and his wife. Despite the attempts of staff, a fire starting in the walls below the second story's flooring near the east wing chimney destroyed "most of the equipment and practically the entire library." Also lost were "records embodying results of tedious investigations." The scientists "promptly resumed" their work in the close quarters of the old "temporary laboratory," a small building used during the very first years of the station. R.E. Coker, at this time Assistant in charge of the Division of Scientific Inquiry helped estimate replacement costs at $92,500, including $4,000 for a scientific library and $2,500 for scientific apparatus. The original building was razed after the fire and replaced; both buildings were quite large and represented substantial government investment in science and inland fisheries (see floor plan in addenda). The new building, measuring some 100 by 55 feet, accommodated sixteen investigators. Contemporary descriptions noted the fact that the laboratory was lighted by electricity. The well-attended dedication on October 7, 1921, featured a brass band and speeches by dignitaries, including Hugh M. Smith, Commissioner of Fisheries, Edward A. Birge, President of the University of Wisconsin, Professor Frank R. Lillie, of the University of Chicago and the Marine Biological Laboratory, Woods Hole, George Lefevre, Professor James G. Needham of Cornell University, as well as the local Congressman. Representatives came from twenty-two universities and colleges, and from fourteen states.[68]

Fairport Station personnel continued their propagation activities. They released infected fish not only on the Mississippi but also on the Cumberland River, on the Ohio River at Louisville, and on the White and Black Rivers of Arkansas. During the summer of 1918, experiments continued.

Fig. 29. Dedication of the new main laboratory building at Fairport Biological Station, 1921. Courtesy Fairport Fish Hatchery, Iowa Department of Natural Resources.

At Lake Pepin, 172 fish of various species infected with the Lake Pepin mucket *(L. luteola)* were retained in an enclosure 12 feet square, placed in shallow water. This "small pen" had a plywood sort of bottom holding a thin layer of sand. By September, they retrieved 11,701 young muckets from the pen, yielding "a little over 80 living mussels per square foot" along with a few other mussels from natural infections.[69]

In 1919, Robert E. Coker published his analysis of the mussel industry in the Bulletin of the U.S. Bureau of Fisheries. Like Smith's report in 1898, Coker reflected a Progressive-era feeling that "conservation" meant the rational and planned use of resources, industry working closely with science to secure the perpetuation of resources. Coker noted and emphasized the impact of the mussel industry in the mussel beds of the Mississippi, using words like "devastation."[70]

Coker, Shira, Clark & Howard

In 1922, the Bureau of Fisheries published the "Natural History and Propagation of Fresh-water Mussels" by R.E. Coker, chief of the Bureau's Division of Scientific Inquiry, Austin F. Shira, director of the Bureau's Biological Laboratory at Fairport, Iowa, and scientific assistants H.W. Clark and A.D. Howard. Coker et al. credited the prior work of Lefevre and Curtis, Simpson, Walker, and Ortmann. This 1922 report is probably most notable for efforts to regularize and put on terms of mass production the station's prior work in propagating mussels. Of course, the station's mission incorporated increasing the supply of mussels to industry. The 1922 report looked into the natural history of fresh-water mussels, including habits, food, habitat, parasites and enemies, unfavorable conditions for mussels, growth of shells and the structure of mussels. Secondly, the report examined the life history and propagation of mussels. This report examined bottom conditions in locations along the Mississippi River, in Indiana, Illinois and Michigan, searching out suitable habitats in natural waters and in canals.[71]

Food habits of mussels

The feeding habits of mussels were of interest to these scientists because the question would arise "whether there is a sufficient food supply in water in which it is desired to promote an abundant growth of mussels." In other words, it was one more facet of putting mussel propagation on an industrial-sized footing. Their literature review and observations seem pointed toward

mussels already past the early stages of growth. W.R. Allen (1914) had described how mussels collected food in his studies at the Indiana University Biological Station at Winona Lake, Indiana. Because the growth rate of mussels was proportionate to the thickness of the shell, and because the growth rate seemed proportionate to the mineral requirements of the mussel, Coker et al. inferred that "the limiting factor of growth is not the organic food supply, but the mineral food supply." They reviewed the observations of Franz Schrader, H. Walton Clark, and Shira himself.[72]

Schrader had found that water two to four inches from the bottom of "well-known mussel grounds" contained solid matter consisting of mineral matter, organic remains mostly from plants, and plankton, mainly green algae and diatoms. Plankton varied from less than one to more than twenty per cent. Mineral matter seldom exceeded five per cent, so most of it was detritus. Dissecting mussels, Schrader found the materials in the stomachs "corresponded to those found in a free state in the water," with no differences between species. Mussels seemed to utilize the materials differently, the detritus undergoing the greatest changes, so Schrader assumed "a comparatively unimportant role as played by algae and diatoms in the food of mussels." Schrader starved mussels for four or five days and then fed them various foods by pipette directly into the intaking siphon, including thread algae, palmellales, detritus (riparian plants were immersed in water for a few days, then macerated with mortar and pestle and strained through bolting cloth–mussels took this readily and digested it well), fresh vegetable material, vegetable fat (olive oil emulsion); he also tried animal matter such as fish meat, tails of tadpoles, blood of Pickerel, and emulsion of fish fat, but the mussels didn't appreciate that cuisine. He foresaw "little likelihood of a shortage of food, for detritus will always be forthcoming," and "only a very little competition among mussels as far as food is concerned," so non-commercial species would not stand in the way of the commercial species getting their fill.[73]

H. Walton Clark found that the "size and apparent health of mussels bear no direct relation to the apparent nutritiveness of the material in the stomach." The thickness of the shell (of interest to the button manufacturer) was partly a matter of heredity, and seemed to be related to current or to mineral content of the water. He found mud was the chief substance in the stomachs of mussels. Examining mussels in the Forth Wayne Feeder Canal in 1908, he found many flagellates, (e.g., Trachelommonas and Phacus) with minute plants (e.g., Scenedesmus, Pediastrum, Botryococcus,), diatoms (Gomphonema, Navicula), a few desmids (Cosmarium), fragments of *Ceratium hirundinella,* casts of the rotifer *Anuraea chochlearis,* and small fragments of confervoid algae.[74]

Coker et al. here remarked that the stomachs of small *L. anodontoides* and *L. luteola* reared in troughs at Fairport" contained only a fine brown flocculent mud, with rarely an occasional diatom." They speculated that since bacteria was found in the stomachs of mussels in the Auglaize River, and since at Fairport tanks with turbid water and mussels had cleared up rapidly, perhaps mussel beds might "be of use in the purification and sanitation of rivers." By 1930, Max Ellis had disproved a rumor that mussels did well in polluted water, showing that mussels were very sensitive to water quality, and that they were "fundamentally clean-water animals and that their ability to adjust themselves to conditions of stream pollution is sharply limited." The authors ventured that "a critical problem is the finding of suitable nourishment for the first month or so of free life, but beyond this the only problem, so far as food supply is concerned, appears to be the avoidance of actually poisonous or harmful substances."[75]

In the fall of 1914, Shira examined the stomach contents of sixty juvenile mussels in Lake Pepin. Four species of Lampsilis, one Quadrula and one Anodonta demonstrated stomach contents ranging 89 to 96 percent organic remains (principally vegetable matter), a trace to six percent inorganic remains (silt, etc.), two to three percent unicellular green algae, and zero to two percent diatoms. Coker et al. went on to point out the living and dead organic materials were "abundantly

suspended in most natural waters," comprising an important food source. The living bodies, or the plankton, was composed of microscopic plants and animals, while the dead organic material was composed of "the remains or fragments of plants and animals in a state of decomposition," also a significant food source.[76]

Fig. 30. The "clam ponds," taken by photographer Oscar Grossheim. The power and pump house is still under construction (c. 1914), and the temporary laboratory can be seen at the right. Courtesy Oscar Grossheim Collection, Musser Public Library, Muscatine, Iowa.

It was unclear at that time how much of the mineral matter necessary for life and shell formation came from the water around mussels and how much came from solid food. In experiments at Fairport, Churchill (1915) showed that mussels could "make use of nutriment which is in solution in the water." This was true for fat, protein, and starch, yet studies of the natural water had not yet been conducted "to prove that such organic substances are present in the waters in quantities sufficient to play an important part in the nutrition of mussels." It was quite clear, however, that dissolved minerals were present in natural waters. Shells were 95 percent calcium carbonate, and 3.5 per cent organic matter, other minerals were present in percentages of less than one per cent, including silica, manganese, iron, aluminum, and phosphoric acid, so "with the possible exception of manganese it is probable that all natural waters contain a sufficient quantity of the minerals to satisfy the needs of mussels." From sundried mussel meats from the Mississippi River contained 7.6 percent moisture, 44 percent protein, 9 percent glycogen, about 3 percent ether extract, and 13 percent undetermined organic material. The remainder was 9 percent mineral matter (mostly phosphoric acid), 8 percent calcium, 3.5 percent silica, .5 percent manganese, and small amounts of sodium, potassium, iron, and magnesium. The authors thought that all natural waters probably contained the requisite minerals for mussel growth, but they hesitated to say if abundant mussel growth was due to any mineral other than calcium. They did know that a deficiency of lime was not favorable.[77]

The United States Geological Survey knew a lot about the mineral content of many streams. The authors assembled information on mineral content of 13 productive and 11 nonproductive rivers. They noted that "within broad limits, the variations in content of silica, iron, magnesium, sodium, and potassium are not significant as affecting productiveness." Nonproductive streams were "either very high in turbidity or very low in calcium, bicarbonate, and nitrate." The Shenandoah was an exception to the rule, having the right conditions but few or no mussels, so there was a possibility for introducing mussels to the river.[78]

Coker et al. also made observations on dissolved gases in the water. They noted that carbon dioxide (also called carbonic-acid gas) was helpful in small quantities but poisonous to animals in large quantities. Carbon dioxide was of interest because it united with calcium carbonate to form bicarbonate, soluble in water. Shells of fresh-water mussels (made mostly of calcium carbonate) were liable to be "attacked by free carbon dioxide in the water and taken up into solution." In soft water, or where the horny covering of a shell was damaged, shells could be damaged (and therefore of lesser value to the button industry).

The scientists and other personnel at Fairport, while performing experiments on feeding fish during the 1920s and 1930s, evidently did not try to propagate phytoplankton, although given P.S. Galtsoff's "Limnological Observation in the Upper Mississippi" published in 1921, they were certainly aware of plankton and its role in river systems. Galtsoff measured and mapped velocity of river current, turbidity, temperature, composition of plankton, and distribution of Copepoda and Cladocera at various locations on the upper Mississippi. Fish culturalists thought in terms of increasing the "productive capacity of ponds." Galtsoff thought ponds relatively simple systems. Plankton could be increased "if the pond is drained and its bottom allowed to overgrow with vegetation. When several months later the pond is again filled with water the zooplankton develops in greater abundance." Another method was "throwing various kinds of soil fertilizers into the ponds," after which the amount of plankton increased.[79]

Feeding the young mussels was a concern that spurred research by E.P. Churchill, Jr. (University of South Dakota Dept. Of Zoology), and Sara I. Lewis (Dept. Of Botany at the University of Iowa). Churchill started the work at Fairport in July of 1921, continued it at the Iowa Lakeside Laboratory at Lake Okoboji, Iowa in August, and during the summer of 1922 Lewis joined the project at Fairport. In 1922 they took advantage of experiments raising *L. Luteola* and *L. Ligamentina* in troughs carried out by A.D. Howard and B.J. Anson. Much of the work discussed basic mussel structure and function, including cilia, gills, siphons, palps, etc. They found that mussels did feed when the water was heavily laden with material; ingestion was accomplished by selection of food material and rejection of the silt, but by "taking a limited amount of all the material present." They tried feeding borax carmine but found that "sooner or later many of the mussels ceased to ingest carmine," and adults rarely ingested any. It is unclear why they tried this experiment, but they mention "the theory that as the mussels approach the adult stages they take less carmine." Mussels just dropped from fish measuring 0.2 to 0.25 mm. long took smaller sized but the same sort of material as larger mussels, mainly protozoa, diatoms, and minute particles of detritus. Mussels 1 mm. long ingested "Euglenas measuring about 60 by 18 micra when elongated and about 25 when contracted," and mussels 2 mm. long ingested red Euglenas 160 by 35 micra.[80]

Mussels consumed mainly "microscopic animal and plant forms and debris or detritus resulting from the decay and disintegration of such forms." Along with that went "everything else small enough to be admitted to the esophagus, not active enough to escape," and not terribly disagreeable. They found "entire diatoms with color, contents, and nucleus" in the rectum and in feces. They found "broken and partly disintegrated plant forms . . . in abundance in the alimentary canal." Some were probably whole when they were ingested. Protozoa, they thought, were "no doubt more easily handled." In experiments with red Euglenas they found that these protozoa were acted on by digestive fluids. They felt that "organic remains in suspension" were a highly important food source. These could be found in abundance in ponds or rivers where "luxuriant plant life is constantly going through a process of disintegration."[81]

It seemed a simple matter to feed growing mussels, even from the earliest stages. It would

be necessary "only to arrange ponds, uncontaminated by sewage or stock, and place in them some of the common water plants and algae. The requisite diatoms, Protozoa, etc., will appear and flourish there, and these, with the detritus from the decay of all the living forms, will supply food for the juvenile mussels in the pond or to which the water from the pond is conveyed." Churchill and Lewis judged that it was "unnecessary to plan any complicated arrangements to provide special food for them."[82]

Bottom conditions

Coker and his associates, like many scientists of their day, made distinctions between natural and artificial conditions. Some natural conditions, such as shifting bottoms, turbidity, sedimentation, drought or floods were unfavorable to mussel life. Artificial conditions "imposed by man" detrimental to mussel life included "the discharge of sewage, industrial wastes, dredging, and the building of wing dams. Dredging destroyed mussels by pumping them up, or shifting the river channel causing new sand bars to bury existing beds. Wing dams changed the course of the current, sedimentation, and the formation of sand bars. Some areas between wing dams near Fairport and at Homer, Minnesota, had grown in with willows, replacing the mussel beds. The clearing of forests that led to irregular stream flows affected mussels as well.[83]

Coker et al. summarized available information on suitable bottom conditions or habitats for sixty-two species of mussels. For *L. higginsi,* Shira had indicated sand as favorable, gravel as preferred, while Howard had found mixed sand and gravel bottoms favorable, and Clark had reported mixed clay and sand bottoms preferred.

Coker et al. noted "luxuriant development of certain mussels in streams where the current is strong." Lakes could also have good circulation of water caused by wave action. Mussels seemed to avoid the main channels and locate themselves nearer shore, at depths from two to 22 feet, but mostly (at Lake Pepin) at 12 to 18 feet. In the artificial ponds at Fairport, *Lampsilis luteola* was seldom found below 3 feet, and when held in crates below 3 feet, they did not thrive, even though in Lake Pepin *L. luteola* was abundant at 8 to 20 feet deep, and found as deep as 25 feet.[84]

Life history

Many questions remained, and the scientists at Fairport took a great interest in tracing the fundamental life history of mussels. For example, they noted that "the process of fertilization in nature has never been observed." They had no idea what excited ovulation or how it was timed to ensure fertilization. Coker, Shira, Clark and Howard had observed male mussels discharging sperm in a large tank at Fairport station, leaving a "long winding furrow which was filled with t white cloud of sperm." Perhaps this was the cause of ovulation. Indeed, just as at Woods Hole, the scientists at Fairport were as interested with basic biology as in questions of importance to (the button) industry. So the 1922 report contained much information on the basic life cycle of mussels, such as when female mussels could be found gravid. *L. higginsi,* for example, had been found gravid in May and September. Interestingly, they list *L. higginsii* as a commercial species. They documented the duration of the parasitic period for nine different species of mussels, for example 10 to 13 days for *L. luteola.*[85]

Natural hosts

Determining the natural hosts of mussels was difficult, starting with illustrating and describing the glochidium taken from gravid mussels (see tables in addenda). Then fish from the river were examined and attempts made to identify the glochidia attached to their gills or fins. It was still an unsure process because some of the naturally occurring infections might not appear in the particular

fish examined. Also, the rate of infection was relatively low in nature. In 1913, 3,671 fish of 46 species were examined, but only 324 or 8.9 percent were infected with glochidia. Regrettably, not even 3 percent were infected with 12 commercially valuable species. The average number of glochidia on a fish ranged from 1 to 416 with a mean of 125. "Infection in nature is a matter of chance," they wrote, and "if it were otherwise, artificial propagation might not be necessary." Given these poor odds, "only because nature is prodigal in the production of glochidia" could mussels "maintain their numbers under natural conditions." The experimental method of determining host fish was easier, because one could simply release glochidia into a tank and see if they became attached to the fish. They found *L. higginsi* used the sheepshead *(A. grunniens)* for a host, finding one natural infection.[86]

Beyond "nature's own provisions": propagation experiments

Coker et al. wrote that "nature's own provisions" adequately brought offspring to the glochidium stage. Artificial aids would "carry the young mussels through the first great crisis," when released glochidia sought a host. The second critical stage was when juveniles dropped from their host fish. Artificial propagation would "give to thousands the chance of life that would ordinarily fall only to dozens." In nature, fish were infected by a relatively small number of glochidia (they do not name a number). But "with the disturbance of natural conditions by the active pursuit of a commercial shell fishery, nature's fair balance is destroyed, and some compensatory artificial aid to the propagation of mussels is rendered necessary."[87]

Coker et al. thought that "operations can be conducted extensively and economically only in the field." They argued that personnel needed to go to the immediate vicinity of a place selected for stocking, catch and infect the host fish there, and "liberate them immediately." They suggested that artificial propagation of fresh-water mussels therefore was "a very different sort of operation" from fish propagation (see "Artificial Propagation" in addenda).[88]

Under the supervision of a Fairport station employee, local crews of 3-4 fishermen put in the river in small motorboats, used to move quickly between sites. They also used one or two flat-bottomed rowboats, in which they evidently placed one or two tanks (ordinary 4-foot galvanized stock tank) and handled fish. The crew chief carried dissecting instruments and a microscope. To procure glochidia, crews visited clammers working on the river, specifically the shellers' boats, examining the day's catch for gravid mussels. Brood pouches could be cut out and placed in water if they could be used the same day, or gravid mussels could be purchased from the shellers and glochidia removed over several days. Sometimes the crews hired shellers to retrieve mussels from the river.

Secondly, the host fish were caught in nets or seines, sorted and placed in the tanks. When the tanks were "comfortably filled," one or more brood pouches were opened, glochidia "teased out in a small pail," and poured into the tanks. An "experienced operator" could "tell at a glance" if the glochidia were ripe. If they freely separated when removed from the brood pouch, this was a good sign. A hand lens would help in this determination, or the operator could drop fish blood or a bit of salt into a small dish with a few glochidia, if the valves began to snap together it was a "sign of maturity and vitality." If the water was changed and not too warm, glochidia could survive a day or two. It was simply a matter of experience for the operator to know how many glochidia to place in a tank and how long to expose the fish. Mostly the fish kept the glochidia stirred up, but personnel might also stir the tank. From time to time the operator would inspect a fish's gills with the hand lens, and when satisfied with the degree of infection would immediately liberate the fish, or transfer them into a different tank. The recommended infection time was 5 to 20 minutes, infection proceeding more rapidly with warmer water temperature. The crews then would kill a few specimen

Fig. 31. "Transferring fish to infection tank. Foreman in boat is pouring the glochidia from a can into the tank." Seining fish in Lake Pepin. Fig. 3 on plate 18, Coker et al. (1919-20).

fish, remove their gills, and in the evenings the foreman counted representative examples of attached glochidia, in an effort to determine the total number of planted glochidia.

Coker et al. strove to achieve the "optimum infection," or the most glochidia without noticeable or appreciable damage to the host fish. That figure was about 2,000 per fish. On 8 inch black bass and white bass infected with *Lampsilis luteola,* 8 inch black bass with *L. Ligamentina,* and on 16 inch gar with *L. Anodontoides* 2,000 glochidia per fish was considered optimal. On 5 inch bluegill, 500 glochidia, on 5 inch crappie 400, on 6 inch yellow perch 1,500 *L. Luteola* were optimal, and on 14 inch channel catfish 1,200 *L. Pustulosa* glochidia was thought best. They were giving to thousands "the chance of life that would ordinarily fall only to dozens."[89]

By the summer of 1921, the Fairport biological station was organizing propagation at Lake Pepin and Lake Pokegama, Minnesota, at New Boston, Oquawka, and Dallas City, Illinois, Fairport, Iowa, at Hannibal and Clarksville, Missouri, and also with rescue crews along the Mississippi in Wisconsin and Minnesota. They claimed 648 million glochidia were released, including the 478 million "infected upon rescued fish by cooperative agents," seven of them paid by the National Association of Button Manufacturers, accompanying seven fish rescue crews operating out of the Homer Minnesota station. A total of 5.8 million fish were "subjected to infection." Superintendent Culler of the Homer station, we believe may be the C.F. Culler who later became district supervisor for the Bureau of Fisheries out of La Crosse, with authority extending all the way to the hatchery in Yellowstone National Park.[90]

Mussel Culture

The second crisis for the aspiring mussel was dropping from the host fish and growing to a sufficient size. Having used techniques of "propagation" to bring the mussels to this stage, Coker et al. (1922) now worked on the techniques of mussel "culture". In 1915, Howard had first reared mussels (Lake Pepin muckets) under control in a crate that floated in the Mississippi River. At that time, Coker evidently had some success with the same species in ponds at Fairport. They designated these methods: 1) a floating crate with closed bottom (used mainly in rivers), 2) a floating crate with open bottom (for ponds), 3) "the bottom crate," 4) pen with wooden or box bottom, 5) concrete ponds, 6) earth ponds, and 7) troughs of sheet metal, wood or concrete tanks, and aquaria.[91]

The floating crate was constructed of 100 mesh to the inch wire cloth on a wooden frame, to prevent washing away of the microscopic mussels in a river's current. This was the floating crate devised by Howard. Infected fish were placed in the crate and subsequently removed after they dropped their mussels. They had good results with the Lake Pepin mucket, and a few Yellow sandshells were obtained, but other mussels did not develop beyond early stages. The scientists found that "even with the crate floating in the river, the conditions within it are not those of the natural habitat of the mussel on the clean current-swept bottom of the river."[92]

At about the same time, Bureau personnel tried using similar equipment at Lake Pepin. Within a floating crate with wooden floor suspended eight feet below the surface, they suspended a

second smaller basket that held infected wall-eyed pike and saugers. This experiment was meant to avoid "losses caused by enemy organisms living on the lake bottom." On the bottom of "one experimental float 10 feet square more than 23,700 young mussels" were counted. The scientists calculated an 84.6 per cent survival rate for the maturing glochidia, and that the system had produced 237 mussels per square foot of crate area.[93]

In artificial earth ponds, Coker and his associates used a floating crate with open bottom. This meant it was closed to fish and open to juvenile mussels, the bottom being made of course-mesh wire cloth (1.5 inches). Infected fish and the crates were kept in the pond until the mussels dropped away. Later, water was temporarily removed from the pond and the developed mussels recovered. They got good results with the Lake Pepin mucket. While Howard had experienced rather poor luck raising mussels in concrete ponds with vertical sides, by 1922 the larger scientific staff was reporting "the usual consistent results" obtained with the robust Lake Pepin mucket *(Lampsilis luteola)*.

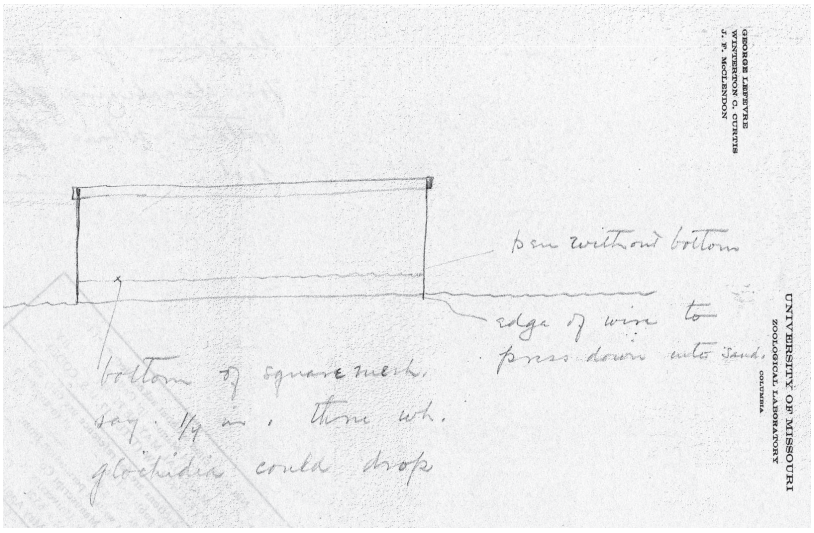

Fig. 32. Drawing of bottom cage, c. 1910-1914. From records of Winterton C. Curtis, courtesy of Western Historical Manuscript Collection-Columbia, University of Missouri.

A crate or "pen" that sat on the bottom of a pond was adapted, to retain infected fish and the "early postparasitic stages of mussels" that scientists planted there. Curtis had drawn such a submerged pen, and Howard had used a bottom-positioned pen to good effect. The pens used by the team of Coker, Shira, Clark and Howard were constructed with either a solid bottom or one of wire mesh that settled a bit into mud on the pond's bottom. A pen of galvanized netting with wooden floor was used in conditions of quiet water (without current). One design had walls of wire cloth extending from the bottom to above the water's surface let the fish "seek their own range of depth" and allowed dropping mussels to "remain close to the bottom of the pond or lake, as is natural for them." Later, the wooden bottom was raised and the mussels collected. Fairport scientists obtained excellent results in Lake Pepin with the Lake Pepin mucket. At Lake City, Minnesota, Roy S. Corwin used such a pen measuring 10 by 10 feet square and 8 inches high with the whole "surmounted by chicken wire" and sunk in a "protected part of Lake Pepin." At the end of the 1920 growing season, 11,000 mussels were collected. It was "the greatest quantity production of mussels yet attained in an inclosure." These had been liberated from 79 artificially infected fish.[94]

Earth ponds "with devices for control of depth and water supply" were stocked with infected fish that remained there the season. They reared "considerable numbers" of Lake Pepin muckets, and a few *L. ventricosa* (pocketbook) in a pond with earth bottom and wooden sides. Accidental plantings in other ponds at Fairport were noted. None of the accidental plantings, however, involved

commercially valuable species.[95]

Troughs at Fairport

Experiments were made in various small dimensioned containers, such as glass aquaria and tank or troughs made of wood, concrete, or sheet metal. These usually were equipped with running water. Special troughs were used at Fairport, beginning perhaps in 1916, and assuredly by 1918, using the Lake Pepin mucket. These troughs were constructed outdoors, and covered from the sun with a simple roof. In 1919, Dr. F.H. Reuling reared two more species, the yellow sand-shell and river mucket, "in considerable quantities in small troughs supplied with naturally clarified river water."[96]

Fig. 33. Constructing the troughs at Fairport Biological Station.
Courtesy Fairport Fish Hatchery, Iowa Department of Natural Resources.

In eight galvanized iron troughs with a supply of water from pond 1D by gravity (via the reservoir that received water from the Mississippi from the pumping plant), assistant F.H. Reuling endeavored to rear mussels. These troughs measured 12 feet long by 1 foot wide by 8 inches deep, were painted with asphaltum, and each had its own water flow from "a common screened supply pipe in the pond." Each trough bottom was covered with a half inch of fine sand. The water supply, pond 1D, remained relatively clear the whole season.

The first year, only 7 *L. siliquoidea* (Lake Pepin mucket) and 4 *L. ligamentina* (river mucket) survived (growing to 6-17,8 mm. and 2.6 mm. respectively). They called it "very encouraging," however, because it was the first time mussels had been artificially reared to that size. In 1918, they reared 746 young mussels using the Lake Pepin mucket. They lacked enough glochidia to get the *L. ligamentina* off the ground. In 1919, Lake Pepin muckets were raised in all five troughs planted. In one, 2,008 were counted (9-17.5 mm.), similar to the growth in the wild. Over 550 *L. ligamentina* were reared (5 to 8.5 mm.), and 2,006 yellow sand-shells were raised in a trough (5.5 to 12 mm.). This was the first record of artificially reared yellow sand-shells in quantity.

The 746 *L. luteola* reared in 1918 were over-wintered in a crate measuring 5 feet square by 8 inches deep that was submerged in an earth pond. In 1919, the crate revealed 238 young mussels, or a survival rate of around 32 percent.[97]

In 1920, H.C. Minch and T.K. Chamberlain conducted experiments in rearing mussels in troughs under a temporary shed, the fourth year of such experiment. The lab data sheet reveals 28 numbered troughs, of which 20 were in use or had an entry. Infections were carried on from June 8 (also the 11th, 12th, & 14th), through July (8, 14, 16-17, 21 & 31) and on to August 3rd and 9th. Gar and Black Bass were used (plus one trough of 5 *I. punc.*), with three to twelve fish in each trough. Anywhere from approximately 408 to 7224 (mostly 3000-5000) glochidia were used in the infection. When inventory was taken October 25 to 30, eleven of the troughs contained juvenile mussels, although two had very few. The most found were in trough 23, where five black bass had hosted *L. luteola* (c. 3736), and 1712 juvenile luteola were found. But then the same species (about 1678 glochidia on ten black bass) were used in trough number 19, and only two mussels were found. It seems that the scientists got inconsistent results in many of their experiments during the 1920s. *L. ventricosa* (c.4980) infecting five black bass in number seven yielded 980 juveniles, and *L. luteola* (c. 4411) on seven black bass in number 16 yielded 857 juveniles.[98]

By 1923, the Bureau of Fisheries felt that enough was known about survival and growth of juvenile mussels "to warrant the establishment of a small rearing system at Fairport." They added 100 to the 42 previously existing troughs at Fairport, each one 16 feet long, 15 inches wide, and 12 inches deep. Black paint covered the bottom of each trough and lids were placed to keep out the light. Darkened troughs, they found, produced twenty-five times as many juvenile mussels as ones open to light. It was assumed that the dark troughs simulated "natural conditions on the bottom of mussel-bearing streams." The troughs were fed by gravity-fed water that had settled out in two ponds before entering the troughs. Lake Pepin or fat muckets were used to infect black bass, and by 1923 they produced 500,000 mussels approximately one half inch in diameter. The 1924 annual report notes that the new troughs were not sheltered by a shed, as were the original ones. The old troughs produced 160,000 young mussels, but the new ones not protected from the sun had a total failure.[99]

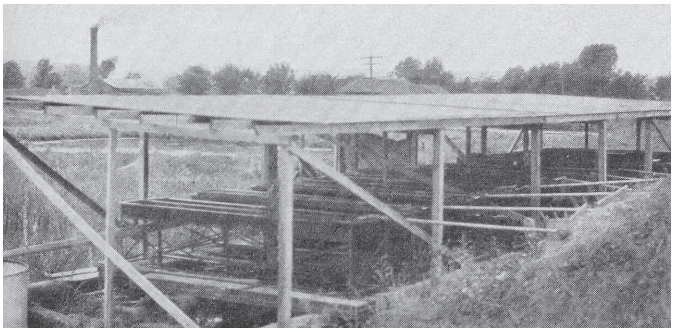

Fig. 34. Troughs at Fairport, shielded from the sun. Fig. 2, plate 2, *Report of the Commissioner of Fisheries* 1920.

Use of the ponds

Six original pages of lab records from 1920 that chronicle mussel experiments in various Fairport ponds survive in the records of R.E. Coker (located in Chapel Hill, North Carolina). Incomplete as they are, they give a bit of insight into how the ponds were used. Pond 1 D, for example, was drained in the springtime, when 13 *L. luteola* were found and replaced in the pond on May 25. Fourteen *L. luteola* and five *A. corpulenta* were added from pond 2 D. Pond 2 D was drawn on May 14, and 136 *L. parva* were removed. After it was refilled, tight bottomed enclosures were placed in the pond to retain infected fishes. Eight of these enclosures were used, most containing bass and one with gar, all of them containing four or five fish each. The infections were performed on June 25-30, and August 14-16, with approximately 1000 to 1500 glochidia per fish. The results were checked October 16 to 18, when they found the bass in enclosure one had yielded one *L. ligamentina,* number two produced seven L. luteola, three produced 60 luteola, and number

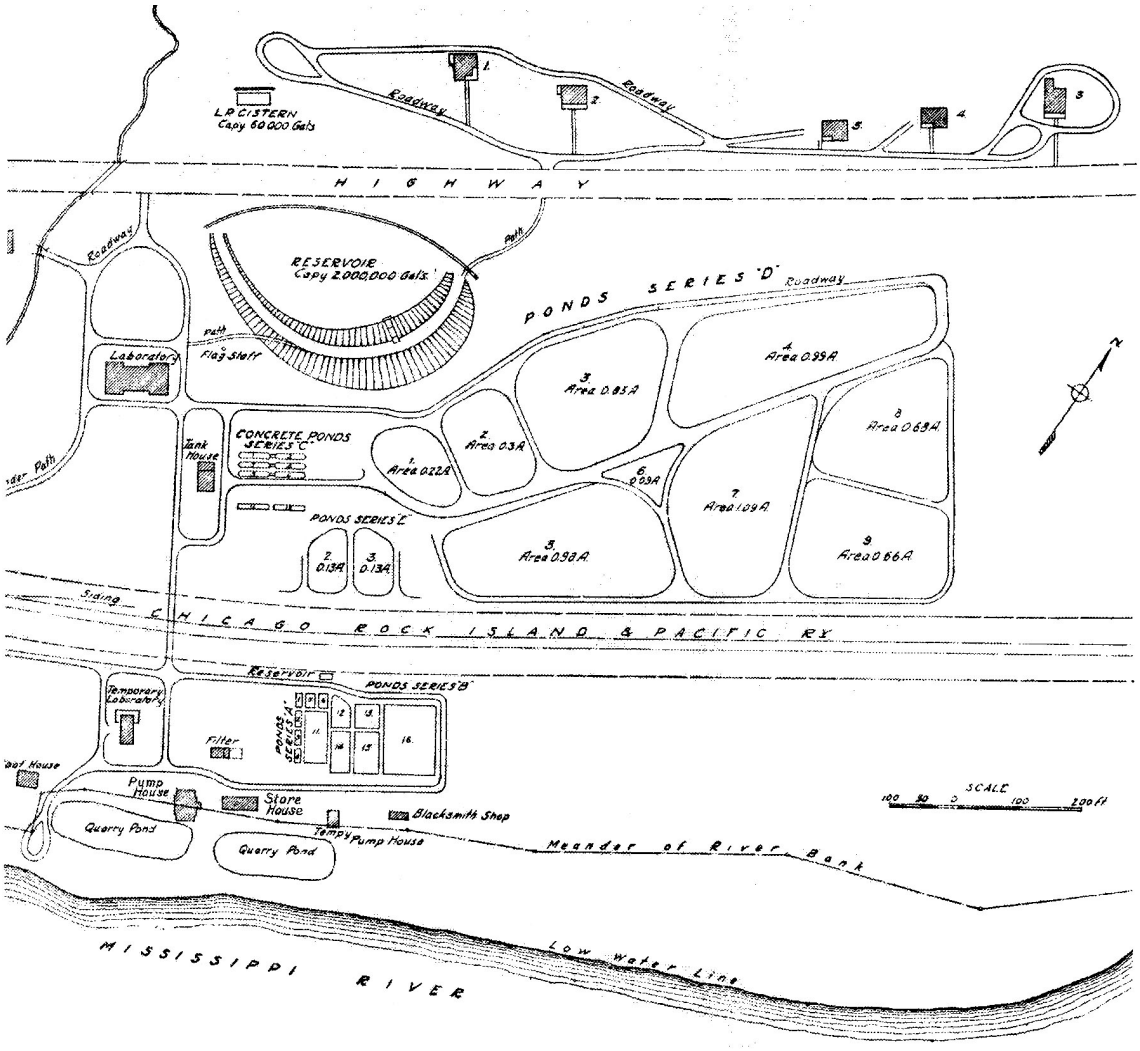

Fig. 35. Map showing existing and planned ponds at Fairport.
From Coker, "Fairport Fisheries Biological Station" (1914).

four 662 *L. luteola.* Enclosures five through eight, bass infected with *L. luteola* and gar infected with *L. anodontoides* failed to produce any juveniles. To find the juvenile mussels, sand in each enclosure was screened through No. 8, 10 and 20 screens.

Pond 3 D was used to measure the growth of *L. luteola* and *A. corpulenta.* When the pond was drawn on May 3, mussels were removed and some of them marked, measured and returned, and ones that had been marked before were again measured. In this way, measurements of 22 individuals were made (in December 1915, May 1916, November 1917, October 1918, and November 1919), although not all of them could be found for subsequent measurement. Oddly, the lab sheet does not specify which species is measured. Shell no. 7, for example, grew from 29.4 mm. To 82.9 mm. in those four years. Pond 8 D was to be used for an experiment with floating open bottom crates, but "owing to the leaky condition of the outlet it was necessary to draw the pond June 8th and install an outlet pipe." Only one marbled mussel was found in the pond, but with wet conditions more could have remained in the mud. Fairport personnel removed 308 living and 28 dead L. luteola, placing them in trough 8, and later in October, the surviving 282 were returned to the pond.

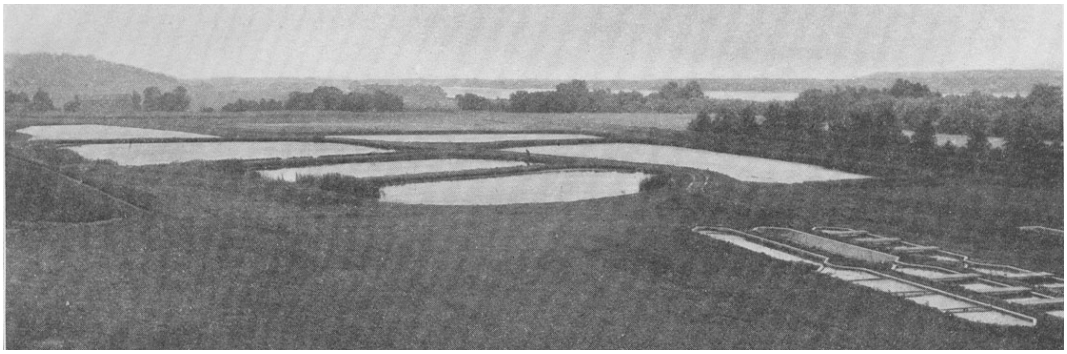

Fig. 36. Series C and D ponds at Fairport.
Plate 77 in Coker, "Fairport Fisheries Biological Station" (1914).

Pond 16B, measuring 0.195 acre, containing large mouth black bass and orange spotted sunfish showed that "under close conditions no material increase in bass will take place even under reasonably favorable food conditions." The cement ponds of series E evidently did not host experiments in retention of bass fry and adult or fingerling *L. humilis* because there was not enough pond space. Series C ponds were "in bad order" for the entire season, except one used by Dr. Howard. In 1931, six new ponds were added at Fairport, designated D11 through D16, and three of the E series and three of the B series were consolidated into larger ponds.[100]

The 1923 annual report from the Manchester National Fish Hatchery in Iowa mentions that their fish had parasitic growth on the gills. In ways similar to the folks at Fairport, they constructed long narrow ponds with a good water supply, earthen bottom and plant growth "to supply them with their natural requirements as closely as possible." Unfortunately, the remedy was "not particularly effective."[101]

For a time, partially-controlled ponds along the Mississippi bottomlands were used in addition to the ponds at Fairport. Around 1935, those ponds along the river were abandoned because the nine-foot channel would change conditions, perhaps reducing their water supply. "Very little can be expected of ponds over which we do not have absolute control," the La Crosse annual report for 1935 stated. The wrong species of fish got into the ponds, sometimes eating the desirable species.

"A distinct departure"

Coker et al. thought their methods "a distinct departure from the methods previously used and gives the operator complete control of conditions throughout." They were encouraged and wished to expand the operations, as well as perform more research into what exact conditions (enemies in troughs, food, artificial feeding, and bottom material) might encourage their growth. Fine sand, they thought, was probably the best bottom material. Coker et al. closed their 1922 report by stating their belief that "the valuable Lake Pepin mucket can be reared in quantities, under conditions of control." In 1923, the Bureau felt that the experiments with the troughs, among other things, gave "an indication of the possible usefulness of controlled methods over the present method" of infecting fish and simply releasing them, "where it is unlikely that more than a 2 or 3 per cent survival results." Mussel rearing, they believed, could be conducted "with results more tangible, cheaper, and less limited by natural physical, chemical, and biological factors."[102]

State of the Art in the 1920s

After reading these reports in the *Bulletin of the Bureau of Fisheries,* and after looking through the surviving lab records, we still are largely in the dark about some of the specific technical questions we'd like to know about, such as the chemical composition of water used in propagating mussels, or how they fed their juvenile mussels. Part of the problem is that most specific data sheets and records were thrown away. This sometimes happens when someone working at an agency retires or moves on. These people often have saved many records, and may be viewed as "packrats." New folks are not personally attached to prior work, attach a lesser value to it, and are more willing to clean house (literally). Secondly, the state of the art was different than it is today. The knowledge base was more basic, so they didn't keep track of some things we wish they might have. Of course, these scientists were far beyond the "vital essences" of the nineteenth century, but their use of "infusoria" gives us an inkling about the state of knowledge. Although chemistry was one of the first sciences to professionalize with formal modes of communication, laboratory standards, courses of study, and one or more professional societies, for our mussel scientists it seems that chemical analysis of the water became a more important concern during the 1930s, with Robert Coker and later Max Ellis realizing the great damage that pollution was working in the Mississippi. Max Ellis and his crew headquartered at the University of Missouri School of Medicine (he was a physiologist) later developed techniques of water chemistry analysis to use on the Mississippi River. While Fairport scientists during the 1920s were aware of mineral content of waters and mussels, there remained a lot to learn about water chemistry. Third, we see how scientists contrasted "natural" and "artificial" conditions. To explain their difficulties in propagation or in raising young mussels, we've seen that they appealed to the idea that something was lacking in the artificial environment provided. To solve the deficiency, whatever it was, Fairport would provide conditions as close to natural as possible. They didn't know what was lacking, but clearly mussels in undisturbed nature had all that they needed. They (Howard in particular) had confidence that getting closer to natural conditions would carry the mussels past the gaps in their own knowledge.

Fig. 37. Staff of the Fairport Biological Station gather in front of the main laboratory building in 1921. Courtesy Fairport Fish Hatchery, Iowa Department of Natural Resources.

Coker's Scheme for Sectional River Closures

Robert Coker was a primary advocate of the idea of closing rivers to mussel harvesting, section by section. The practice was initiated on Lake Pepin (1919-24) and for a time appeared successful. T. K. Chamberlain and J.B. Southall made surveys of Lake Pepin Mussel populations in 1923 and 1924. Immediately following the closures, harvests increased by thirty per cent, even before the season was half over. The sectional closures lasted several years, but around the year 1933, the Minnesota and Wisconsin legislatures repealed (or allowed to lapse) the legislation, when it appeared that mussels were not breeding there in numbers.

Evidently, state legislatures did not embrace closures, nor did they act in concert, despite the pleading of scientists and efforts of the Bureau of Fisheries. At that time, the questions included "who owns the mussels?" and issues of riparian rights. In 1920, for example, the "Barrett bill" was debated in Kentucky, a measure that would have regulated mussel harvest. They were still talking in 1926, but no action was taken. Laws were proposed in other states as well, and Coker watched the legislative sessions with great interest.

Closed seasons were fought by local clammers, some of whom argued that although a particular bed might be fished out, there were plenty of mussels elsewhere. They also argued a closed season would only profit the wealthy, while the small scale clammer could "illy afford to be thrown out of employment."[103]

Disappointment at the Fairport Biological Laboratory

The early 1930s seemed tumultuous at Fairport. The staff was re-organized in 1930. One of the assistants, Richard Zalesky, wrote to Elmer Higgins in Washington, calling Dr. Wiebe "the bunk" as well as an "unhuman supervisor," and resigned his position. In 1933, Frank Bell was appointed Commissioner of Fisheries. When he resigned six years later, the *Fisheries Service Bulletin* noted that "a shake-up in the fish cultural activities of the Bureau followed Mr. Bell's appointment, which resulted in the closure of unproductive stations." Bell's actions may well have affected the Fairport Biological Laboratory. By 1933, fish culture operations at Fairport began to increase, while efforts aimed at the propagation of mussels began to decrease.[104]

In his book about the history of California fisheries, Arthur McEvoy traces the boom and bust of three major fisheries over time. Scientists mis-read cues from nature and misinterpreted data, demonstrating how difficult it was to understand wild species in marine environments. A similar phenomenon was involved in the story of mussel populations on the Mississippi. One of the great problems was the lag time between action and information. McEvoy notes that "a given level of fishing effort has a far greater impact on the population when the stock is at low levels than when it is abundant. If a seiner can find fish, it will take huge catches even as it wipes out the last schools in a population." Similarly, harvesters continued taking mussels even at low population levels, when by all apparent indications there were plenty of mussels for the taking. At various times, popular wisdom remained at odds with reality or with the latest scientific knowledge. Even within the Bureau, it seemed there was debate about the relative success of the mussel propagation program that may have stemmed from inter-departmental competition for funds. Although scientists had claimed success for their methods of mussel propagation, by 1926 the Bureau's Washington office reported that "natural causes have contributed more to the increased production of sand shells than has the innoculation of fishes with the young of this species."[105]

Despite the 1929 official optimism of Bureau of Fisheries Director Elmer Higgins, it seems that at Fairport itself, despair set in as it became apparent that mussel populations had been devastated. Thomas K. Chamberlain, Fairport Station director in 1930, wrote that Pepin was "simply gone" as a mussel producing body of water. Chamberlain wrote to Elmer Higgins (Division of

Scientific Inquiry) on February 13, 1930, conveying data showing "the complete breakdown of all fisheries in Lake Pepin." Evidence included reported declines in the catches of the regular commercial fishery, the infection crew's declining catch of game fish intended for infection, and a detailed mussel survey. Apprentice Fish Culturist George W. Davis reported that the upper end of Lake Pepin was filling in with silt of a foul nature, most probably from packing plants in south St. Paul. Scientists had been aware of pollution problems from as early as 1913, when S.A. Forbes, director of the Illinois Natural History Survey, had written to Dr. H.F. Moore, in charge of the Bureau of Fisheries' Division of Scientific Inquiry. He worried that the subject of pollution "is so infinitely complex . . . . that I fear life is too short for me ever to complete this work according to my first intention . . . ." From St. Paul to Keokuk, the Mississippi River in 1930 appeared to Chamberlain "just about a thing of the past" as a producer of fish and mussels. He reported the fishermen "as bitter against the Keokuk Dam as ever, claiming that no fish come up through the locks." As early as 1926, the host fish (skipjack) for the ebonyshell mussel *(Quadrula ebenus,* a highly valuable species for button manufacture) was evidently missing above the Keokuk dam. Without the host fish, there was no hope for the glochidia. It seemed mussels in the wild were doomed. Chamberlain urged Higgins to drop the work in Lake Pepin and "advise the states to throw the entire river open to unlimited shelling," giving as a reason the failure of the Minneapolis sewage control project. Chamberlain noted "the nine foot channel proposition" as "an additional reason for throwing the river wide open pending the completion of the engineering work."[106]

Between about 1930 and 1932, the Bureau of Fisheries changed policy twice, restricting mussel harvest then opening it up again. Two things were going on. First, after all the work at Fairport Station, Coker surmised that the artificial propagation and release of growing mussels could not keep up with the harvest. Regardless of how many mussels the station produced, the insatiable harvest consumed the product, and, it seemed, a bit more. Additionally, river conditions had been altered enough to create an environment that did not encourage mussel growth and reproduction. Historian Harriet B. Carlander suggests the bureau opened up mussel harvest because it became apparent Dr. Ellis's new method of propagating mussels (without host fish in artificial nutrient) "would be unavailing in maintaining the supply in waters where natural conditions had been so altered." Fairport scientists did not give up on technique, in other words, but rather came to believe that the river had become inhospitable for the growth of mussels. Certainly, low harvests after fishing restrictions were lifted indicate that mussel stocks were severely depleted by the early 1930s. By 1932, commercial harvesters and "mussel diggers" (sportsmen or those who gathered mussels for the table) were at odds, blaming each other for declining mussel populations. Advising the Izaak Walton League before their meeting with the Pearl Button Manufacturers Association, Max Ellis called for "the closing of fresh-waters to mussel fishing during the major fishspawning season."[107]

Contemporary conservationists had in mind supply of a major industry, rather than the survival of any particular species. Carlander suggests that "the only hope for the continuance of the freshwater pearl button industry seemed to lie in the artificial propagation of mussels under controlled water conditions on 'farms.'" Attention seemed to shift to a factory model of completely artificial mussel production, but it did not seem to catch on, partly due to a shift to plastic buttons during the 1940s.[108]

Max Mapes Ellis

The fourth major character in the attempt to rear mussels at Fairport, and perhaps one of the more colorful, or at least persistent personalities in this story, was Max Mapes Ellis. He confidently predicted he could propagate ten to a hundred times more than his predecessors. Like Coker, he ended up working on more general pollution and habitat problems, at the same time as funding for his mussel propagation work dried up. A physiologist at the University of Missouri, Ellis began work on mussels at Fairport by 1925, and maintained absolute confidence in this work until 1942, when Elmer Higgins at the Washington office of the U.S. Fish and Wildlife Service (organized in 1940 out of the former Bureau of Fisheries) cut off his funding.

We know that Ellis began his work at Fairport by 1925, when Thomas K. Chamberlain directed the station. Ellis found that ultraviolet rays of sunlight were fatal to glochidia, clearing up the reasons why mussels seemed to do better in the dark. Secondly, he discovered that the "acid-alkali balance of the blood of the fish to the glochidia encysted in its gills" was important. This factor had significance for developing Ellis's pet project, propagating mussels without the parasitic cycle.

Fig. 38. Max Mapes Ellis, inspecting bottom samples on the Mississippi River near Oquawka, Illinois, 1931. Courtesy of Cornelia Motley and Philip V. Scarpino.

By 1926, Ellis believed he was well on the way to eliminating the parasitic stage of the mussel life cycle in laboratory propagation. This concept can be found mentioned as early as 1916 in the *Report of the U.S. Fish Commissioner,* under the activities of the biological laboratories. It's fair to imagine that the idea may have come out of the Woods Hole Marine Biological Laboratory.

Working with his spouse, Marion D. Ellis, Max Ellis started with an artificial infection of *L. fallaciosa* Smith (the Creeper or Slough Sand-shell) on its natural host, the short-nosed gar, *Lepisosteus platostomus* Rafinesque. He then dissected glochidia out of their cysts at eighteen and at ninety-six hours after encystment, noting that the ones at 18 hours didn't look any different than glochida fresh from a gravid mussel's marsupial pouch. These glochidia were immediately transferred to one of several experimental solutions and observed. In one of the solutions, glochidia grew twelve days until they developed as much as the control glochidia encysted on fish. This batch was transferred to river water where they "made their final transformation in less than a half hour." Actually, he noted, the *in vitro* glochidia made it through the entire process a bit more

quickly than the control group, but didn't hazard a guess as to why. For three weeks, these young mussels were watched, and to Ellis's surprise, not a single one died. Normally, one would expect "a rather high mortality" on the first few days after a natural parasitic cycle.[109]

The successful solution, he wrote in a 1926 issue of *Science,* contained "sodium chlorid, potassium chlorid, calcium chlorid, sodium bicarbonate, dextrose and a mixture of amino-acids, together with small quantities of phosphates and traces of magnesium salts" (see addenda). He found that solutions "containing only inorganic salts were neither adequate neither to produce growth and differentiation nor to maintain glochidia already well started on their way to transformation." So, depending on the particular solution employed, he noted one could demonstrate 1) "parasitic life on the fish is not essential", 2) encystment provided glochidia protection against bacterial and protozoan enemies, and 3) that the glochidium "is a true parasite while on the fish, receiving essential food substances from the host fish." While Ellis seems to argue against himself, this seems to be Ellis's convoluted way of saying that success of the *in vitro* specimens depended on the solution used, that the nutrient solution must provide the essential food substances.[110]

The obvious problem with this work was that the glochidia had been dissected off their encystments on host fish. There is no indication in the 1926 *Science* article that Ellis had taken glochidia directly from a gravid mussel and placed them in one of his solutions. Perhaps he was trying to satisfy his curiosity about the function of encystment. Very soon after that publication, the Ellis method started to utilize glochidia removed directly from the marsupial pouch. At any rate, Ellis now believed he had made a breakthrough to propagating mussels. If he could skip the parasitic stage, he could raise as many mussels as the equipment allowed. Indeed, he envisioned rows upon rows of apparatus looking much like round glass jars, full of developing and transforming glochidia. A later explanation of this system described its foundation on a "physiological nutrient solution . . . based on the amino acids, easily obtained from waste fish and from animal flesh, to which acids certain commercial chemicals are added. The mussel culture apparatus consists of a number of small units containing the solution, each unit capable of handling a large number of glochidia at a time."[111]

Although Ellis wrote that he intended to publish "detailed data" on his experiments with the solution, he never published the specific formula. In fact, his secretive behavior regarding his experiments eventually seemed to frustrate Elmer Higgins, director of the Branch of Scientific Inquiry at the U.S. Bureau of Fisheries.

In the summer of 1926 at Fairport Station, Ellis completed his nutrient solution "which would carry mussel glochidia through the same metamorphosis they would normally undergo as parasites upon fish." Only individual glochidia "were so carried through, difficulty being experienced with bacteria associated with the glochidia," multiplying and destroying the glochidia. In 1927, Ellis employed "a method of sterilizing the glochidia directly after being taken from the marsupia of the parent mussels" which did not injure the glochidia. Unfortunately, a further description of this sterilizing technique is not evident in the archival sources. He then was able to carry through groups, first dozens, then hundreds at a time. By 1927, he felt his nutrient solution was perfected.[112]

In the fall of 1927 and the spring of 1928, Ellis took a sabbatical leave to tour European laboratories and work with colleagues. He used what he learned to improve Fairport's lab techniques and expand the numbers of mussels produced. He based himself out of the University of Glasgow in Scotland, working under the direction of Professor D. Noel Paton and with the daily cooperation of Professor E.P. Cathcart, a protein-chemist. Ellis was specifically interested in studying the guanidines from a physiological point of view, "the relations between the guanidines, blood and muscle," guanidine poisoning, and comparisons between invertebrates and vertebrates.

Ellis wrote to Guy L. Noyes, dean of the Medical School at the University of Missouri, advertising the offer of "the Button men" to fund a fellowship that would pay for lab assistants and supplies for Ellis's lab at the University of Missouri, and pointing out the connection between mussels and his other work: "The raising of these embryos in artificial nutrient solutions has opened up new approaches to several physiological problems, the actions of various salts, ions, vitamins and metabolites on development, differentiation, cell-composition and tissue-composition being gross problems now in hand. These are not without their medical contacts, in fact part of my interest in cataract came from certain findings on the mussel embryos, and I hope to advance the cataract work through this proposed laboratory." Ellis visited the Marine Laboratory on the Island of Great Cumbrae, Frith of Clyde where he enjoyed the privileges of the "Coates Research Room and Table." He visited several medical labs in England, and then traveled to Holland, Germany, Czechoslovakia, Austria, Switzerland, and Belgium. Paton's personal introductions made "our sojourn here in Europe pleasant as well as profitable," in the sense of all that he learned at several European research laboratories. Upon his return, Ellis designed six units of apparatus to culture mussels, each to handle "upwards of half a million glochidia." Although ripe glochidia were scarce, the equipment got a fair trial. Unfortunately, no diagrams or photos of the equipment survived.[113]

During 1928, Ellis reported almost all the gravid mussels collected from the field were infected with a protozoan parasite known as Clark's bug, believed to belong to the genus *Conchotherius.* This was harder to get rid of than other bacteria infecting glochidia. The protozoa seemed to multiply rapidly and foil Ellis's new equipment. Ellis and Chamberlain traveled to several states but had difficulty finding mussels free of the parasite. In the lab at the University of Missouri, Ellis and his assistants devised a method to separate out healthy from infected glochidia. In 1928, Ellis also discovered that the glochidia of *Lampsilis anodontoides* (yellow shandshell) and *L. ligamentina* (river mucket) were not held in the brood pouches overwinter in a ripe stage, as was previously thought. The glochidia only ripened just before their release in spring. This meant that in previous years all the propagation work that had been done after midsummer was of little value.[114]

Archival evidence suggests Ellis did indeed produce juvenile mussels. The first plants of juvenile mussels were planned for 1928, at least nine and perhaps as many as fifteen to be conducted 50 miles apart in Minnesota, Wisconsin, Indiana, Kentucky (the Ohio River and the Cumberland), Arkansas (the White and the Black Rivers), and on the Mississippi River between Iowa and Illinois. Ellis hoped to plant one million cultured mussels during the summer of 1929.[115] In 1929, Ellis reported that he intended to develop "individual mussel culture units" to handle more glochidia. He claimed to have tripled the capacity of the units over six months, so now each unit would handle 1.5 million at a time. Ellis wrote that "several such units have been operated to capacity, several times producing some five or six million young mussels" over the summer and fall. By producing so many young mussels in the "few mussel culture units," Ellis assumed "that the large-scale production of mussels is established as economically feasible." He removed 2 million mussels produced at Fairport to Columbia by automobile, "where they arrived in perfect condition," showing that they could be "transported safely to streams for planting." The best survival rate, he thought, could be obtained by transporting young mussels during the first three days following metamorphosis, or three weeks after that time.[116]

By 1930, Ellis had a staff of eleven working at the Bureau of Fisheries' Columbia field unit, housed in eight rooms of the University of Missouri's Medical Building, and organized as part of the graduate school. Max Ellis, Marion Ellis, and Amanda Merrick had completed evaluating the blood

of fresh-water mussels, comparing stressed populations to groups theoretically not under stress. They were attempting to assess the effects of "progressive changes in stream conditions," including navigational improvements in the river, and particularly municipal and industrial pollution that had "materially altered the natural habitats" in the Mississippi drainage. Mussels were subjected to varying concentrations of potassium salts (potassium chloride, potassium carbonate, and potassium sulphate, in 0.10, 0.25, & 0.50 percent solutions), magnesium salts (magnesium sulphate and magnesium chloride, in solutions of 0.25 , 0.50, and 1/00 percent), and sodium and calcium salts (solutions of 0.25 to 1.00 percent). They found that although small quantities and proportions of inorganic salts were present in mussel blood, those salts were essential for life activities. These salts were balanced against each other, and mussels tolerated them only within rather narrow limits. Mussels proved to be very sensitive to "changes in water composition," including concentration of salts and pollution. The team also determined something of practical importance in the transportation of mussels. They iced down some mussels, discovering that the cold numbed them too much, so that the adductor muscles relaxed, the shells gaped open, and the water they harbored spilled out. Those mussels died much more quickly than mussels packed in "moist sphagnum or other damp material." Disappointingly, there are no further clues in their publication regarding the specific salts Ellis used in his nutritive solution.[117]

Changing to the "Ellis Method"

In early 1930, The Bureau decided to put the "Ellis method" on a producing basis. Fish Commissioner Henry O'Malley wrote "it is our intention to operate this apparatus on a commercial basis at the Fairport, Iowa, Laboratory of the bureau as rapidly as a supply of healthy glochidia can be obtained." Elmer Higgins, Chief of the Division of Fishery Biology, planned to put two mobile units into the field, each capable of producing 25,000,000 to 50,000,000 juvenile mussels. Higgins wrote that assistants, "oddly enough, will probably be women trained in hospital and bacteriological technique," since the task required a "great degree of manual skill as well as training in sterile procedure." Ellis and crew were on the lookout for favorable localities "in waters of suitable chemical composition known to be definitely free from deleterious domestic or trade wastes, and free from sudden fluctuations in water level." The Bureau wanted assurances from the states that mussels would enjoy protective legislation.[118]

The U.S. Bureau of Fisheries seized upon Ellis's new method with enthusiasm. By 1930, the Bureau clearly distinguished between the "controlled natural propagation" method, and the new "artificial propagation" or Ellis method. The older method called for infecting rescued fishes, was practiced exclusively from 1915 to at least 1925, and was materially improved by Ellis. The natural infection method continued to be used during the 1930s, but the Bureau wanted to switch to the Ellis method because of the pollution situation in the rivers. The button manufacturers preferred the original method, believed it worked well, and distrusted the new-fangled technology. For its part, the Bureau came to doubt the reported numbers of planted (encysted) glochidia prior to 1924.[119]

In 1931, the Fairport Station added a new series of troughs in the aquarium room, and the "old lab" (probably the original temporary lab) was fitted out with a series of troughs, presumably to help Ellis with his work. Meanwhile, Ellis experimented with food for mussels, suggesting that "mussels may be fed various inexpensive foods successfully and the health and activity greatly improved." He did not say what that food was. He also concluded that "the calcium content of the water can be controlled and a calcium level suitable for proper shell growth" could be obtained "by the simple expedient of splashing the intake water through piles of limestone rubble."[120]

The problem of habitat

Notwithstanding his perennial optimism, by 1930 Ellis found a dire situation for mussels in the Mississippi River. In the portions of the Mississippi, Ohio and Tennessee Rivers that he studied, Ellis found no replacement of yellow sandshells less than 6 years of age or ebonyshells less than 9 years of age. This was distressing because these were the two of the most important commercial species. In the upper Mississippi, he found only two of fifteen commercial species, the maple-leaf and the hickory-nut, replacing themselves fast enough to maintain the species. The Bureau of Fisheries reported a "startling decline in mussel production" in the Upper Mississippi river. Lake Pepin was the prime example: in 1914-15, the lake had produced 3,000-4,000 tons of commercial shells *(Lampsilis luteola* a primary species), in 1919, 200 tons; in 1924 after the four year closure, it produced 2,000 tons, but the catch again fell off rapidly, in 1926 producing 164 tons and in 1927 only 50 tons. In 1929, areas that had been closed for five years were re-opened, and officials estimated production of commercial species at a disappointing 600 tons. With detailed sampling, the Bureau estimated a 70 per cent drop in the total mature mussel population in just one year. In 1931, Ellis reported "no conditions suitable for planting yellow sandshells" on the Ohio River between Cairo, Illinois, and the mouth of the Green River, or on the Tennesee River across Kentucky.[121]

Furthermore, Ellis was having great difficulty finding enough brood-stock, because the brood pouches of gravid yellow sandshell, slough sandshell, Lake Pepin mucket, river mucket and pocketbook mussels "were found to be heavily infested with bacteria and infusoria." The unit inspected over 6,000 gravid mussels in 1930, finding few suitable for propagation work, many of them having "black masses filling units of the marsupium normally occupied by conglutinates of glochidia." Ellis wrote that "in addition the usual bacterial flora to be expected in any decomposing mass of tissue, one particular organism" similar to *Bacillus proteus,* comprised the main organism in these infections. In the spring of 1930, the Bureau requested button manufacturers to find gravid mussels, pack them in wet moss or wet gunnysacking and ship them express "in an ordinary wooden box, candy pail, or small keg" to Dr. Ellis at the University of Missouri. By the late 1930s, the only places he found with small quantities of good quality gravid yellow sandshell were in northeastern Arkansas and southern and central Texas. Ellis simply could not find enough brood spawn to propagate them in numbers. Aside from disease, these were the places that still had good river conditions. Finding enough gravid mussels was one of his biggest problems.[122]

Fig. 39. M.M. Ellis "collecting bottom samples from cruiser with Peterson dredge." Fig. 3 in Ellis, "Detection and Measurement of Stream Pollution," 1937.

The first problem was pollution. As early as 1923, Fairport reported that its mussels had become infected with a ciliate (Conchopthirius)

that invaded the marsupia and destroyed glochidia. Sewage entering the Mississippi from Davenport, Rock Island, and Moline was thought to be the cause. Fairport scientists feared that pollution of the Mississippi River would negatively affect their trough experiments "by destroying the juveniles as soon as [they were] dropped" from their host fish. In 1930, Elmer Higgins [Chief, Division Of Scientific Inquiry] thought "the outstanding need" was "a thorough physical, chemical, and biological study of all actual or potential mussel-producing waters in the Mississippi and Gulf drainage to discover waters favorable to the extension of mussel culture" and "an urgent need for a thorough study of the biological and physiological effects of the various polluting substances found in streams." Progress in mussel culture, wrote Ellis, was limited by not knowing "the fitness of inland waters to support aquatic life . . . . Conditions are becoming so serious in these waterways that prompt action is needed in providing ways and means for disposing of domestic sewage and trade wastes other than by using the rivers as open sewers."[123]

The second problem was erosion silt. Ellis judged that silt directly smothered mussels "in localities where a thick deposit of mud is formed," and young mussels were particularly vulnerable to oxygen deprivation brought on by silt "blanketing the sewage and other organic material which in turn produce an oxygen want . . . ." Pollution and silt added up to a serious situation that threatened "extensive and rapid reduction of the mussel fauna . . . almost to extermination . . . if the erosion and pollution problems are not solved, in view of various improvements for navigation now existing or already authorized throughout the Mississippi, Ohio and Tennessee drainages." Because of the great changes in river conditions from 1925 to 1930, Ellis wrote, "the present problem of mussel culture is not one of propagation, either natural or artificial, but the maintenance of a suitable habitat for a period of at least five years to allot maturing of the mussels planted."[124]

Ellis's pollution studies

From 1932, Max Ellis was placed in charge of "investigations in interior waters," consisting of the mussel propagation and the pollution studies. We surmise that it was Ellis who started the pollution study in 1930. From 1934, the pollution study was called F.P. 41, "Stream Pollution Studies in the Middle West." The work was centered in Ellis's lab at the University of Missouri in Columbia. Scientists surveyed 800 miles of the Mississippi, various streams in 21 states, as well as mining and natural alkali pollution in Idaho, North Dakota, and Montana. Mining, mine wastes, and the processing of metals were perceived as problematic, as well as other industrial processes such as tanneries that created wastes that ended up in rivers. Ellis developed assay techniques, publishing an article on the detection of stream pollution in 1937. He detected, measured, and documented chemicals in rivers including sodium chloride, acetic acid, hydrochloric and sulphuric acids, tannic and tartaric acids, the salts of eight metals, including aluminum potassium sulphate (tannery wastes), lead nitrate (mining and smelting wastes), and ferrous sulphate (wire and tin-plate mill waste). These studies continued through 1940.[125]

The pollution studies must have taken quite a bit of time, reducing the amount of energy Ellis could put into the mussel propagation work. Similarly, the attention of the Bureau of Fisheries was increasingly diverted toward the pollution studies. The pollution investigations on the Mississippi River were first mentioned in the Bureau's 1930 *Annual Report.* Beginning in 1934, we see that the Bureau's *Annual Report* has more to say about pollution studies than about mussel propagation, and beginning in 1938, the report simply does not mention mussel propagation. Through 1947, Ellis continued to publish on the subject of water pollution with the Fish and Wildlife Service.

Fig. 40. Pollution studies field crew engaged in stream-side operations, equipped with chemicals, sampling outfits, dredges, and seines. Fig. 5 in Ellis, "Detection of Stream Pollution" (1937)

Decline of the Fish Rescue Program & Associated Propagation

In 1930, the Bureau of Fisheries announced that "due to pollution in the upper Mississippi Region," it would no longer use the method employing rescued fish" to infect host fish and release them into rivers. Assuredly, pollution was a big concern, but the fish rescue program was coming to its end for other reasons. The fish rescue program, according to archival sources, was discontinued about the time the nine-foot channel was dredged on the Mississippi, or when lock and dams reduced the overflows. For example, the La Cross station's annual report for 1941 notes that no rescue work was performed at La Crosse or Genoa, "due to the water levels maintained by the U.S. War Department since the canalization of the Mississippi River." The La Crosse annual report for 1942 declares that rescue work was "no longer required since the nine-foot channel, except a very limited amount where water stage is exceptionally low and then only in the upper reaches of the pools." Additional archival evidence shows that as late as 1948 Iowa was still conducting fish rescue with good success, and the Fish and Wildlife Service was still performing "test hauls" in overflow areas below lock and dam No. 10.[126]

The records of the fish rescue work yield clues into the reduction of mussel propagation work. Annual reports for the combined fish rescue and mussel propagation work had columns for numbers of fish rescued, and among other items a column for the number of "larval mussels." For example, H. L. Canfield, Superintendent of the La Crosse station, reported in 1928 that 145 million fish were rescued, and 1.9 billion larval mussels, predominantly *L. luteola* (grass mucket), *L. ligamentina* (river mucket), and *L. ventricosa* (pocketbook), released in a state of parasitism on suitable host fishes. In 1930, they reported rescuing 20 million fish and releasing 1.8 billion glochidia. Although fish rescue continued, the 1931 report from La Crosse contained the note "no mussels," and the explanation that "mussel life has been almost wiped out." Adult mussels had become sterile through bacterial attacks on the larval mussels, adults perished because of polluted

water, and the river bottom was "entirely unfavorable for larval mussel growth and development." Each year through 1937, "no mussels" appeared in the column for larval mussels. Beginning in 1938, nobody bothered to enter any notation, and in the La Crosse annual report for calendar year 1943, the column for larval mussels no longer appeared.

The Homer Station also suspended infection work, as of its 1931 annual report, but continued the fish rescue work. The Homer Station closed as a regular station in 1934 after rescuing 20 million fish that year, but continued operations as did Lynxville, Marquette and other stations that carried out instructions from the Commissioner of Fisheries. In 1935, all the gear for the Upper Mississippi River Wildlife and Fish Refuge was stored at the Homer Station, and all the refuge's boat repair, motor repair, carpenter and blacksmith work, as well as seine and net repair was carried out there. Homer suspended rescue operations entirely in 1939, conducted no fish cultural operations in 1941 (but did lots of repair work), and by1943 the ponds were out of operation.[127]

Each year during the 1930s the Bureau of Fisheries' Annual Report included Elmer Higgins's "Progress in Biological Inquiries," the report of the Division of Scientific Inquiry. In 1933, Higgins wrote that "Research activities at the Fairport (Iowa) laboratory . . . have been entirely discontinued, owing chiefly to a lack of sufficient funds." Budget cuts due to the Great Depression could have restricted the Bureau's options in the early 1930s (before public works programs got underway). At this time the U.S. Bureau of Fisheries' Division of Fish Culture began to use the station predominantly for propagating warm-water pond fishes.[128]

As of July 1st, 1933, funds for operating the Fairport Station as a biological laboratory were cut off, and foreman Leslie H. Bennett took charge, "with a view to raising as many fish as possible with what money could be utilized for that purpose." The station retained two apprentice fish culturalists and the foreman, and the large lab was closed and all its equipment stored or transferred, presumably to some other Bureau of Fisheries station. The cottages stood unoccupied by 1934, and cottage #4, "formerly occupied by the shell expert," was in bad shape, while the director's cottage was "rapidly showing signs of the effects of being left vacant and neglected." Foreman Bennett suggested that in the local climate "unoccupied buildings are susceptible to rapid decay," and noted that in the large lab "the dampness is penetrating." In 1945, the lab building evidently housed POWs and their guards, who did some repair, painting and upkeep. The main lab may have been torn down by 1955.[129]

Ellis moves the mussel propagation to Texas

In 1932, "a large-scale experiment . . . on the growth, survival, feeding, and general health" of mussels was initiated at the U.S. Bureau of Fisheries' Ft. Worth station. This was undoubtedly the work of Ellis, sanctioned and supported by the Bureau. The Bureau built "raceways having various types of bottoms over which water of different depths [was] maintained," in which hatchery personnel planted mussels. They marked the mussels and at intervals emptied the water for direct inspection. The "economic species of Texas" were planted there, as well as "important species from Indiana, Iowa, Arkansas, Illinois, and Missouri." Tests gave them hope that "a very large number of mussels may be successfully crowded into a small space if proper water and food conditions" were provided. They claimed to have more than 6,000 adult mussels and more young mussels planted. Noting the "great difficulty encountered in obtaining suitable breeding stock," the Ft. Worth raceways and holding ditches would protect female fresh water mussels "to some extent from the inroads of bacteria and other organisms," and the glochidia was utilized for propagation "when properly matured." The Fort Worth Station had suitable water and relatively warm winters.[130]

Here again we note an important transition in thinking about the chances for recovery of

mussels in their native habitat. In 1930, Bureau Commissioner Henry O'Malley had written that "the maximum production without recourse to artificial propagation apparently has been reached." "The particular objective," Ellis wrote in 1932, "is the determination of the maximum number of fresh-water mussels which may be raised successfully in a given area by artificial propagation." What this means is that by the early 1930s, the Bureau was looking not to the river for the salvation of industries based on mussels, but to completely artificial propagation, what we might call "mussel farms." This is substantiated by the 1931 Annual Report of the U.S. Bureau of Fisheries, which mentions that the "transfer of attention from the reestablishment of the mussel beds in the natural habitats in the larger rivers, as the Mississippi and Tennessee, to the production of artificial beds in controlled habitats has made necessary extensive studies on the physiology of the fresh-water mussel."[131]

In 1933, Ellis wrote that in the raceways the volume of water was much less than in a river. Therefore, "proper bottom conditions" in a raceway "requires the constant flow of a large volume of water, so directed that the current will scour the bottom free of silt deposits." Even a quarter-inch of silt in the raceway "soon killed out even the adults" of most species. If decomposing algae or other organic matter was thrown into the equation creating a high oxygen demand, the deadly effect was increased. Of the commercial species, the Yellow sandshells seemed to fare the worst, and the River mucket from Indiana to resist the silt the best. The best survival in silty conditions was "made by the maple-leaf shell." Ellis thought that "the volume of water required for the power scouring of raceway bottoms would be too large and too expensive to be practical under most conditions of mussel farming, if large numbers of mussels are to be handled in small areas and all of the available space utilized."[132]

Ellis thought that since large volumes of water were necessary, "it was not feasible to raise mussels in large enough numbers on the bottom to make the project commercially practical, especially with the silt hazard." To step around the silt problem and to increase the number of mussels in a raceway "to a commercially desirable figure," he started experimenting with three types of crates placed in the raceways. Crates contained trays arranged in tiers that kept mussels out of the mud. Ellis thought 3 to 10 times as many mussels could be raised in such crates as might occupy the same space on the bottom. He crowded them intentionally to see how many could be supported, with and without "artificial feeding." Ellis also examined the effects of light, the spread of mites, and the growth of algae, as he worked with 10,000 mussels.[133]

Ellis carried on experiments in "food and food storage" at Columbia. He looked for the "ability of mussels to utilize various types of cheap material as food." Over 18 months, he determined that the Yellow sandshell could survive complete starvation for 10 to 18 months.

During the mid- to late-1930s, despite the problems with river conditions and notwithstanding ongoing difficulty in securing funds for his work, Ellis sustained his efforts. He continued to release juvenile mussels in the Mississippi, the Illinois, and other rivers where the mussel populations were failing. In 1936, the Ellis method was field tested in Arkansas, and indications were that equal increases in mussel populations resulted from the established method of mussel propagation and from the Ellis method. Research showed that plants from either propagation method resulted in about 24 % more [one and two-year old] mussels than control areas. The plants were composed of just two species, the Wabash mucket and the yellow sandshell, around 60% planted in Indiana and the rest in Arkansas. During the summer of 1936, about 40 million mussels, about half-and-half Yellow sand shell *(Lampsilis anodontoides)* and River mucket *(Actinonaias carinata),* were planted in locations 5 to 7 miles long on the White and Black Rivers in northern Arkansas. Ellis planned to sample and monitor those plants for the next five years. They hoped to double their plants in 1937, and there is evidence that they planted mussels in rivers that summer and again in 1938. Oddly

enough, this report is about our best clue as to what species Ellis was raising with his new method.[134]

The older method of "controlled natural infection" was used alongside the Ellis method all through the 1930s. In 1941, Edward W. Bailey, Acting Chief of the Division of Fishery Biology, reported that planting operations using natural propagation attained 2,292,000,000 fixed glochidia (estimated to be in a parasitic state). He wrote that 1.4 billion had been planted in Indiana and 0.9 billion had been planted in Arkansas. A new method introduced that fall placed the host fish "in tubs containing special fluids designed to cleanse their gills." Unfortunately Bailey did not go into further detail about the fluid. The effective rate of infection would be much better than before, when many glochidia initially became attached to their host, but fell off all too soon. With confidence he suggested that most of the glochidia would attach themselves to a host, and thus reported numbers could be considered "practically a minimum," a net infection rather than a gross infection.[135]

In 1940, the Bureau of Fisheries was subsumed in a general reorganization of federal agencies, with most of its functions taken over by the Fish and Wildlife Service in the Department of Interior. In December 1940, Ellis and Bertis A. Westfall departed Columbia Missouri to survey mussels in the lower Rio Grande Valley, central Texas, and southern Arkansas. During the summer of 1941, Ellis had been in touch with state officials, establishing a cooperative program between his laboratory and the states of Texas, Arkansas, and Indiana. Ellis pleaded with Elmer Higgins, suggesting that "in view of the complete program which now involves cooperation between three states," Higgins should visit to see in one place "our local planting, transplanting, and shipment for stocking." Ellis defended the mussel propagation efforts. He reminded Higgins that the last time they had met with the button manufacturers at the Bureau's office in Washington (1938), Ellis had pointed out the deteriorating condition of the St. Francis River from a sand-bottomed to a mud-bottomed stream. "Worthless" (to button manufacturers) mussels like the "creeper" and the "floater" were moving into portions of the St. Francis. But mussel propagation was "very successful where river conditions have permitted a fair trial." Still the optimist, Ellis wrote Higgins of mussel men telling him of "the surprising rise in the yellow sand population in the areas where we planted those shells."[136]

It is curious that annual reports from the Ft. Worth, Texas station (built in 1928 on 31 acres 7 miles west of the city) found at the D.C. Booth Historic Fish Hatchery do not mention the raceways that Ellis built for mussel culture, nor for that matter do they mention anything about mussels. The 1943 annual report does mention a lab building maintained by the Division of Fishery Biology. The 1955 annual report suggests that the building formerly used as a laboratory was converted into a third residence in 1946.[137]

The secret

The button manufacturers had funded a part of Ellis's work, and as early as 1929 they wanted a demonstration of his progress. Ellis advanced various excuses, reluctant to give any such demonstration. His biggest concern was that his technique might be stolen. In a letter to the chief of the Bureau of Fisheries, Elmer Higgins, he shared his worry regarding the "constant effort of reporters and certain spies to get into my laboratory and make away with the method . . . we have to be constantly on our guard." This was hardly in the spirit of scientific inquiry. After all, Ellis had taken a sabbatical leave in Europe, where he gained ideas for his laboratory techniques. Ellis became obsessed with protecting his method of mussel propagation, particularly his innovation of skipping the parasitic stage. Higgins advised Ellis that theft of his idea would not be a worry if he would merely apply for a patent. Even before the patent was granted, his method would be secure.

Unfortunately, because he did "not want to disclose the apparatus or formulae," he made a conscious decision not to put the formula in writing or publish his techniques.[138]

In 1941, Edward W. Bailey asked Ellis if he meant to use the entire $20,000 that had been allotted for mussel propagation and distribution. In 1942, the Fish and Wildlife Service had kept Ellis's work going by borrowing $7,000 from the appropriation for the propagation of food fishes. On March 2, 1942, Bureau chief Higgins wrote Ellis without ceremony that the allotment for mussel culture was scheduled for the savings estimates in the next fiscal year, and "no funds for this purpose will be available after July 1, 1942." Certainly, diversion of funds toward the war effort (following on the heels of a major economic depression) may have necessitated the cutting of all but the most essential operations. For example, the *Report of the United States Commissioner of Fisheries for Fiscal Year 1940* was not printed until 1950! Many activities in American conservation simply lost all their energy when the war began, as nearly everyone focused on that struggle. Yet there were other things at work, such as the changing river conditions. It does seem curious that Higgins and Bailey seemed supporting and basically optimistic about propagation through the fall of 1941. Perhaps Higgins was frustrated with Ellis's refusal to make a demonstration, or possibly he felt Ellis's new method (or mussel propagation in general) was ineffective. Finally, perhaps the pleas of the button manufacturers fell on deaf ears as people decided the better days of that industry were gone and momentum shifted to the Upper Mississippi River Improvement Association. It seems that newsletters and annual reports relate good information, celebration and hoop-la when a program begins, yet when a program ends, one finds no admission of defeat or clear explanation when a program ends. This is where letters or diaries sometimes will be revealing, but here we are left wondering.

Archival records show one last effort to obtain funding for mussel propagation. In 1948, Congress directed the Fish and Wildlife Service to spend $25,000 of money already allotted for fish propagation to propagate mussels. "From headquarters at Carterville, Illinois," plants of yellow sandshells and river muckets were conducted in the White, Black and St. Francis Rivers in Arkansas, the Mississippi River in Iowa, and the Wabash River in Illinois and Indiana. The Fish and Wildlife Service protested that "a greatly expanded program of investigations would be needed to learn whether mussel propagation activities are serving a useful purpose." The language of the complaint implied that the pearl button industry had declined and was a relatively small industry, and the study to determine the value of mussel propagation activities would cost more than the program itself. "In view of doubt as to the value of present mussel propagation activities and inability to assess the worth of mussel propagation" without spending a lot of money, the Fish and Wildlife Service recommended dropping the propagation activities.[139]

There are good reasons to believe that Ellis successfully propagated a limited number of mussel species while skipping the parasitic state as he claimed. While he may have been eccentric, Ellis was a careful scientist, and during his career published many articles on physiology, mussels, and water pollution. He had a career and a reputation that he would have hesitated to besmirch with spurious claims. Secondly, lab work since that time confirms that a limited number of species can indeed skip their parasitic stage, including *Lasmigona subviridis* and *Strophitus undulates (=edentulus)*. Ellis was dealing in the realm of strange-but-true scientific fact. Yet there are also reasons to doubt the practical effectiveness of a method that sought to avoid the parasitic stage. The ability to skip the parasitic stage is not a widespread phenomenon in mussels, and *in vitro* metamorphosis does not seem consistently repeatable in the lab for all the reported species—it is at the least a tricky business. There remains the possibility that the juvenile mussels Ellis perceived as viable may have perished quickly after their release.[140]

Ellis's secretive behavior has ensured a frustrating paucity of clues regarding his secret formula and his laboratory apparatus. The most specific mention of the formula remains his mention of chemical groups in his 1926 *Science* publication. To complete the image of the obsessed scientist, busy with secret formulas and beakers full of mysterious amino acids, it seems that Max Ellis carried the specific secret of his nutritive solution to his grave.

Yet the story did not end there. In 1982, Billy G. Isom and Robert G. Hudson published information on the solution they used for in vitro culture of *Ligmia recta* and *Lampsilis ovata* (see addenda). Like other scientists before them, Isom and Hudson suggested that technique could serve conservation as well as industry. Isom and Hudson mentioned that their artificial medium included salts modified from the "unionid Ringers" solution Ellis used in 1930 when working on the blood of healthy and stressed mussels. Ellis et al. were testing "the validity of the normal values which were obtained from the various analyses of mussel blood," by dissecting away almost the entire foot of a mussel, immersing it in different mediums (including this salty solution, distilled water, tap water, and river water), and checking for continued activity. Ellis et al. made no mention of glochidia. They called the solution "unionid ringers," after the "'Ringer's fluid' commonly used for studies of vertebrate tissues." Their composition included sodium chloride at .153 percent, calcium chloride at .012 percent, potassium chloride at .015 percent, magnesium chloride at .010 percent, di-basic sodium phosphate at .009 percent, and sodium bicarbonate, to adjust the pH value to pH 7.9.

Notes

1 A concise history of the industry is found in James Lee Anthony, "Growth and longevity of freshwater mussels (Bivalvia: Unionidae) with application to their commercial fisheries," Master's thesis, Iowa State University, 2000, esp. 91-94. Historical sources include Hugh M. Smith, "The mussel fishery and pearl button industry of the Mississippi River," *Bulletin of the U.S. Bureau of Fisheries* 18 (1898): 289-314; H.M. Smith, "The pearl-button industry of the Mississippi River," *Scientific American* 81 (1899): 86-87; and Robert E. Coker, "Fresh-water mussels and mussel industries of the United States," *Bulletin of the U.S. Bureau of Fisheries* 36 (1921): 11-89. On coaxing workers to use shells efficiently, see file 200, Winterton C. Curtis Papers, Western Historical Manuscripts Collection, University of Missouri, Columbia, Missouri (hereafter cited as WCC Papers).

2 Anthony, 94-98; Hugh M. Smith, "Mussel Fishery and Pearl Button Industry"; Mussel names and historical notes on name changes can be found in Donna Turgeon et al., *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks* (Second Edition, Bethesda, Maryland: American Fisheries Society, 1998), e.g., 185.

3 Arthur MacEvoy, *The Fisherman's Problem: Ecology and Law in the California Fisheries, 1850-1980,* (Cambridge: Cambridge University Press, 1986), 91; W.C. Curtis to B.W. Evermann (U.S. Fisheries Bureau), c. May-June 1907, file 2, WCC Papers, WHMC.

4 Three accounts are of interest: Philip V. Scarpino, *Great River: An Environmental History of the Upper Mississippi, 1890-1950,* (Columbia, Missouri: University of Missouri Press, 1985); Harriet B. Carlander, *History of Fish and Fishing in the Upper Mississippi River,* (Rock Island, Illinois: Upper Mississippi River Conservation Committee, 1954); and Alice Outwater, *Water: A Natural History* (New York: Basic Books, 1996), 117-31.

5 R.E. Coker, A.F. Shira, H.W. Clark, and A.D. Howard, "Natural history and propagation of fresh-water mussels," *Bulletin of the U.S. Bureau of Fisheries* 37 (1922): 75-181, (hereafter cited as Coker et al.); *Report of the United States Commissioner of Fisheries* for 1920.

6 R.E. Coker, A.F. Shira, H.W. Clark, and A.D. Howard, "Natural history and propagation," on Glochidum theory, see 136; George Lefevre and Winterton C. Curtis, "Studies on the reproduction and artificial propagation of fresh-water mussels," *Bulletin of the U.S. Bureau of Fisheries* 30 (1910): 105-202.

7 Jane Maienschein, *100 Years Exploring Life, 1888-1988: The Marine Biological Laboratory at Woods Hole* (Boston: Jones and Bartlett Publishers, 1989), 23; Winterton C. Curtis, "History of the Department of Zoology, University of Missouri," Bios 20, No. 3, October 1949; file 91, Winterton C. Curtis Papers, Western Historical Manuscript Collection, University of Missouri, Columbia, (hereafter cited as WCC Papers, WHMC).

8 Curtis, "History of the Department of Zoology."

9 File 59 & 60, WCC Papers, WHMC.

10 File 200, WCC Papers, WHMC.

11 File 16, WCC Papers, WHMC.

12 Original field notes, some laboratory records, plans for research and plans for investigations are located in the WCC Papers, WHMC.

13 Thanks to Kevin Cummings at the Illinois Natural History Survey for helping us clear our confusion over Lefevre and Curtis's use of metanevra and fragosa, and the common use of "mapleleaf." In 1922, Coker et al. referred to the "Maple-leaf, Quadrula lachrymosa (Lea)."

14 George Lefevre and Winterton C. Curtis, "Reproduction and Parasitism in the Unionidae," *J. Experimental Zoology* 9 (1910): 79-115, plus 5 plates.

15 Lefevre and Curtis, "Reproduction and Parasitism," 99.

16 Lefevre and Curtis, "Reproduction and Parasitism," 100.

17 George Lefevre and Winterton C. Curtis, "Studies on the Reproduction and Artificial Propagation of Fresh-Water Mussels," *Bulletin of the U.S. Bureau of Fisheries* 30 (1910): 105-202, 156. See also George Lefevre and W.C. Curtis, "Experiments in the Artificial Propagation of Fresh-Water Mussels," *Bulletin of the.U.S. Bureau of Fisheries* 28 (1908): 615-626. This paper was not actually delivered at the 4th International Fisheries Conference in September, 1908. Evidently Lefevre and Curtis were too consumed with university duties to attend. File 75 & 76, WCC Papers. "Nature is prodigal . . ." found in "Statement of the Principal Facts in the Life History of Our Freshwater Mussels and of the Means Proposed for Increasing the Supply," c. July 1907, file 201, WCC Papers, WHMC.

18 M. Braun, "Postembryonale Entwicklung von Anodonta," *Zool. Anz.* (1878), 1; F. Schmidt, "Beitrag zur Kenntniss der postembryonalen Entwicklung der Najaden," *Arch. Naturgesch*., Jg.51, (1885); Lefevre and Curtis, "Reproduction and Parasitism," 103; Lefevre and Curtis, "Studies on the Reproduction," 157.

19 Lefevre and Curtis letter to Evermann, 21 March 1908, 22 pages, file 70, WCC Papers.

20 Lefevre and Curtis, "Studies on the Reproduction," 164.

21 Lefevre and Curtis, "Studies on the Reproduction," 164-65.

22 Lefevre and Curtis, "Studies on the Reproduction," 165.

23 Lefevre and Curtis, "Studies on the Reproduction," 165.

24 Lefevre and Curtis, "Studies on the Reproduction," 182.

25 Lefevre and Curtis, "Studies on the Reproduction," 183-84; The story of their first success was included in Lefevre's 23-page presidential address to the Central Branch of the American Society of Zoologists, meeting in Urbana, Illinois, on April 5, 1912 (File 213, WCC Papers).

26 File 203, file 78, WCC Papers, WHMC. There was plenty of political maneuvering when Hugh Smith was appointed to the office of Fish Commissioner. Some scientists, such as Coker, preferred another candidate. Caswell Grave wrote to Robert E. Coker on 22 May, 1913, expressing his discontent with leadership at the Bureau of Fisheries: "the grudge which I am bearing the present bosses of the Bureau only got a little deeper. I suppose they are going ahead on the very wise principle that the fewer there are in the Bureau who understand their problems and are capable of independent research along the more promising lines, the fewer there will be to see their blunders." Box 1, REC Papers, SHC-UNC.

27 George Lefevre and Winterton C. Curtis, "Metamorphosis without Parasitism in the Unionidae," 6 page manuscript, March 25, 1911, File 80, WCC Papers; the information also was printed in Lefevre and Curtis's "Studies on the Reproduction and Artificial Propagation of Fresh-Water Mussels," *Bulletin of the U.S. Bureau of Fisheries* 30 (1910): 105-202.

28 "Statement of the Principal Facts in the Life History of Our Freshwater Mussels and of the Means Proposed for Increasing the Supply," File 201, WCC Papers, WHMC; Lefevre and Curtis, "Studies on the Reproduction," 182.

29 "Maps Relating to Mussel Investigations, 1914, 3 items," RG 22, Div. of Scientific Inquiries; Cartographic Branch, NARA, College Park, Maryland; RG 22 refers to Record Group 22, Records of the Fish and Wildlife Service [and its predecessor, the Bureau of Fisheries], National Archives and Records Administration, College Park, Maryland (hereafter cited as RG 22, NARA).

30 Lefevre and Curtis, "Studies on the Reproduction," 176.

31 Lefevre and Curtis, "Studies on the Reproduction," 191.

32 Lefevre and Curtis, "Studies on the Reproduction," 185.

33 For 1907 "Tentative Plan," see file 200, WCC Papers, WHMC; Lefevre and Curtis, "Studies on the Reproduction," 190.

34 Winterton C. Curtis, "History of the Department of Zoology," 81.

35 *History of Muscatine County,* 305, Musser Public Library, Muscatine, Iowa.

36 J.B. Hunn, "'Woods Hole' on the Mississippi," *Fish and Wildlife News* (Aug., Sept., Oct., 1989): 17. On details of site selection, see file 77, WCC Papers; more on Evermann's involvement in Box 1, Robert E. Coker papers, Southern Historical Collection, University of North Carolina, Chapel Hill, (hereafter cited as REC Papers, SHC-UNC).

37 "Work of the Fairport Station," *Fisheries Service Bulletin,* No. 27, August 1917, Fish-347, D.C. Booth Historic Fish Hatchery, Spearfish, South Dakota (hereafter cited as DCB); Robert E. Coker, "The Fairport Fisheries Biological Station: Its Equipment, Organization, and Functions," *Bulletin of the U.S. Bureau of Fisheries* 34 (1914): 383-406; R.E. Coker, "The Fisheries Biological Station at Fairport, Iowa," Appendix I to the *Report of the U.S. Commissioner of Fisheries* for 1920, 1-12; "Investigation of Inland Fisheries," *Report of the United States Commissioner of Fisheries* 1928, xi; on shipments to Japan, see Box 11, E121 RG22 NARA.

38 Robert E. Coker, "The Fairport Fisheries Biological Station," 383-406; Details on construction can be found in Boxes 13 to 16, E118, RG22, NARA. See also "Brief History of the U.S. Fish Cultural Station, Fairport, Iowa," 2 page typescript, Iowa DNR fish hatchery at Fairport (copy at DCB); Fairport Annual Reports, Fish 42, Box 3, DCB.

39 Coker et al., "Natural History and Propagation," 137.

40 Coker et al., "Natural History and Propagation," 137.

41 Harriet B. Carlander, *A History of Fish and Fishing in the Upper Mississippi River,* Upper Mississippi River Conservation Committee, 1954, 28-39, 47. In the city cemetery (East side) of Manchester, Iowa, the grave marker of Carl Albin (1881-1916) refers to his hard work at the fish hatchery.

42 On the dispute of use of the Curlew, see files 70-72, WCC Papers, WHMC.

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44 Coker et al, 162; Hugh M. Smith, "When the Father of Waters Goes on a Rampage," 369-83; Carlander, 47.

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47 "Fresh-water mussels," *Report of the Commissioner of Fisheries,* 1922, 21-22.

48 Thaddeus Surber, "Notes on the Natural Hosts of Fresh-Water Mussels." *Bulletin of the United States Bureau of Fisheries* 32 (1912): 101-116, + plates 29-31; quote on 114.

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53 Arthur Day Howard, "Experiments in the Culture of Fresh-Water Mussels," *Bulletin of the Bureau of Fisheries* Vol. 38 (1921-22): 63-89, [Document No. 916, May 12, 1922, Washington, D.C.: Government Printing Office, 1922], see esp. 64-65.

54 Howard, "Experiments in the Culture," 64-65.

55 Howard, "Experiments in the Culture," 64-65.

56 Howard, "Experiments in the Culture," 64-65.

57 Howard, "Experiments in the Culture," 64-65.

58 Howard, "Experiments in the Culture," 70.

59 Howard, "Experiments in the Culture," 72.

60 Howard, "Experiments in the Culture," 73.

61 Howard, "Experiments in the Culture," 74.

62 Howard, "Experiments in the Culture," 74.

63 Howard, "Experiments in the Culture," 76-7.

64 Howard, "Experiments in the Culture," 86.
65 Biographical information from finding aid for R.E. Coker Papers, SHC-UNC; H. Eugene Lehman, "Robert Ervin Coker," *The Journal of the Elisha Mitchell Scientific Society* 84 (No. 2, Summer, 1968):332-37.
66 Robert E. Coker, "Water-Power Development in Relation to Fishes and Mussels of the Mississippi," Appendix VIII to the *Report of the U.S. Commissioner of Fisheries* for 1913 [also identified as Bureau of Fisheries Document No. 805]; Coker to S.A. Forbes, 12 September, 1913, INHS Chief's Subject File, UILLA.
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68 Fire accounts in Box 14, E117, RG 22, NARA; Dedication written up in Fisheries Service Bulletin (November 1, 1920, No. 66); See also R.E. Coker, "The Fisheries Biological Station at Fairport, Iowa," Appendix I to the *Report of the U.S. Commissioner of Fisheries* for 1920, 1-12, esp. 3-4.
69 "Immediate need of Lab Building," 2 p. mss., December 1917, Box 14, E117 RG 22, NARA; See Arthur Day Howard, "Experiments in the Culture of Fresh-Water Mussels," 77-78; Coker et al., 166.
70 R.E. Coker, "Fresh-water mussels and the mussel industries of the United States," U.S. Bureau of Fisheries Document 865, Washington, D.C.: U.S. Bureau of Fisheries, 1919; also published in *Bulletin of the U.S. Bureau of Fisheries* 36 (1917-18): 11-89.
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72 W.R. Allen, "The food and feeding habits of fresh-water mussels," *Biological Bulletin*, Marine Biological Laboratory, Woods Hole, Mass., 27 No. 3 (1914), 127-46 + 3 plates.
73 Coker et al., 88-91.
74 Coker et al., 91-92. Mussels taken at Lost Lake, Indiana, contained "such organisms as Microcystis aeruginosa, Pediastrum boryanum, and P. Duplex, Coelastrum microporum, Botryococcus braunii, Scenedesmus, Melosira crenulata, Coconema cymbiforme, Navicula, Epithemia argus, Fragilaria, Cocconeis pediculus, and Lyngbya aestuarii.
75 Coker et al., 93.
76 Coker et al., 114.
77 Coker et al., 114-116.
78 Coker et al., 114-116, see also Table 9 on page116 detailing minerals in rivers.
79 P.S. Galtsoff, "Limnological Observations in the Upper Mississippi," *Bulletin of the United States Bureau of Fisheries* 39 (1923-24): 347-438.
80 E.P. Churchill, Jr., and Sara I. Lewis. "Food and Feeding in Fresh-water Mussels." *Bulletin of the United States Bureau of Fisheries* 39 (1923-24): 439-71, see 463, 468.
81 Churchill and Lewis, "Food and Feeding," 468-69.
82 Churchill and Lewis, "Food and Feeding," 469.
83 Coker et al., 124-25.
84 Coker et al., 111-12.
85 Coker et al., 138.
86 Coker et al., 151-52, 163.
87 Coker et al., 160, 163.
88 Coker et al., 160.
89 Coker et al., 162.
90 "Fresh-water mussels," *Report of the United States Commissioner of Fisheries* 1921, 35.
91 Coker et al., 163-64.
92 Coker et al., 164.
93 "Fresh-water Mussels," *Report of the United States Commissioner of Fisheries* 1923, 13-14.
94 Howard, 77-78; Coker et al., 164; Howard reported Corwin's pen as measuring 10 feet square, Coker et al. no doubt refer to the same pen but describe it as 12 feet square.
95 Coker et al., 164.

96 Coker et al., 165; "Fresh Water Mussels," *Report of the United States Commissioner of Fisheries* 1920, 24.
97 Coker et al., 166; See also "Report of Pond Experiments with Fish and Mussels, Season of 1920," Box 1, REC Papers, SHC-UNC.
98 "Report of Pond Experiments [1920]," Box 1, REC Papers, SHC-UNC.
99 Carlander, 47; see *Fisheries Service Bulletin*, Feb. and Oct. 1923; "Biological Station, Fairport, Iowa," *Report of the United States Commissioner of Fisheries* 1920, 4-9; "Fresh Water Mussels," *Report of the United States Commissioner of Fisheries* 1920, 24; "Fresh Water Mussels," *Report of the United States Commissioner of Fisheries* 1923, 13.
100 "Report of Pond Experiments [1920]," Box 1, REC Papers, SHC-UNC; Fairport Annual Report, 1931, Fish 42, Box 3, DCB.
101 Manchester NFH (Iowa) Annual Report, 1923, Fish-347, Box 2, DCB.
102 Coker et al., 166; "Fresh Water Mussels," *Report of the United States Commissioner of Fisheries* 1923, 14.
103 J.P. Albee (Prairie CuChien, Wisconsin) to Commissioner of Fisheries, June 10, 1908, File 73, WCC Papers, WHMC.
104 Box 19, E121, RG22, NARA.
105 MacEvoy, *The Fisherman's Problem,* 148; Lewis Radcliffe (Acting Commissioner) to W.P. Pickett 22 Sept., 1926, file Mussels 1926-29, Box 11, E121 NARA.
106 Carlander, 48; Chamberlain to Higgins, 13 February, 1930, Box 19, E121, RG22, NARA; Chamberlain to Asst. In Charge, Div. Of Inquiry, 12 Feb., 1930, Box 19, E121, RG22, NARA; S.A. Forbes to H.F. Moore, 22 January 1913, 43/1/5-1, IHNS Chief's Subject file, UILLA.
107 Carlander, 48-49; Anthony, 100; Ellis's recommendation to Izaak Walton League dated 14 December, 1932, File 840.3, Box 672, E 269, RG 22, NARA.
108 On plastic buttons, see Anthony, p. 94.
109 M.M. Ellis and M.D. Ellis, "Growth and Transformation of Parasitic Glochidia in Physiological Nutrient Solutions," Science 64 (No. 1667, December 10, 1926): 579-80.
110 M.M. Ellis and M.D. Ellis, "Growth and Transformation," 579-80.
111 Lewis Radcliffe [acting Commissioner] to D.M. Dow [Australian Commissioner], 15 October 1929, Box 11 E121 RG22, NARA.
112 Henry O'Mally [US Fish Commissioner] to Henry B. Ward [Zoology Dept., U. Illinois] 19 January 1928, Box 19, E121, NARA.
113 Letter Ellis to Dean Guy L. Noyes, 4 May, 1928, and letter to Noyes 30 January, 1928, File 74, Collection #3651, School of Medicine Records, WHMC.
114 "Mussel Culture," Report of the United States Commissioner of Fisheries 1928, 670-71.
115 Thomas Chamberlain to Elmer Higgins, 3 May 1928, Box 672 E 269; Chamberlain to Guy Amsler (Arkansas F&G), 29 March, 1929, Box 19 E121; RG 22, NARA.
116 "Fresh-water mussel investigations," Report of the U.S. Commissioner of Fisheries 1930, 1120.
117 M.M.Ellis, Amanda D. Merrick, and Marion D. Ellis, "The Blood of North American Fresh-Water Mussels Under Normal and Adverse Conditions," Bulletin of the Bureau of Fisheries 46 (1930): 509-542, esp. 540.
118 Henry O'Mally to Buel A. Williamson, 22 April 1930, Box 11 E121 RG22 NARA; on women in labs, see letter Higgins to W.P. Pickett [President National Assoc. of Button Manufacturers], 6 November 1940, Box 672 E 269 RG 22 NARA; Elmer Higgins, "The Fresh-Water Pearl Button Industry and the Relations of the Bureau of Fisheries Thereto," 5 April 1930, Box 672, E269, RG22, NARA; Bureau of Fisheries, "State of the Mussel Fishery and policy of Conservation and Propagation of Mussels," 3 March 1930, Box 19, E121, RG22, NARA.
119 See also "Proposed program of fresh-water mussel culture for the season of 1941," USDI FWS, E269 RG 22.
120 "Mussel propagation," [US. Bureau of Fisheries] Report of the Commissioner with Appendices 1932, p. 144-45; "Fresh-water mussel investigations," Report of the United States Commissioner of Fisheries 1933, 376-77.

121 Bureau of Fisheries, "State of the Mussel Fishery and policy of Conservation and Propagation of Mussels," 3 March 1930, Box 19, E121, RG22, NARA. Summary sheets of data for the Lake Pepin surveys 1928-29 can be found in Box 19, E 121, RG22, NARA; on river conditions, see Brown to Barrett, 20 November, 1931, File 840 Box 672 E269 RG 22, NARA.

122 Box 19, E121, RG22, NARA.; M.M. Ellis, "Memorandum of Propagation and Natural Replacement of Fresh Water Mussels." Box 672, E269 RG22, NARA. N.d., but other dated materials suggest c. 1930; "Investigations of mussels and pollution in interior waters," Report of the United States Commissioner of Fisheries, 1931, 621-25.

123 Lewis Radcliffe (Acting Commissioner) to W.P. Pickett 22 Sept., 1926, file Mussels 1926-29, Box 11, E121 NARA; Elmer Higgins, "The Fresh-Water Pearl Button Industry and the Relations of the Bureau of Fisheries Thereto," April 5, 1930, Box 672, E269, RG22, NARA.

124 M.M. Ellis, "Memorandum on Propagation and Natural Replacement of Fresh Water Mussels," n.d., 3 page mss., RG 22 E269 Box 672, NARA.

125 See Ellis, "Detection . . . . of Stream Pollution," 1937, Fish 280; "Report on Status of F.P. 41, Stream-Pollution Studies," Fisheries Service Bulletin No. 235, 1 December 1934, DCB.; "Summer Pollution Surveys," Fisheries Service Bulletin No. 304, 1 September 1940, DCB.

126 Annual Report, Genoa, Wisconsin station, Fish 42, Box 16, DCB; Annual Report, La Crosse, Wisconsin station, Fish 42, Box 16, DCB. See also Fish 327, DCB.

127 Annual Reports, La Crosse Station, 1928-1941, Box 16, & Annual Reports, Homer Station, Box 6, Fish-42, DCB.

128 Report of the United States Commissioner of Fisheries 1936, p. 379; Carlander, 56. The 1934 annual report of Fairport station also details the end of the biological station's functions; "Annual Report of the Fairport Iowa Station," Box 3, Fish 42, DCB.

129 Fairport Annual Reports, 1933-1942, Boxes 2 & 3, Fish-42, DCB.

130 "Mussel propagation," [US. Bureau of Fisheries] *Report of the Commissioner with Appendices* 1932, 144-145; "Mussel investigations," Report of the United States Commissioner of Fisheries 1932, 524-25; M.M. Ellis, "Memorandum on Propagation and Natural Replacement of Fresh Water Mussels," n.d., 3 page mss., RG 22 E269 Box 672, NARA.

131 O'Malley to Buel A. Williamson, 22 April 1930, Box 11 E121 RG22, NARA; "Mussel propagation," Report of the United States Commissioner of Fisheries 1932, 144-145; "Mussel investigations," *Report of the United States Commissioner of Fisheries* 1932, 524-25.

132 "Fresh-water mussel investigations," *Report of the United States Commissioner of Fisheries* 1933, 376-77.

133 "Fresh-water mussel investigations," *Report of the United States Commissioner of Fisheries* 1933, 376-77.

134 Higgins to Director, U.S. Fish and Wildlife Service, 3 December, 1940, Box 672, E 269, RG 22, NARA; "The Bureau's Program of Mussel Propagation," n.d., c. 1940, Box 672, E269, RG22, NARA; "Mussel propagation," *Report of the United States Commissioner of Fisheries* 1936, 57; *Report of the United States Commissioner of Fisheries* 1937, 64-66; *Report of the United States Commissioner of Fisheries* 1938, 73-76.

135 Edward W. Bailey, "Memorandum for Mr. Jackson," 3 November 1941, File 840.5 Box 672 E269 RG22, NARA; Higgins memo for Director, 3 December 1940, File 840 Box 672 E269 RG22 NARA.

136 On the Rio Grande survey, see "Mussel surveys begun," *The Service Survey* (U.S. Fish and Wildlife Service), Vol 1, No. 1, January, 1941, DCB; On relationship between Ellis & Higgins, see Ellis to Higgins, June 17, 1941, Box 672, Entry 269, RG 22, NARA.

137 Annual Reports, Fort Worth Texas Station, FY 1940-1943, 1955; Fish 42, Box 12 and Box 6, DCB.

138 Ellis to Chamberlain, 13 May 1929, [and other letters in] Box 19 E121 RG 22, NARA.

139 See Box 672, Entry 269, RG 22, NARA.

140 Personal communication, historian Philip Scarpino, November 28, 2001; personal communications from malacologists Rafael Araujo, Bill Lellis, Steve Fraley, Dick Neves, Bob Summerfelt, and John Downing, Dec. 4-11, 2001; see B.G. Isom and R.G. Hudson, "In vitro culture of parasitic freshwater mussel glochidia," *The Nautilus* 96 (1982, No. 4): 147-151; see also M. Pekkarinen, M. and Hansten, C., "Success of metamorphosis of the lake mussel (Anodonta anatine) glochidia in different hosts and in vitro," *Proceedings of the 50th Annual Meeting of the Scandinavian Society for Electron Microscopy* (Espoo and Helsinki, Finland, 7-10 June 1998): 115-16.

Biographical List

Many of these folks held Ph.D.'s; we've noted those we could identify

Allen, Edgar	Early worker at Fairport, later professor of anatomy at U. Missouri
Anson, B.J.	Worked with Arthur Day Howard; Fairport employee
Arey, L.B.	Studied encystment of glochidia at Fairport, c. 1920-24, held Ph.D., associated with Northwestern University Medical School.
Barney, R. L.	Director, Fairport Biological Station c.1921-23, Propagated Terrapin turtles in South Carolina for USBF
Bennett, Leslie H.	Foreman in charge, Fairport Station, c. 1935-38
Canfield, A. L.	Fairport superintendent (not director), 1917
Chamberlain, Thomas K.	Assistant in Fairport's early days, Fairport Station director 1924- c. 1930. Probably served on Ecological Society of America's Research Committee on Fresh-water Fish and Fisheries
Churchill, E. P.	Studied feeding habits of mussels, c. 1922-23 at Fairport, held Ph.D.
Clark, H. Walton	Worked at Fairport station, with Surber
Coker, Robert E.	Zoologist, held Ph.D. Studied mussels early on, worked for the bureau of Fisheries, first director of Fairport Station in 1914, took charge of the Bureau's Division of Scientific Inquiry (1915-22), then moved to the U. of North Carolina, where he completed his career writing books about the sea. Served on Ecological Society of America's Research Committee on Fresh-water Fish and Fisheries.
Copper, Fay A.	Foreman in charge, Fairport Station, c. 1940
Corwin, Roy S.	Scientific Assistant, Lake Pepin work, c. 1920
Culler, [C.F.?]	Homer (Minn.) Station superintendent, presumably the C.F. Culler who became District Supervisor for the Bureau of Fisheries out of La Crosse, Wisconsin c. 1924.
Curtis, Winterton C.,	Zoologist and professor, U. Missouri Dept. of Zoology, held Ph.D.
Danglade, Ernest	Performed wide-ranging early mussel surveys.
Davis, H. S.	In 1916 was with University of Florida, worked on protozoan parasites at Fairport Lab. In 1930 returned to Fairport in charge of fish propagation work. In 1953 published *Culture and Diseases of Game Fishes.*
Ellis, Max Mapes	Placed in charge of mussel research in 1930. A physiologist and professor at the School of Medicine at the University of Missouri. Worked on water pollution during later 1930s.

Evermann, Barton W.	Ichthyologist, worked at U.S. Bureau of Fisheries c. 1904, later Director of California Academy of Sciences, associated with the San Francisco Museum of Natural History.
Grier, N.M.	From Dartmouth College, conducted surveys of Upper Mississippi between Lake Pepin and La Crosse, 1920-25, held Ph.D.
Higgins, Elmer	Director, U.S. Bureau of Fisheries
Howard, Arthur Day	Research Assistant, Fairport Lab, held a Ph.D.
Isley, F.B.	Worked on mussel growth and development.
Jones, Richard O.	Senior mussel culturist for Ellis in 1940-41.
Koontz, A.R.	In 1916, studied rearing of glochidia on artificial media at Fairport.
Lefevre, George	Zoologist, University of Missouri
Moore, Dr. H.F.	Associated with the U.S. Bureau of Fisheries, served on Ecological Society of America's Research Committee on Fresh-water Fish and Fisheries, held Ph.D.
Moore, Emmeline	Worked on aquatic biology at Fairport c. 1919, particularly plants in pond fish culture
Reuling, F.H.	Worked with the outdoor troughs at Fairport. Held Ph.D.
Smith, Hugh M.	Researcher, later Commissioner (director) of the Bureau of Fisheries. Early on, he called for preservation measures for the fresh-water mussels.
Southall, J.B.	Surveyed mussels and mussel beds on Mississippi River and on Lake Pepin, 1924-25; employee of Fairport Biological Station, photographer
Surber, Thaddeus	Research Assistant, Fairport Lab., later with U.S. Bureau of Fisheries in Homer, Minnesota, served on Ecological Society of America's Research Committee on Fresh-water Fish and Fisheries
Surber, Eugene W.	In charge, U.S. Fisheries Experimental Station, Leetown, West Virginia, 1938
Shira, Austin F.	Fairport Station Director, 1917-1920. Co-author with R.E. Coker
Westfall, Bertis A.	Accompanied Ellis on reconnaissance in Texas and Arkansas, 1940-41, held Ph.D.
Wilson, Charles Branch	Early mussel survey with Danglade
Wiebe, A.H.	A supervisor at Fairport Station, held Ph.D.
Wylie, R.B.	Director, Iowa Lakeside Laboratory c. 1923, held Ph.D.

Resources

Two books of particular interest should be mentioned regarding the history of the U.S. Bureau of Fisheries on the Mississippi River: Harriet Carlander's *History of Fish and Fishing on the Mississippi River* (1954), and Philip Scarpino's *Great River: An Environmental History of the Upper Mississippi River* (1985).

Several libraries have complete or near-complete runs of the main publication of the U.S. Bureau of Fisheries, *Bulletin of the United States Bureau of Fisheries.* These include the Biology Laboratory at the University of Illinois, Parks Library at Iowa State University, and the Department of Interior's library in Washington, D.C. A set is also available at the USFWS Research Center in La Crosse, Wisconsin. The *Bulletin of the United States Bureau of Fisheries* went through several name changes, but a catalog search using that title should reveal the call number. Similarly, the annual reports from the Bureau changed their title several times, but for many years the title remained *Report of the United States Commissioner of Fisheries.*

Annual Reports of the United States Bureau of Fisheries (with the invaluable "Progress in Biological Inquiries"), appendices to the *Bulletin of the United States Bureau of Fisheries,* and the Economic Circulars of the Bureau are more difficult to find. A near-complete run of all these materials is available at the Department of Interior's library in Washington, D.C., in the Main Interior Building. For one-stop research, this is a very fine facility. These materials might be available at a major depository library, such as the National Archives branch in Kansas City, Missouri. A near-complete run of the Annual Reports is available at the USFWS library in La Crosse, Wisconsin, and Iowa State University's Parks Library retains copies of the Annual Reports in remote storage. The monthly newsletter of the Bureau of Fisheries, *Fisheries Service Bulletin,* is a useful resource. It was replaced by *The Service Survey* in January, 1941. Both can be found at the D.C. Booth Historic Fish Hatchery in Spearfish, South Dakota.

In the bibliography below, you will find some of the citations will mention at least one location where an article might be found. We note which items can be found at the Musser Public Library in Muscatine, Iowa. If no mention is made, the item should be available at a major university library. Local libraries can obtain some items through interlibrary loan.

This story could not be told without consulting manuscripts. Finding fewer than twenty pages of original lab data in the archives, however, was a disappointment. A few years ago, historian Philip Scarpino had arranged to inspect Max Ellis's equipment and papers that were stored in the attic of a science building on the campus of the University of Missouri, but discovered everything had been discarded. If anyone should discover more records in the proverbial attic, pertinent to the history of mussels and the U.S. Bureau of Fisheries, they should contact the D.C. Booth Historic Fish Hatchery in Spearfish, South Dakota, to provide the papers a proper home.

The Records of the U.S. Bureau of Fisheries (Record Group 22, particularly Entries 269, 117, & 121) at the National Archives in College Park, Maryland, contained very good records from the Bureau's central office. The D.C. Booth National Historic Fish Hatchery in Spearfish, South Dakota, is an excellent resource. The Robert E. Coker papers at the University of North Carolina in Chapel Hill were very helpful. We also consulted the papers of Winterton C. Curtis, and a few records pertaining to Max Ellis in the records of the School of Medicine, both located in the Western Historical Manuscript Collection at the University of Missouri in Columbia, Missouri.

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Key:

DCB	D.C. Booth Historic Fish Hatchery, Spearfish, South Dakota
MIBL	Main Interior Building Library, Department of Interior, Washington, D.C.
Musser Lib.	Musser Public Library, Muscatine, Iowa
REC Papers	Robert E. Coker papers, Southern Historical Collection, University of North Carolina, Chapel Hill, North Carolina
SHC-UNC	Southern Historical Collection, University of North Carolina, Chapel Hill, North Carolina
U. Ill. Bio. Lib.	University of Illinois Biology Library, Champaign, Illinois
UILLA	University of Illinois Archives, Champaign, Illinois
WCC Papers	Winterton C. Curtis Papers, Western Historical Manuscripts Collection, University of Missouri, Columbia, Missouri
WHMC	Western Historical Manuscripts Collection, University of Missouri, Columbia, Missouri
NARA	National Archives and Records Administration, College Park, Maryland.

Addenda

1) Breeding Record of *Quadrula metanevra.* Circa 1909. From file 210 in the records of Winterton C. Curtis, Western Historical Manuscripts Collection, University of Missouri, Columbia, Missouri.

2) Record of Infection Experiment for *Lampsilis subrostratus* and *L. rectus.* April 20, 1909. From file 207 in the records of Winterton C. Curtis, Western Historical Manuscripts Collection, University of Missouri, Columbia, Missouri.

3) Table 1, Infections with hooked and hookless glochidia. 1910. From file 211 in the records of Winterton C. Curtis, Western Historical Manuscripts Collection, University of Missouri, Columbia, Missouri.

4) Lefevre, George, and Curtis, Winterton C. Part IV, "The Parasitism," pp. 156-75 in "Studies on the reproduction and artificial propagation of fresh-water mussels." *Bulletin of the U.S. Bureau of Fisheries* 30 (1910): 105-202.

5) Collection and Infection of Fishes during month of July, 1927. Illustrates fish rescue and infection records once held at Fairport. From Box 16, Fish-42, D.C. Booth Historic Fish Hatchery.

6) Floor Plan for the 1914 Fairport Laboratory. Pp. 389-90 in Coker, Robert E., "The Fairport Fisheries Biological Station: Its Equipment, Organization, and Functions." *Bulletin of the U.S. Bureau of Fisheries* 34 (1914): 383-406.

7) "Mussel Propagation, by Experiment and Practice." Pp. 399-402 in Coker, . "The Fairport Fisheries Biological Station . . . ." *Bulletin of the U.S. Bureau of Fisheries* 34 (1914): 383-406.

8) Tables 1-4, from Howard, Arthur Day, "Experiments in Propagation of Fresh-Water Mussels of the Quadrula Group." *Report of the U.S. Commissioner of Fisheries* for 1913, Appendix IV.

9) Floor Plan for the 1920 Fairport Laboratory. Pp. 6-7 in Coker, R.E. "The Fisheries Biological Station at Fairport, Iowa." Appendix I to the *Report of the U.S. Commissioner of Fisheries for 1920,* 1-12.

10) Coker, R.E., A.F. Shira, H.W. Clark, and A.D. Howard. Table 6, 8, 9, 15, 16; Table 18, Commercial Mussels and Their Hosts; Table 19, Number of Species of Fish Known to Serve as Hosts for Certain Species of Mussels, & Table 20, Number of Species of Commercial Mussels Known to be Carried as Parasites by Certain Fishes, pp. 116, 152-54 in "Natural history and propagation of fresh-water mussels." *Bulletin of the U.S. Bureau of Fisheries* 37 (1922): 75-181.

11) Coker, R.E., A.F. Shira, H.W. Clark, and A.D. Howard. "Artificial Propagation," pp. 160-66, in "Natural history and propagation of fresh-water mussels." *Bulletin of the U.S. Bureau of Fisheries* 37 (1922): 75-181.

12) M.M. Ellis and M.D. Ellis, "Growth and Transformation of Parasitic Glochidia in Physiological Nutrient Solutions," *Science* 64 (No. 1667, December 10, 1926): 579-80.

13) Isom, Billy G., and Robert G. Hudson, "In Vitro Culture of Parasitic Freshwater Mussel Glochidia," *The Nautilus* 96 (No. 4, 1982): 147-51.

FRESH-WATER MUSSEL INVESTIGATIONS

Breeding Record of Quadrula metanevra

1907-08

		1 2 3	4 5 6	7 8 9	10 11 12	13 14 15	16 17 18	19 20 21	22 23 24	25 26 27	28 29 30	31	Total
NOT GRAVID	Jan.				10 (? ♂ or ♀)								
	Feb.												
	Mar.												
	April												
	May												
	June					1			3	1			
	July			2	2	3	1 26	1	10	10	3		
	Aug.	5	4 6	4	4								
	Sep.												
	Oct.												
	Nov.										17		
	Dec.										? ♂ or ♀		68+
EARLY EMBRYOS	Jan.												
	Feb.												
	Mar.												
	April												
	May												
	June		2		1								
	July	1		1	3		1 2 1		5				
	Aug.	1											
	Sep.												
	Oct.												
	Nov.												
	Dec.												18
LATE EMBRYOS	Jan.												
	Feb.												
	Mar.												
	April												
	May												
	June									1			
	July						1	1	3				
	Aug.		1	1									
	Sep.												
	Oct.										1		
	Nov.												
	Dec.												8
GLOCHIDIA	Jan.												
	Feb.												
	Mar.												
	April												
	May												
	June												
	July					2							
	Aug.		1 1										
	Sep.												
	Oct.												
	Nov.												
	Dec.												4
		1 2 3	4 5 6	7 8 9	10 11 12	13 14 15	16 17 18	19 20 21	22 23 24	25 26 27	28 29 30	31	

1) **Breeding Record of *Quadrula metanevra*. Circa 1909. From file 210 in the records of Winterton C. Curtis, Western Historical Manuscripts Collection, University of Missouri, Columbia, Missouri.**

RECORD OF INFECTION EXPERIMENT

Series XI No. 12 Date April 20/09 Place Columbia, Mo.

Tank No.

Mussel *Lampsilis subrostratus* and *L. rectus*

Collected at *L. subrostratus* from pond near Columbia
L. rectus from Wabash river (Cox)

Remarks

Glochidia, quantity used Gills, partly filled, from six *subrostratus*
" from 1 *rectus*

Maturity Ripe

Remarks

Fish Large mouthed black bass 27
Sun-fishes Number infected 240

Collected Bass from La Crosse, Wis; at Sunfishes from pond near Columbia.

Size

Remarks

Temperature of water, containing fish

Containing mussels During infection 21° C

Mode of infection Infected in tubs
Exposure - 15 minutes

Behavior of fish and glochidia during infection

Moderate gill infection on bass
Slight " " " sunfishes
April 20-26, 6 bass died.
April 27 - Young mussels began to drop off (7 days). They are very active from first & thrust out the long caudates foot toward the bottom of dish.
May 5 - Last mussels came off, i.e., the young mussels continued to come off during 9 days.

Miss Young Unfortunately it is impossible to distinguish between *L. subrostratus* & *L. rectus* in this experiment

2) **Record of Infection Experiment for *Lampsilis subrostratus* and *L. rectus*. April 20, 1909. From file 207 in the records of Winterton C. Curtis, Western Historical Manuscripts Collection, University of Missouri, Columbia, Missouri.**

Table 1

Infections with hooked glochidia

Experiment	Date	Mussel	Fish	Exposure	Young mussels liberated	Duration of parasitism	Average temperature during parasitism
1	Dec. 3, '09	Symphynota complanata	Apomotis cyanellus Apomotis cyanellus	15 min.	Dec. 17-19	14-16 days	16° C.
2	Dec. 17, '09	Symphynota complanata	Pomoxis annularis Apomotis cyanellus	15 min.	Jan. 1-4, '10	15-18 days	16.3°
3	Jan. 7, '10	Symphynota complanata	Pomoxis annularis	12 min.	Jan. 18-21	11-14 days	16°
4	Apr. 5, '10	Symphynota complanata	Apomotis cyanellus	30 min.	Apr. 14-18	9-13 days	17.8°

Infections with hookless glochidia

5	Feb. 19, '10	Lampsilis ligamentina	Apomotis cyanellus	9 min.	March 5-12	14-21 days	17.8°
6	Mar. 6, '09	Lampsilis ligamentina	Apomotis cyanellus Micropterus salmoides	10-15 min.	Apr. 7-11	32-36 days	19.1°
7	Apr. 8, '09	Lampsilis ligamentina	Apomotis cyanellus Micropterus salmoides	10-15 min.	Apr. 27-May 1	19-23 days	20.3°
8	Apr. 13, '10	Lampsilis subrostrata	Apomotis cyanellus	8-15 min.	May 2-8	19-25 days	18.1°
9	May 2, '10	Lampsilis ligamentina	Apomotis cyanellus Micropterus salmoides	7-10 min.	May 15-26	13-24 days	18.1°
10	May 3, '10	Lampsilis subrostrata	Apomotis cyanellus	50 min.	May 17-25	14-22 days	18.1°
11	July 29, '09	Unio complanatus	Perca flavescens	7-14 min.	Aug. 12-14	14-16 days	23°
12	Aug. 5, '08	Quadrula plicata	Micropterus salmoides	30 min.	Aug. 17-	12- days	24.4°

3) Table 1, Infections with hooked and hookless glochidia. 1910. From file 211 in the records of Winterton C. Curtis, Western Historical Manuscripts Collection, University of Missouri, Columbia, Missouri.

4) Lefevre, George, and Curtis, Winterton C. Part IV, "The Parasitism," pp. 156-75 in "Studies on the reproduction and artificial propagation of fresh-water mussels." *Bulletin of the U.S. Bureau of Fisheries* 30 (1910): 105-202.

IV. THE PARASITISM.

ARTIFICIAL INFECTION OF FISH.

In any investigation which attempts to ascertain the facts of most importance for the artificial propagation of a species, attention is at once directed to those points in the life history where wholesale destruction of the individuals is most likely to occur. These points of wholesale waste are usually to be found in the earlier part of the individual's existence rather than during its adult life and are often preventable by artificial means. In common with other animals which must overcome the chances of parasitism, the Unionidæ produce enormous numbers of eggs, the great majority of which are by virtue of the brooding habit of the female mussel carried safely through their embryonic period and discharged as glochidia. We have not attempted to estimate the numbers of glochidia carried by full-grown adult females, but anyone who has seen them taken from the gills knows that they must be numbered by the hundreds of thousands, or even millions, and had these glochidia any great chance of survival and development to the adult stage the supply of mussels would far exceed anything which has ever been known in nature. When, however, the next stage of the larval history is sought for in nature, it becomes apparent that we have reached a point in the life cycle where the destruction and waste of individuals is wholesale and probably in excess of that which occurs at any other stage. There is no evidence, save in the case of the species *Strophitus edentulus*, the metamorphosis of which we have discussed under another heading of this paper, that any one of the Unionidæ can pass beyond the glochidial stage without becoming a parasite upon some fish, for the failure of glochidia to develop when left in water has been observed by all investigators since Leeuwenhoek.

The large element of chance involved in this shift from parent to fish, which has already been emphasized in our discussion of the glochidium, is again apparent when fish are examined in nature with a view to determining the abundance of the parasitic larvæ under the conditions of natural infection, for all investigators agree that the parasites exist in numbers which are insignificant when compared with the masses of glochidia which occur in the parent mussels. Only an occasional fish is found to be infected and it thus becomes clear that the purely accidental nature of the infection makes necessary the production of glochidia in such abundance as to overcome by sheer force of numbers the chances of destruction. Fish become infected in nature by occasional glochidia, but the chance that any fish will carry under natural conditions the number of glochidia which our experiments have shown that individual fish are capable of carrying, when artificially infected, is a negligible quantity. Here, then, we have the point of greatest destruction in the life cycle of the Unionidæ; and the point of attack for artificial propagation is clear. The fish must be made to carry more glochidia. Under experimental

laboratory conditions it is found that a given fish may carry successfully a load of glochidia so much in excess of what the same fish would ever be likely to carry in nature that there is no reason why a single fish should not be made, under the conditions of artificial infection, to do the work which a thousand fish perhaps could not do in the state of nature. This has been from the first our main point of attack, and, with this in view, we have studied the parasitism, first, by the infection of small lots of fish in aquaria and, later, by the infection of fish in larger numbers in a hatchery. Other points in the life cycle, as for example the stage immediately following the parasitism, may be found by later work to be places of wholesale destruction; we are convinced, however, that there can be no other where the mortality reaches such proportions as it does when the countless glochidia are spread upon the bottom and left to the chance that will bring them in contact with the parts of a fish's body suitable for their parasitism.

Throughout our experimental infections we have made use of small fish, usually those under 6 inches in length, because such fish are more easily collected in numbers and because we have not had proper facilities for the keeping of larger individuals. Where small numbers of fish are used and each individual can be carefully watched, the attainment of what may be termed an "optimum" infection in every case may be secured with no great difficulty, and by following the methods practised by various investigators ever since Braun (1878) and Schmidt (1885), we have obtained unlimited material whenever necessary. If the glochidia are placed in shallow dishes and in water just deep enough to cover all parts of the fish, the latter will usually keep the water sufficiently agitated to insure a proper suspension of the glochidia and tolerably constant results will follow.

It is very necessary that the glochidia be so distributed in the water as to come in contact with the proper parts of the fish, and, in most cases, to guard against over rather than under infection. Active fish, such as the rock bass (*Ambloplites rupestris*), and the large-mouthed black bass (*Micropterus salmoides*), are very favorable for gill infections, since they keep the water so well agitated that the glochidia hardly settle to the bottom at all, while their strong respiratory movements draw the suspended glochidia continually against the gills. With fish like the crappie (*Pomoxis annularis*), which when undisturbed move about quietly and whose respiratory movements are less vigorous, the water must be stirred to keep the glochidia suspended, or be so shallow that the fish are always near the bottom. The smaller gill slit of the crappie is another factor which makes for a very light infection in fish under 2 inches in length, since the glochidia reach the gills by way of the mouth and not from the opposite direction. For fin infections, sluggish fish like the German carp (*Cyprinus carpio*) need little attention, and the darters (*Etheostoma cæruleum spectabile*), which habitually rest upon the bottom for considerable periods, become quickly loaded with glochidia upon both fins and gills; although, as we shall see, the latter fish appears to be particularly adapted for ridding itself of the entire infection.

In the account which follows, we are discussing the results obtained from the infection of fish in small numbers and kept under careful observation in the laboratory.

There is no reason for believing that larger numbers of fish would present any more serious difficulties than are to be expected in the keeping of any fish in large numbers within a restricted space; and, if one could insure as uniform and careful an infection of the larger numbers, we have every reason to believe that such infections would prove as successful as those here described.

INFECTIONS WITH HOOKED GLOCHIDIA.

For the infections with hooked glochidia, we have used principally *Anodonta cataracta* from Falmouth, Mass., the species studied by Lillie (1895). With these we infected German carp under 6 inches in length and, unless otherwise stated, the following account refers to this combination which gives typical results. A smaller number of infections, made with *Symphynota complanata* and *S. costata* upon carp and other fishes, are referred to in a supplementary manner. The glochidia of *A. cataracta* become attached in large numbers to the fins (fig. 19–25, pl. IX and X) and gills of the carp. They are also found upon the other external parts which offer the condition of a soft scaleless epithelium like that of the fins; thus, the region about the anus, the edge of the operculum, the lips and in very heavy infections, even the soft area of the ventral surface between the mouth and pectoral fins may become heavily loaded. Within the mouth cavity, the gill filaments and also the gill bars and rakers become well covered. The glochidia which attach to these mouth parts do not remain, for, although the fish may be carrying many of their fellows upon its external parts, in about one week after the infection all glochidia have disappeared from the gill filaments, which then become as clean as though never infected. Scattered glochidia may remain upon the other internal mouth parts, for specimens are occasionally seen well embedded and in advanced stages of their metamorphosis, but in the main these parts also will become free of glochidia.

The general distribution upon the individual fins may be seen by reference to figures 19 to 25, plates IX and X, which show how great a proportion of the glochidia become attached to the fin margins. If a fish is carefully watched, as its slight movements stir up the glochidia during the infection, the latter are seen continually falling upon the upper faces of the pectoral and pelvic fins. They may even be collected with a pipette and heaped upon a motionless pectoral fin, remaining there for some minutes without more than an occasional specimen becoming attached. The margin of the fin is so much more favorable for attachment, that it is often thickly set with glochidia, when none are found upon the fin surface, and this despite the fact that glochidia must, during infection, strike against the surface of the fin many times for every time that one of them comes in contact with a fin margin. It is, therefore, the margin of the fin for which this glochidium is best suited, and, once fastened there, it is almost certain to remain and become embedded by the growth of the host's epithelium.

Considered in a more detailed way and with reference to the parts of the glochidium, we may explain this more frequent attachment to the margin as due to the fact that when the glochidium strikes against any flat surface the sensory hairs are not stimulated and the glochidium, which, as we have already shown in the case of the hooked forms,

responds principally to tactile stimulation, does not receive the stimulus to permanent closure which is given by the presence of any foreign object inserted between the valves. When a specimen does become attached to the surface of a fin, as is sometimes the case (fig. 21 and 22, pl. IX, fig. 25 and 32, pl. X), it presumably gains its hold by catching upon one of the ridges formed by the fin rays, for the hooks could hardly be used upon a perfectly flat surface. Glochidia sometimes hold to the surface of a fin by a shred of tissue, under which their hooks have caught, remaining there after all the neighboring specimens are completely overgrown (fig 25, pl. X), only to be torn off later without having caused any noticeable hypertrophy of the fin tissue. Figures 25 and 32, plate X, show that glochidia may become overgrown either flat against the surface or upon edge, and figure 24, plate IX, shows a young mussel leaving a surface attachment after a parasitism of 74 days.

The behavior and reactions of glochidia are of course significant in connection with the actual attachment when once the glochidium is brought in contact with a suitable part of the fish's body and receives the normal stimulus to close its valves. The bringing of the glochidium against just that part of the fish is a matter of the chance distribution in the water. Hence the distribution of the glochidia to the several fins is determined solely by the number likely to be brought in contact with a given part of the body. Those fins which brush against the bottom are always the more heavily loaded and the numbers elsewhere depend upon the extent to which the glochidia are kept suspended in the water. The importance of the mucus for the glochidia of *Symphynota* and of the larval thread for those of *Anodonta* and *Unio* in tangling the glochidia into masses and drawing others against the fish when a single one has become attached has probably been exaggerated, as explained in the section of this paper which deals with the function of the larval thread.

Optimum infections, as we shall term those which are close upon the limit of the number of glochidia which a fish can safely bring through the metamorphosis, often show the glochidia very closely set one after another, as in figures 22 and 23, plate IX, and figure 25, plate X, and several hundred may be safely carried by a fish 3 or 4 inches in length. Prolonged exposure causes so heavy an infection of the margins (fig. 19 and 20, pl. IX) that the fin tissue appears unable to overgrow the mass of glochidia, and they then remain attached without overgrowth for a week or more.

Figure 19, plate IX shows how on a part of the fin having no overcrowding normal embedding occurred, while in the more crowded areas the glochidia were still uncovered even seven days after infection. In the middle upper margin of this fin it would seem that the overgrowth might well have taken place, for many cases like figure 25, plate X, have been observed in which glochidia as closely set were properly embedded. The failure of overgrowth in this region is probably due to the presence immediately after infection of a greater number of glochidia many of which have since been detached. In all cases of this kind a smaller number will finally become embedded than in an infection where the fin has received more nearly the optimum load (fig. 21, 22, 23, pl. IX, and fig. 25, pl. X), for the great majority drop off when the fin becomes so mutilated

that bacterial or fungus infection sets in. These over-infections sometimes cause such hypertrophy that the fins become swollen and the rays so drawn together that it is impossible for them to spread out normally. Often the fins are raw and bleeding for some days and show red areas within where the blood vessels have become abnormal. The fish are likely to die from this or from the similar injury to their gills, and these over-infections are unsatisfactory if one wishes to bring through their parasitism the maximum number of glochidia.

The steps in the implantation of the glochidium by an overgrowth of the fish's tissue may be seen in figures 21 and 22, plate IX, and figure 25, plate X. Figures 21, plate IX, and 26, plate X, show the glochidium 3½ hours after attachment to the fish's fin. Most of the glochidia have bitten deep enough in from the margin to have a good hold for their hooks. The beginning of the hypertrophy appears as a faint mass of tissue, seen with its nuclei in the detailed figure 26, plate X. At the end of 12 hours the overgrowth is well advanced and sometimes, as in figure 27, plate X, shows different stages even in neighboring glochidia. The ragged edge of the host's tissue rises up crater-like about the glochidium, meeting above in a delicate mass, the nuclei of which are shown. Figure 22, plate IX, shows that in 24 hours most of the glochidia are more than half covered, whether upon the edge or the surface of the fins. At the end of 36 hours (fig. 25, pl. X) optimum infections of the carp show all the glochidia which have obtained a proper attachment well embedded, and from this time onward the only change which is visible in whole mounts is a slight increase in the opacity of the cyst, which renders the internal structure of the glochidium less distinct (fig. 23, pl. IX). Some of our infections show embedding in as short a time as 6 hours (*Symphynota*), and Harms (1909) gives 10 to 12 hours as the time which he observed in *Anodonta*, so the time given for the figures above referred to is the maximum for hooked glochidia which have been well located. Glochidia upon the fin surface become embedded in a similar manner and are then in a very secure position (fig. 22, pl. IX, fig. 25 and 32, pl. X).

INFECTIONS WITH HOOKLESS GLOCHIDIA.

Our experiments in artificial infection with hookless glochidia have been more extensive because this is the type of glochidium found in the species of mussels which are of commercial importance. Species of the genus *Lampsilis* (*ligamentina*, *recta*, *anodontoides*, *ventricosa*, *subrostrata*, and *luteola*) have been the most frequently used, but infections have also been made with several species of *Quadrula* and one of *Unio*. The list of fishes employed as hosts for hookless glochidia is also more extensive and we are, therefore, able to make statements which we know to be of wider application than those made for the hooked glochidia.

When the same fish is used, the results for the several species of *Lampsilis* are very uniform and we can thus discuss the parasitism of this genus as a whole; but we do not find the same mussel giving uniform results with all species of fish. The glochidia of this genus have been used successfully for the infection of blue-gill sunfish (*Lepomis pallidus*), yellow perch (*Perca flavescens*), crappie, large-mouth black bass, rock bass,

the red-spotted sunfish (*Lepomis humilis*), and the green sunfish (*Apomotis cyanellus*). As with the hooked glochidia, the infections have all been made upon fish under 6 inches in length, upon which these glochidia remain in numbers only on the gill filaments, although during infection some may become attached to and even embedded upon fins and other external parts. Harms (1908) concludes that the hookless type persists in much greater numbers on the fins of small than of large fish, and that the hooked type will survive upon the gills if large fish are used. It is doubtless true that the size of the gills and fins is an important factor in determining the place of attachment for each type, since the hookless form is better adapted for holding to a delicate surface like a gill filament or a fine fin, while the hooked type seems likely to be easily torn from such a surface. When the hookless form does once become established upon an

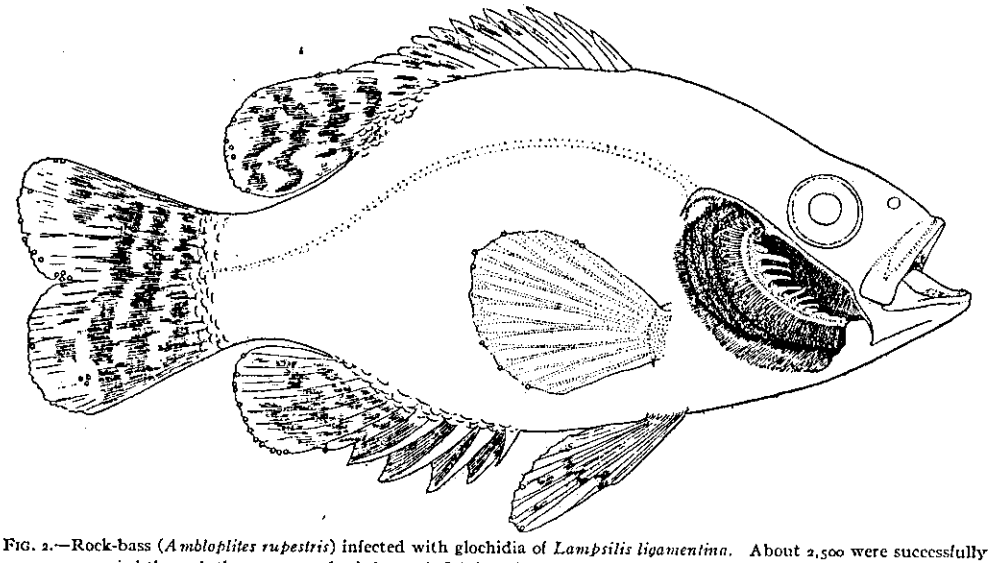

FIG. 2.—Rock-bass (*Ambloplites rupestris*) infected with glochidia of *Lampsilis ligamentina*. About 2,500 were successfully carried through the metamorphosis by each fish in this infection. Note the large number on the gills.

external part, it will develop there without mishap, as shown by the figure of a hooked and a hookless glochidium developing side by side upon the margin of a fin (fig. 29, pl. x). Within the mouth cavity these glochidia become attached to the gill bars and rakers, if these parts are covered by a sufficiently delicate epithelium, though they are always found in the greatest numbers upon the gill filaments. In most of our infections the filaments are more heavily infected toward their outer ends (fig. 43, pl. xi), the distribution varying somewhat with the species of fish. For example, successful infections of rock bass with *Lampsilis ligamentina* show about seven glochidia upon the distal third of the filament to one upon the proximal two-thirds; of large-mouth black bass about 3 to 1, and of yellow perch about 1½ to 1—differences which are probably due to some particular configuration of the mouth parts, which causes the glochidia to fall more upon one region of the filaments than another.

In a fish which will carry a given glochidium successfully, over-infection of the gills is easily accomplished and easily fatal, although species of fish differ greatly in the amount of infection they are able to withstand without serious mortality. In one of our most successful combinations (rock bass infected with *Lampsilis ligamentina*), fish 4 inches in length were estimated to be carrying in the neighborhood of 2,500 glochidia, an average of more than two for every filament of the gills and yet there was almost no mortality among the fish. A rock bass from this infection is shown in text figure 2, which also illustrates the distribution of the glochidia on a single fish. In this case the success of so heavy an infection is perhaps explained by the distribution of the glochidia upon the gill filaments, for we found by count that there were about seven near the tips to one on the proximal two-thirds of the filament, and thus the greater part of every filament was left unchanged and in full functional condition, while in other infections (large-mouth black bass with *L. ligamentina*), where a much greater proportion of the glochidia were upon the sides of the filaments, the mortality of the fish was heavy, although the amount of infection was much less. A gill of the latter fish infected with these glochidia is shown in figure 39, plate XI. The number estimated for this fish, which was 4 inches in length, being only 450, is less than the optimum.

Implantation upon the filaments occurs in a manner similar to that of the hooked glochidia upon the external parts, but much more rapidly. Figures 35, 36, 37, and 38, plate XI, show the appearance at 15 minutes, 30 minutes, 1 hour, and 3 hours, respectively, after infection, and our observations, showing that the cyst is completed within from 2 to 4 hours, agree with what Harms (1909) has found for gill infections. The proliferation will even continue after the gill has been cut from the fish and placed in a watch glass for observation under the microscope (fig. 54 and 55, pl. XIII). An immediate result of the cyst formation is the obliteration of the lamellæ upon either side of the gill filament, which thus becomes smooth and slightly swollen in the vicinity of the glochidium (fig. 43, pl. XI). Figures 34 and 43, plate XI, show the general and detailed appearance of the cysts and the diversity in the angles at which the glochidia are attached.

The older statement that the hooked glochidia are fin and the hookless gill parasites finds, therefore, confirmation from our work, although it would be better to say that the hooked attach most successfully to large strong margins like those of the fins, and the hookless to soft and fine filamentous structures like the gills in fish of moderate size. The reactions of the two types of glochidia to mechanical and chemical stimuli, with respect to the part they play in attachment, have already been discussed.

SUSCEPTIBILITY OF FISHES TO INFECTION.

The susceptibility of different fishes to infection is a matter which has not been sufficiently considered by any previous investigators. We have evidence that some species are much less susceptible than others to one or the other type of glochidium, and that in these cases any considerable infection is an impossibility. The most striking instances of this are the German carp, certain minnows, and the darters.

In the case of the carp, while the fish is admirably suited to carrying the hooked glochidia of *Anodonta* and *Symphynota*, we have never been able to secure a successful infection of the gills with the hookless glochidia of the genus *Lampsilis*. The disappearance of the hooked glochidia of *Anodonta* and *Symphynota* from the gills of the carp may be due to the pulling away of these large and heavy glochidia from the delicate gill filaments, as suggested in our consideration of the survival of the two types of glochidia upon fins and gills, respectively. The disappearance of the hookless glochidia of *Lampsilis* from both gills and fins of the carp can not be explained in this manner; it suggests rather that there may be some reaction of the host's tissues comparable to the processes which confer immunity against parasitic bacteria in higher vertebrates. With minnows (*Notropis cayuga* and *N. lutrensis*) 2 to 4 inches in length, we have not been able to secure any considerable infection with the glochidia of *Symphynota complanata*, for, although they will attach in large numbers during infection, they all drop from the fins and gills within a few days. The fins of these minnows are much more delicate than those of the carp, and the explanation is perhaps that so large a glochidium is easily torn away; but the large-mouth black bass has hardly a delicate fin, and for this fish we have records of infections where no glochidia of *S. complanata* became attached during an exposure sufficient for the attachment of many to the gills. In this latter case, the extreme activity of the fish must be considered as a factor which might keep the hooked glochidia from attachment to the fins.

Darters (*Etheostoma cæruleum spectabile*) 1½ to 2 inches in length can not be infected successfully with the glochidia of *Lampsilis*, for although they may fasten so thickly to the fins that many fish die during the first day after their exposure, the surviving fish will slough off considerable portions of the fins and within a week show only the healed and regenerating parts as an indication of their recent experience. The gill slits were so small in these fish that only an occasional glochidium was found upon them.

Such cases as these are of great importance and should be followed up to determine whether the simple mechanical conditions like over-infection, delicacy of fin, or configuration of the mouth parts can give a satisfactory explanation; or whether the histological changes of which the fish is capable, under stimulation by the glochidium, must be regarded as the cause of its immunity. We have not carried out a sufficient number of experiments to feel sure that the simpler explanations can be excluded. In any case, it is interesting that fish like the minnows and darters, which live close to the bottom, are not likely to become heavily infected by some of our most common glochidia.

BEHAVIOR OF FISHES DURING INFECTION.

The behavior of the fish during infection is a matter of some importance and has been already mentioned in an incidental manner. The rock bass, large-mouth black bass, and blue-gill sunfish, which are very active and which consequently exhibit powerful respiratory movements, are well adapted to artificial infection, and the proper suspension of the glochidia in the water is secured by the movements of the fish alone. The crappie, which are sluggish and easily killed by handling, require some special device to

insure the optimum infection and are not well suited for work on a large scale because of their behavior during infection. Fish which rest upon the bottom are sometimes not so favorable as they might seem because they do not move about enough to keep the glochidia in motion. While other features may be of greater importance, the behavior of the fish as affecting the distribution of the glochidia in the water should always be considered in deciding how useful any fish may be for purposes of infection.

INFECTION OF FISH IN LARGE NUMBERS.

The infection of fish in large numbers has been attempted with a view to determining the feasibility of extending the methods described above to wholesale infections of fish in a hatchery. As a result of two such attempts, we have no doubt that the successful development of the methods needed for infection in connection with the artificial propagation of mussels is only a matter of a little study in a properly equipped station. In December, 1907, about 25,000 small fish, under 6 inches in length, were placed at our disposal at the substation of the Bureau at La Crosse, Wis., and we were able on this occasion to infect by wholesale methods about 12,000 blue-gill sunfish, 3,700 yellow perch, 7,000 catfish, 2,000 crappie, 150 rock bass, 150 carp, and 100 roach. The greater number of these fish were infected with the glochidia of *Lampsilis ligamentina*, and, considering the fact that this was our first experience with so large a number of fish, the results were satisfactory. Smaller lots were infected with the glochidia of *L. anodontoides* and *L. recta*, the results giving every indication that these two species are essentially like *L. ligamentina* in the conditions of their development. The most successful infections were obtained by placing from 100 to 200 fish in a common galvanized iron washtub about two-thirds full of water. It was found that by adding to this body of water the glochidia obtained from two or three specimens of *Lampsilis*, and, when it seemed necessary, stirring the water by hand, tolerably constant results could be secured. Our difficulties were with over- rather than with under-infection. It was also possible to use the same tub a number of times without changing the water or adding to the stock of glochidia. Infection was also attempted by lowering the water in the large retaining tanks of the station to a depth of 4 inches and confining the whole number of fish which had been held in the full tank to this much smaller body of water. This method was found, in the absence of any attempt to keep the glochidia properly distributed through the water, quite inadequate and it became necessary to reinfect these fish in the tubs.

The mortality of the fish in these experiments was decidedly in excess of what one might expect for uninfected fish kept under similar conditions, a result clearly due to the over-infection which is the one thing most to be guarded against. At the end of six weeks some of the remaining fish were liberated in the west channel of the Mississippi River at La Crosse, a locality which we then believed might be suitable for this species of *Lampsilis*.

These infections were made under conditions of limited time and equipment and were wholly tentative, the aim being to make a test of our methods on a large scale. We revisited La Crosse a month after the infection, making careful examinations of the

fish and by shipping several hundred to Columbia were able to follow the development of the glochidia under the conditions in our laboratory. The results were probably as favorable as could have been expected under the circumstances.

In December 1908 a similar infection was attempted with about 6,200 large-mouth black bass and 3,800 crappie in the station of the Bureau at Manchester, Iowa. Upon this occasion the glochidia of *Lampsilis ligamentina* were again used in a majority of the infections, similar results being obtained with *L. anodontoides*, *recta*, and *ventricosa*, which were used for the minor infections. The black bass took the glochidia very readily and, having had only a limited experience with this species of fish, we gave them an amount of infection equal to that which had been carried successfully by the rock bass infected at La Crosse in the previous experiments. The infection was estimated at from 2,000 to 2,500 glochidia to a fish 4 or 5 inches in length. This proved entirely too heavy for the large-mouth black bass and the mortality among them amounted to about 55 per cent in the 30 days they were under observation. By the third day after the infection the hypertrophy of the gill tissue was so great as to be at once noticeable to the eye, and this was clearly the cause of death. An infection of not more than 1,000 glochidia per fish would have been more nearly the optimum load.

The crappie did not take the infection well despite longer exposure, the reason for this being the size of their gill slits and their behavior as already discussed, and we do not consider small fish of this species favorable for infection with any of the glochidia from mussels which are of commercial importance.

Thirty days after these infections the surviving fish were liberated in the Maquoketa River near Manchester, in a situation where the conditions were favorable for mussels and where the presence of a dam below the point of liberation, together with the absence of mussels of this species, made it seem possible that at some later period their appearance in this locality might be traced to this experiment. We have never made any subsequent examination of this stretch of the river with this in view, a thing which should be done by one of the parties engaged in the field work of the mussel investigation.

These two experiments in the wholesale infection of fish, while disappointing in some respects, give no indication of any insurmountable difficulties. It is fair to conclude that a little experimentation under hatchery conditions will make it as easy to carry the glochidia through their metamorphosis in large numbers as we have found it in small lots of fish kept in aquaria. The high mortality of the fish, being so clearly a matter of over-infection, is a thing which can be guarded against without reducing too greatly the load of glochidia which the fish may carry. It is then only a matter of discovering the most suitable species of fish and finding out how best to handle them in large numbers.

One thing which seems necessary for the rapid and uniform infection of fish in large numbers is a device which will bring about a uniform distribution of the glochidia in the water during the whole period of the fishes' exposure. Without something of the sort it will hardly be possible to handle large numbers of fish with constant and uniform results. We have tried, though not very extensively, two means of effecting

this. The first consisted of a two-bladed propeller fastened in the middle of the bottom of a tub and rotated slowly, there being enough space in the water above the blades to allow the fish room to escape the stroke. This device was not very satisfactory, but as it was operated by hand and the blades roughly constructed, effective use might be made of a more carefully adjusted mechanism of this type. A second and more promising device consists of a branched system of iron pipes bored with many small holes (text fig. 3), through which fine jets of water are forced out at the bottom of a tank. The amount of pressure in these fine jets can be easily regulated from the main supply pipe, and the height to which the glochidia will be driven from the bottom is thus controlled. The tank may be allowed to overflow at the top and the glochidia

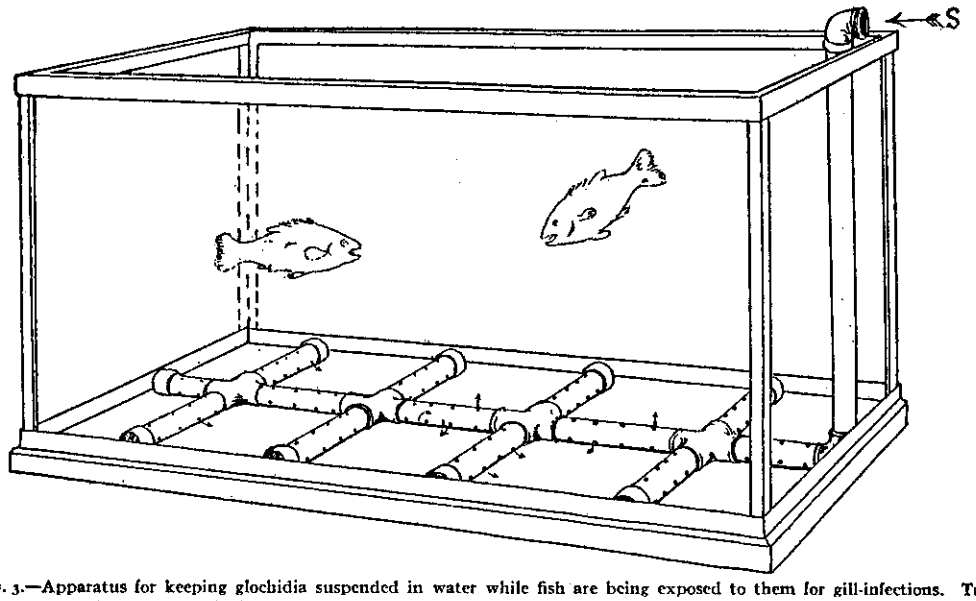

FIG. 3.—Apparatus for keeping glochidia suspended in water while fish are being exposed to them for gill-infections. Tap water entering at S issues in fine jets through the very small holes placed along the top and sides of the pipes on the bottom of the aquarium, and an even distribution of glochidia throughout the water is thereby maintained. By regulating the force of the water entering the pipes at S the glochidia are prevented from rising to the top of the aquarium and escaping with the overflow.

prevented from being carried off in the overflow by so adjusting the force of the jets that the glochidia will not rise quite to the surface. This device keeps the glochidia suspended in a very uniform way, and it may prove to be just what is needed for the uniform infection of large numbers of fish.

CONDITIONS NECESSARY FOR SUCCESSFUL INFECTION.

Three factors should be considered in attempting the infection of any species of fish with glochidia, namely, the uniform suspension of the glochidia in the water, the reaction of the glochidia when stimulated by mechanical or chemical contact with the fish, and the reaction of the fish's tissues after the glochidium has become attached.

In any attempted infection of fish in large numbers, careful tests should first be made upon a few fish in small dishes, with microscopic examination of the infected parts from fish killed during the time of infection and for several days following, or until it is clear that the glochidia have become safely established in their host's tissues. After even limited experience one learns approximately the number of glochidia needed and can determine roughly their suspension in the water by taking samples at random in a pipette, which when held against the light shows clearly the individual glochidia. During infection it is possible to pick out individual specimens and by lifting up the operculum of the living fish, examine the gills with a hand lens. The glochidia are then seen individually and the progress of the infection can be watched. Fin-infecting glochidia may be seen individually if a fish is placed in a small dish against a black background.

It is not difficult to determine by these means the optimum time for the exposure. When 100 fish 5 to 6 inches in length are taken and the contents of a single marsupium of a large *Lampsilis* is placed in an ordinary washtub, infections may be obtained somewhat as follows: Rock bass, exposed 30 to 40 minutes, 2,000 to 2,500 glochidia on gills of each fish; large-mouth black bass, exposed 15 to 20 minutes, 500 to 1,000 glochidia on gills; crappie, exposed 20 to 30 minutes, 200 to 400 glochidia on gills; yellow perch, exposed 20 minutes, 400 to 600 on gills; German carp (with *Anodonta*), exposed 30 to 40 minutes, 200 to 500 on fins. These figures are given as starting points for anyone attempting artificial infections and can not be taken as representing the results of precise determinations of optimum infections for the fish in question, because the means for determining the numbers and distribution of the glochidia have been only approximate. It will probably always be necessary, in the practice of artificial infection on a large scale, to have the fish examined microscopically by a properly trained observer, and this will be particularly true in the beginning of this work in hatching establishments, because the practical details of artificial infection on a large scale have yet to be solved.

DURATION OF THE PARASITIC PERIOD.

According to the experience of previous observers, the duration of the parasitic period varies inversely with the temperature of the water (Schierholz, 1888; Harms, 1907–1909). Although we have found this to be true in general, our experiments have not shown so definite a relation between temperature and parasitism as has been described by Harms, for example, and it is quite possible that other factors, which are obscure, exert a modifying influence upon the length of time the glochidia remain on the fish. Harms found that the glochidia of *Anodonta* completed the metamorphosis in 80 days at a temperature of 8° to 10° C; in 21 days at 16° to 18°; and in 12 days at 20°; while in the case of the hookless glochidia of *Unio* (which are gill parasites) the period was 26 to 28 days at a temperature of 16° to 17°. He is inclined to attribute the somewhat longer time required for the metamorphosis of *Unio* to the fact that the glochidia in this genus when discharged are in a less advanced stage of development than are those of *Anodonta*—a difference that exists between all hookless and hooked glochidia.

A few typical cases, selected from our records of infections are given in the accompanying table, which illustrates the far greater variability in the parasitic period than that observed by Harms.

TABLE SHOWING INFECTIONS WITH GLOCHIDIA.

Experiment.	Date.	Mussel.	Fish.	Exposure.	Young mussels liberated.	Duration of parasitism.	Av. temp. during parasitism.
HOOKED GLOCHIDIA.				*Min.*		*Days.*	°*C.*
1	Dec. 3, 1909	Symphynota complanata.	Apomotis cyanellus		Dec. 17–19	14–16	16.0
2	Dec. 17, 1909	do	do	15	Jan. 1–4	15–18	16.3
3	Jan. 7, 1910	do	Pomoxis annularis. Apomotis cyanellus	15	Jan. 18–21	11–14	16.0
4	Apr. 5, 1910	do	Pomoxis annularis. Apomotis cyanellus	12	Apr. 14–18	9–13	17 8
HOOKLESS GLOCHIDIA.				30			
5	Feb. 19, 1910	Lampsilis ligamentina	Apomotis cyanellus	9	Mar. 5–12	14–21	17.8
6	Mar. 6, 1909	do	do	10–15	Apr. 7–11	32–36	19.1
7	Apr. 8, 1909	do	Micropterus salmoides. Apomotis cyanellus	10–15	Apr. 27–May 1	19–23	20.3
8	Apr. 13, 1910	Lampsilis subrostrata	Micropterus salmoides. Apomotis cyanellus	8–15	May 2–8	19–25	18.1
9	May 2, 1910	Lampsilis ligamentina	do	7–10	May 15–26	13–24	18.1
10	May 3, 1910	Lampsilis subrostrata	Micropterus salmoides. Apomotis cyanellus	50	May 17–25	14–22	18.1
11	July 29, 1909	Unio complanatus	Perca flavescens	7–14	Aug. 12–14	14–16	23.0
12	Aug. 5, 1908	Quadrula plicata	Micropterus salmoides	30	Aug. 17	12	24.4

In the case of *Symphynota complanata*, which has hooked glochidia essentially like those of *Anodonta*, the period varied from 9 to 18 days at average temperatures of 17.8° to 16° C., as compared with Harms's 21 days at practically the same temperature. At lower temperatures, about 10°, we have recorded a period of 74 days for *S. costata*.

The absence of a close correspondence between the temperature and the duration of the parasitism has been much more conspicuous in the case of hookless glochidia, which have shown not only a remarkable range in the period but a considerable irregularity in different experiments made at about the same temperature. The shortest period recorded by us was seven days in an infection of black bass with the glochidia of *Lampsilis subrostrata* and *L. recta* in April when the average temperature during the parasitism was 20.5°, but this unusual time was only observed in this one instance. A still more remarkable case, but at the opposite extreme, was an infection of black bass and crappie with the glochidia of *L. ligamentina* and *L. recta* which remained on the fish for 13 to 16 weeks. The infection was made in November and the young mussels were liberated during a period of about three weeks in the following February and March; during the parasitism the temperature varied from about 16° to 18.° The cause of the extreme duration in this case is not known, for in no other experiment at the same temperature has the parasitism lasted for more than 25 days.

As may be seen in the table, with hookless glochidia (aside from the extreme cases mentioned) the variation in the period has been from 12 to 36 days at average temperatures ranging from 24.4° to 17.8°; but even at practically the same temperature the difference may be quite marked, as in experiments no. 8 and no. 9. Experiment no. 6 should be noticed as being a case in which, contrary to expectation, quite a long period (32 to 36 days) was recorded at 19.1°, whereas in other experiments (no. 5 for example) the time was only 14 to 21 days at the lower temperature of 17.8°.

It would seem clear that, although within certain wide limits the duration of the parasitism is dependent upon the temperature of the water, nevertheless other factors may enter into the case to either accelerate the metamorphosis or prolong it over a period which is much longer than the usual duration of the parasitism. These factors would seem to be associated with individual physiological differences in the interaction between the fish and the parasite and are probably nutritive in nature, for on one and the same fish some glochidia may remain several days longer than others.

As may be seen from an examination of the table, in which the period of liberation is given in each experiment, not all of the young mussels leave the fish at the same time, but, on the contrary, the liberation may occupy a week or more. Harms found that it required from 5 to 6 days, the greater number leaving the fish during the middle of the period. Our experience has usually been in accord with these observations, but we have found the period to be somewhat more variable, from 2 to 11 days, or even much longer.

IMPLANTATION AND CYST FORMATION.

As has been described, the glochidium attaches itself to the fish by closing its shell firmly over some projecting region which can be grasped between the valves, like the free border of a fin or a gill filament. In so doing, a portion of the epithelium and underlying tissue, including blood vessels and lymphatics and varying in amount with the extent of the "bite," becomes inclosed within the mantle space of the glochidium. This tissue early disintegrates into its cellular constituents, which are taken up by the pseudopodial processes of the larval mantle cells, and, as Faussek (1895) has described, are utilized as food during the early stages of metamorphosis. In figure 60, plate XV, drawn from a glochidium six hours after attachment to a fin, the disintegrated tissue, consisting of loose epithelial cells, blood corpuscles, and fibers which lie scattered in the mantle cavity, is seen in the process of being ingested by the mantle cells. Figure 61, plate XV, shows a later stage, 24 hours after attachment, in which the detritus has been entirely taken up, and the mantle cells are now heavily charged with food material.

Almost immediately after attachment proliferation of the epithelium begins as the initial step in the formation of the cyst which eventually incloses the entire glochidium. The overgrowth of the larva has been described by Faussek (1895) and Harms (1907–1909) as a healing process on the part of the fish's tissues, resulting from the irritation caused by the wound. The proliferation starts around the line of constriction produced by the pressure of the edges of the valves on the epithelium, and, since the glochidium lies between and prevents the immediate closure of the lips of the wound, the extending

epithelium is forced to slide up over the surface of the shell on all sides, until the free margins meet and fuse over the back of the larva, as may be understood by reference to figures 59 to 61, plate XV, and 35 to 38, plate XI.

So rapid is the overgrowth, especially in the case of implantation on the gills, that it would seem that something more than the mere mechanical irritation produced by the glochidium is concerned in causing the proliferation of the epithelium. We have, therefore, carried out a series of experiments with a view to determining whether or not a chemical stimulus is provided by the larva, and by using various methods have studied the action of glochidial extracts on the epithelium of both fins and gills. The results have been entirely negative, although the question has by no means been settled by the experiments which have been thus far attempted. By further improvements in the technique, some of the difficulties involved in the investigation, which is still in progress, may be overcome.

The process of implantation and cyst formation may be readily observed on the filaments of an excised gill, which under favorable conditions will live long enough in a dish of water to enable one to see the glochidium completely covered by the proliferated epithelium. Figure 54, plate XIII, drawn from the living excised gill, shows the distal end of a single filament bearing a glochidium of *Unio complanatus* which has become nearly covered by the walls of the cyst. In this case the gill was cut from the fish two hours after the infection and the drawing was made an hour later; immediately after the excision of the gill this particular glochidium was hardly half covered. The same glochidium was kept under observation, and two hours later (five hours after the infection) the sketch was made which is reproduced in figure 55, plate XIII. By this time the cyst, which is seen to have very thick walls, was completed, and formed a prominent mass near the end of the filament. Shortly afterwards the tissues of the gill began to disintegrate, but for at least three hours they remained alive and the proliferation of the epithelial cells proceeded rapidly, the entire process of cyst formation taking place in a perfectly normal manner.

The histological changes which the epithelium undergoes in the formation of the cyst have been studied in this laboratory by Miss Daisy Young, and, as her results will soon be published in detail, only a brief reference will be made in this place to the essential points involved in the cellular changes occurring during implantation of the glochidium.

Figure 59, plate XV, shows a very early stage, 15 minutes after attachment, in the formation of the cyst on the fin of a fish which had been infected with the glochidia of *Symphynota complanata*. The section is taken transversely through the glochidium and the free border of the fin on which the parasite has a firm grip. The mass of tissue, consisting of epithelial cells, connective tissue, and blood vessels in the mantle chamber of the glochidium, is the edge of the fin which was inclosed between the valves when attachment was effected. Already the proliferation of the epithelium is beginning in the neighborhood of the constriction, where two mitoses may be seen on the right in the figure. At the edges of the wound caused by the closure of the shell some of the

epithelial cells are undergoing degeneration, while on the left of the section quite a patch of these cells is sloughing off, a not infrequent occurrence. The region of most active growth and multiplication of cells is just below the line of constriction, and, as the cells at this level increase in number, they appear to push those lying above them up over the outside of the shell, so that the actual covering of the glochidium is due largely to this mechanical gliding of the epithelium over its surface. Sections give no conclusive evidence of amitotic division, while mitoses are generally abundant in the region of active proliferation. An intermediate step in the process of implantation is illustrated in figure 60, plate xv, less highly magnified than the last figure, which shows a glochidium about half covered in six hours after attachment. The free edges of the cyst wall eventually meet over the dorsal side of the glochidium, where they then fuse. Figure 61, plate xv, shows a case of complete implantation on a fin at the end of 24 hours; now the epithelial covering is continuous and the glochidium entirely inclosed. The wall of the cyst is seen at this time to be quite thick, but it usually becomes thinner later on as the cells composing it flatten down. In the last two figures the mantle cells of the larva clearly show epithelial nuclei and cell detritus which have been ingested.

In figures 62 and 63, plate xv, two stages are represented in the formation of the cyst on gill filaments, taken at one hour and three hours, respectively, after attachment. The glochidia are those of *Lampsilis ligamentina*. In figure 62, plate xv, the proliferation has made some progress, especially on one side, and three or four mitotic figures are seen just below the glochidium and near the raw edge of the constricted epithelium. A large mass of the tissues of the filament is also shown in the figure inclosed within the mantle chamber of the glochidium. Figure 63, plate xv, represents a stage when the process is nearly completed and the edges of the epithelial covering have met but not yet quite fused. The cyst wall in this case is much thinner than that shown in figure 61, plate xv, but its thickness is quite variable.

In about one week after attachment, as a rule, the wall of the cyst begins to assume a looser texture, the intercellular spaces becoming infiltrated with lymph, and from this time on to the end of the parasitic period there is little further change in its structure.

Before liberation of the young mussel, the valves open from time to time and the foot is extended. By the movements of the latter the cyst is eventually ruptured, its walls gradually slough away, and the mussel thus freed falls to the bottom.

Portions of the wall of the cyst often adhere to the shell after liberation, while, if the young mussel has hooks, it may hang for a time by shreds of the fin in which the hooks are embedded, as seen in figure 24, plate ix.

METAMORPHOSIS WITHOUT PARASITISM IN STROPHITUS.

In a brief paper (1911) we have recently announced the discovery that in the genus *Strophitus* Rafinesque the metamorphosis takes place in the entire absence of parasitism, and, since the life history of this form is without a parallel in the Unionidæ, so far as is known, reference may be made again to the interesting conditions which obtain in its development.

It has been known for a long time that in *Strophitus* the embryos and glochidia are embedded in short cylindrical cords which are composed of a semitranslucent, gelatinous substance, and that these cords, which are closely packed together, like chalk crayons in a box, lie transversely in the water tubes of the marsupium. The blunt ends of the cords are seen through the thin lamella of the outer gill, which in this genus, as in *Anodonta* and others, constitutes the marsupium. The position of the masses of embryos, while contained within the gill, is so unusual that Simpson in his "Synopsis of the Naiades" established a special group, the Diagenæ, for *Strophitus*—the only genus of the family in which this peculiarity exists. In other genera the embryos are conglutinated more or less closely to form flat plates or cylindrical masses, each one of which is contained in a separate water tube and lies vertically in the marsupium.

So far as we are aware, Isaac Lea (1838) was the first to observe this interesting arrangement which he described and figured, rather crudely to be sure, in *Strophitus undulatus* (*Anodonta undulata*). In several subsequent communications (1858, 1863) he added further details and illustrations, and also mentioned the occurrence of the transversely placed cords, or "sacks," as he called them, in *S. edentulus*. He recorded the former species as being gravid from September until March, and described the extrusion of the cords from the female, as well as the remarkable emergence of the glochidia from the interior of the cords after the latter have been discharged.

> The sacks were discharged into the water by the parent from day to day, for about a month in the middle of winter. Eight or ten young were generally in each sack, but some were so short as only to have room for one or two. Immediately when the sacks came out from between the valves of the parent, most of the young were seen to be attached by the dorsal margin to the outer portion of the sack, as if it were a placenta.

The essential points in these observations have since been verified by other investigators. Sterki (1898), following the suggestion of Lea, has called the cords, which differ strikingly from the conglutinated masses of *Unio* and other genera, "placentæ," thus indicating that he considered them to have a nutritive function. He also described the extrusion of the glochidia, when placed in water, and their attachment to the cord "by a short byssus thread whose proximal end is attached to the soft parts of the young." He further states that the glochidia are inclosed in the placentæ when the latter are first discharged, and that after their extrusion they remain attached for some time.

Strophitus edentulus, which Ortmann (1909) regards as identical with *undulatus*, is a rare species in all of the localities in which we have collected mussels, and, until recently, our only observations on this form were made upon a few gravid individuals which were taken in the Mississippi River near La Crosse, Wis., during the summer of 1908. Mention has already been made of our records with reference to the breeding season of *Strophitus*.

After verifying the main observations of Lea and Sterki, so far as was possible at that season of the year, we examined the glochidia carefully with a view to determining whether their subsequent life history would exhibit any peculiarities, as might be suspected from their relation to the cords. At that time we did not observe the normal

discharge of the cords by the female; but we removed them from the marsupium, placed them in water, and, after the glochidia had emerged (fig. 46, pl. XII), employed various means to bring about their attachment to fish. None of these attempts, however, was successful, although the fish were left in small dishes containing many cords for as long a time as 12 hours. In the light of these results, which indicated the inability of this glochidium to attach itself to fish, and in view of the fact that the cords so evidently seemed to be a nutritive device, we felt it to be highly probable that in this species the metamorphosis would be found to occur in the absence of parasitism—a prediction which has been recently verified.

On February 6, 1911, a single female of *Strophitus edentulus*, which had been kept in the laboratory since the preceding November, was seen discharging its cords from the exhalent siphon. The discharge continued until March 25, and during that time the cords were thrown out in varying numbers from day to day. They measured from 2 to 10 mm. in length and about 1 mm. in diameter, although they became more or less swollen after lying in the water for a time. Each cord contained from 10 to 24 glochidia arranged in an irregular row. In many cases the glochidia emerged from the cords in a few minutes after the latter were discharged, and then usually remained attached by the thread in essentially the same manner as has been described by Lea and Sterki (fig. 46, pl. XII). The thread, which is apparently a modified larval thread, is continuous at its distal end with the egg membrane, which generally remains embedded in the cord; so intimate, in fact, is the union between the two that at times the membrane, adhering to the thread, is dragged out of the cord when the glochidium is extruded, in which case, of course, the glochidium becomes entirely detached from the cord.

All attempts to infect fish with these fully formed glochidia were again unsuccessful, even when the exposure was of long duration. Within a few days the extruded glochidia died in spite of every effort to provide the most favorable conditions for their maintenance.

When the cords first began to be discharged, one of our students, Miss Daisy Young, happened to notice that not all of the larvæ were extruded, and that among those which remained in the cords some had lost the larval adductor muscle, possessed a protrusible foot, and showed other signs of having undergone the metamorphosis. Upon careful examination this was found to be true, and it was discovered that these young mussels—for such they undoubtedly are—are subsequently liberated by the disintegration of the cord *after having passed through the metamorphosis in the entire absence of a parasitic period.* We, therefore, have concluded that the emergence from the cords in the glochidial stage is premature, due possibly to some change which has taken place in the gelatinous substance surrounding them as a result of free contact with the water, or to release from the pressure to which they are subjected while in the marsupium. It is perfectly evident that these glochidia neither become attached to fish nor undergo any further development; they have simply come out too soon and are lost.

The young mussels, on the other hand, which have developed inside the cords, when liberated by the disintegration of the latter or removed directly by teasing, are found to

have reached as advanced a stage of development as is attained by any unionid at the time it leaves the fish. They closely resemble the young of *Anodonta* at the close of the parasitic period, and upon examination have been found to possess the following structures: The anterior and posterior adductor muscles; the ciliated foot; two gill buds on each side; a completely differentiated digestive tract, including mouth, esophagus, stomach intestine, and anus; liver; the cerebral, pedal, and visceral ganglia; otocysts; the rudiments of the kidneys, heart, and pericardium; while they also show a slight growth of the permanent shell around the margin of the shell of the glochidium (fig. 45, pl. XII). The larval muscle has completely disappeared, although some of the mantle cells of the glochidium, as well as the hooks of the shell, are still present. They crawl slowly on the bottom of the dish by the characteristic jerking movements of the foot, after the manner of the young of other species at a corresponding stage, although the valves of the shell gape more widely apart and the foot is shorter and less extensible. We have not succeeded as yet in keeping them alive for more than 10 days, but it is difficult in the case of any species to maintain young mussels of this age under laboratory conditions.

One of these young mussels after removal from the cord is shown in figure 45, plate XII, in which many of the organs of the adult or their rudiments are clearly indicated. A comparison will show that it is essentially as advanced in its development as the young of *Anodonta* when it is liberated from the fish (cf. Harms's figures, 1909, and also our fig. 47, pl. XII, of *Symphynota costata*).

The conclusion is inevitable that we have here to do with a species which has no parasitism in its life history, although the presence of hooks and other typical glochidial structures would indicate that it has originated from ancestors which possessed the parasitic stage like other fresh-water mussels. The cord is undoubtedly to be interpreted as a nutritive adaptation which arises in the marsupium during the early stages of gravidity, since the young embryos are at first contained in an unformed viscid matrix and the cords are a later product.

The whole history of this exceptional species warrants a more detailed study, and Miss Young is now engaged in such an investigation. When her work is completed we hope that it may include the entire course of development, the method of formation of the cords, and the rearing of the young mussels during a much longer period than has thus far been possible.

V. ATTEMPT TO REAR GLOCHIDIA IN CULTURE MEDIA.

Since the relation of the glochidium to the fish is essentially a nutritive one, it seemed to us that it should be possible to rear the larvæ through the metamorphosis artificially, provided a suitable nutritive medium could be found, and accordingly a series of experiments, with this object in view, were undertaken at our suggestion by one of our students, Mr. L. E. Thatcher. Although the result has thus far been entirely negative, we have not despaired of ultimate success, and, since the experiments are to be continued, a brief mention of the methods employed may be made in this place.

It was natural to suppose that the blood of the fish would offer the most favorable nutritive conditions for the development of the glochidia, and hence it has been used in most of the experiments, which, moreover, have been made in the spring, when the water in the laboratory was comparatively warm and the metamorphosis, if it had occurred, would have taken place as rapidly as possible.

The glochidia of *Lampsilis ligamentina* and *L. subrostrata* were carefully removed from the marsupium with a sterilized pipette and then repeatedly washed in distilled water in order to obtain them as free as possible from bacteria and other organisms. A drop of blood was next taken from a fish's heart and placed on a cover glass and a few glochidia immediately introduced into it. The cover glass was then inverted over a hollow slide containing a moist piece of filter paper, and the chamber sealed with vaseline. Every precaution was taken to avoid contamination by bacteria. As soon as the glochidia came into contact with the blood, of course they snapped shut in the manner already described and in doing so inclosed some of the corpuscles, which it was to be presumed would be ingested by the mantle cells. Although in some cases bacteria and infusoria, probably introduced with the glochidia, appeared, in a majority of the cases the cultures remained free from foreign organisms. In the latter event the glochidia lived for a few days, but finally died without showing any indication of further development. Experiments were tried with the blood of the frog and of *Necturus*, and also with extracts of fish's tissues, bouillon and other nutritive media. In all, however, the results were negative. The failure may possibly have been due to insufficient aeration, and experiments are now being devised in which oxygen is to be introduced into the moist chambers, and it is hoped that we shall yet succeed in rearing the glochidia in nutritive media through the metamorphosis.

VI. POST-LARVAL STAGES.

BEGINNING OF THE GROWTH PERIOD AND LIFE ON THE BOTTOM.

The changes occurring during the parasitism and by means of which the glochidium becomes transformed into the young mussel, ready for life on the bottom, are more properly described by the term development than by the word growth. The latter process becomes the conspicuous feature only when the miniature mussel has left the fish. From this time onward there are very few changes to which the term development may be strictly applied; for, with the exception of the outer gill, all the important organs of the animal have been laid down and have assumed something of their definitive structure (fig. 47, pl. XII).

As soon as they are liberated from the fish the young mussels become quite active and move about on the bottom of a dish by means of the foot (fig. 18, pl. VIII, and fig. 48, pl. XII), securing a hold by flattening the ciliated distal end against the bottom, and then drawing up the body after the characteristic fashion of lamellibranchs. In these movements the cilia of the foot play an active part; they beat vigorously while the foot is being extended, and apparently are effective in part at least in causing the protrusion. When

5) Collection and Infection of Fishes during month of July, 1927. Illustrates fish rescue and infection records once held at Fairport. From Box 16, Fish-42, D.C. Booth Historic Fish Hatchery.

DEPARTMENT OF COMMERCE
BUREAU OF FISHERIES
Form 611 a

COLLECTION AND INFECTION OF FISHES DURING MONTH OF July, 1927

BIOLOGICAL STATION, FAIRPORT, IOWA

Mussel Propagation Lake Pepin Substation Lake City, Minn. Total Glochidia 18,189,050

FISHES COLLECTED, INFECTED, AND LIBERATED

WHERE PROCURED	WHERE LIBERATED	L. M. BASS	S. M. BASS	SUNFISH	CRAPPIE	SAUGER	Sauger Walleye	PICKEREL	Wisc. Pike	YELLOW PERCH Large	PERCH Small	CHANNEL CATFISH	GOLDEN SHINER	TOTAL	Species and Number of Glochidia: L. luteola Glochidia
Lake Pepin.															
Stockholm Haul		2		10	8	6	18		5	2	58			109	127,800
Canfield Haul	Lake Pepin			19		18			1		499			537	163,900
Huffman Haul		1		14	22	182	451		3	338	633			1644	2,675,300
Randal "						14	28			14	60			116	160,000
Long Point "		1		4	5	88	146		11	62	787			1104	855,700
2nd Creek "		10		8	1	9	73			36	103			240	361,800
Mackey Shore "		2		2		89	122			48	227			490	758,700
Nehart " Haul		4		15	22	780	696		37	209	505			2268	5,124,200
Rowe "				11	3	30	137		6	81	901			1169	792,100
Camp Dodo "						5	55			37	479			576	301,900
Gilbert Creek "				11	42	30	241		1	59	1039			1423	1,053,000
Matson Pt. "				8	10	50	343		3	22	799			1235	1,327,700
Central Pt. "				2	10	194	160		8	173	449			996	1,605,000
West Island "		3		31		94	288		1	117	1351			1885	1,534,250
Patterson's "				12		8	18			10	34			82	119,400
Babbits Pt. "		3		4	2	16	39			21	295			380	251,500
Lake City "				5		7	19		3	12	4			50	118,900
Hospital "				6		40	103		2	68	461			680	624,100
Stem Pt. "		1		6		9	48		6	12	78			160	231,800
														15,144	18,189,050

Fishes collected from Lake Pepin 15,144

Fishes rescued .....

Fishes propagated .....

TOTAL 15,144

Of these 15,144 were infected with 18,189,050 glochidia and liberated.

GOVERNMENT PRINTING OFFICE

6) Floor Plan for the 1914 Fairport Laboratory. Pp. 389-90 in Coker, Robert E., "The Fairport Fisheries Biological Station: Its Equipment, Organization, and Functions." *Bulletin of the U.S. Bureau of Fisheries* 34 (1914): 383-406.

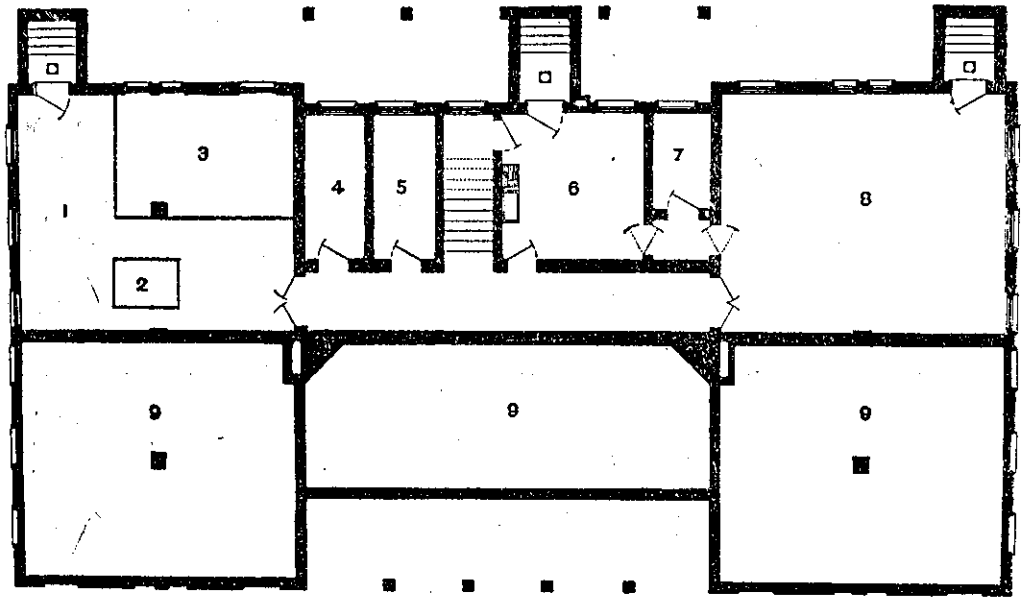

FIG. 1.—Plan of basement of laboratory. 1, Furnace room; 2, steam boiler; 3, coal bin; 4, store room; 5, toilet; 6, kitchen; 7, pantry; 8, dining room; 9, not excavated.

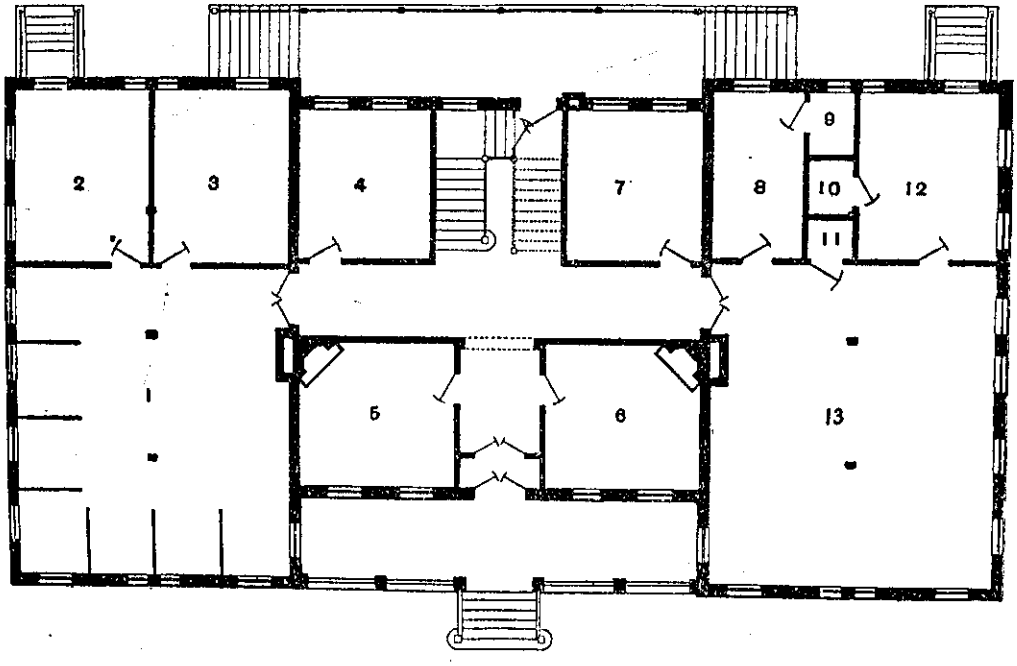

FIG. 2—Plan of main floor of laboratory building. 1, General laboratory; 2, library; 3, chemical laboratory; 4, sterilizing and embedding room; 5, general office; 6, director's office; 7, stock room; 8, packing room; 9, closet for office storage; 10, alcohol closet; 11, janitor's closet; 12, preparation room; 13, museum.

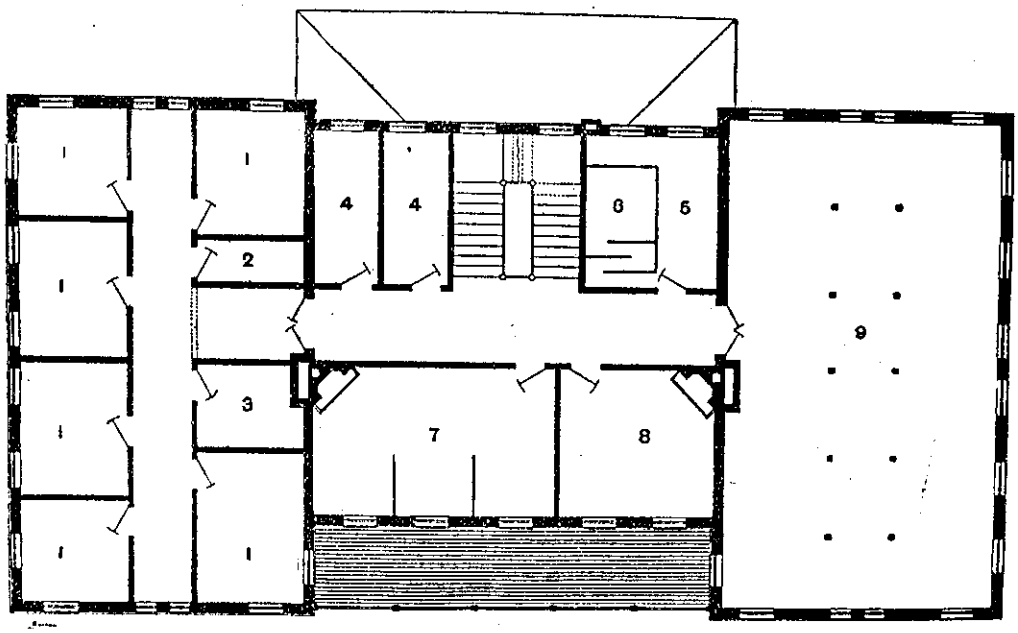

FIG. 3.—Plan of second floor of laboratory building. 1, Six bed chambers; 2, linen closet; 3, janitor's closet; 4, two bathrooms; 5, photographic room; 6, dark room; 7, north laboratory; 8, director's laboratory; 9, west wing.

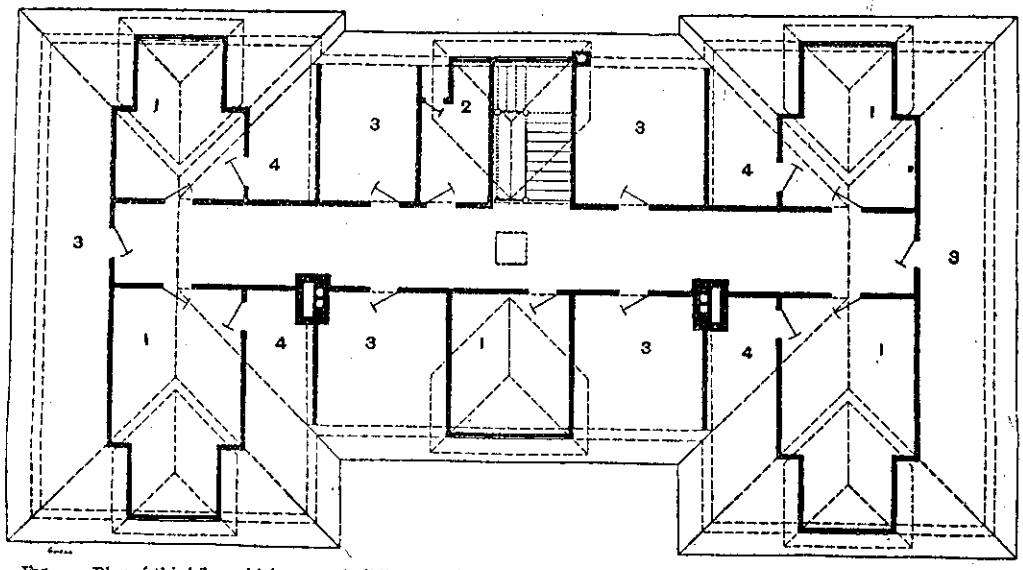

FIG. 4.—Plan of third floor of laboratory building. 1, Five bed chambers; 2, bathroom; 3, six dark storage chambers; 4, four large closets.

7) "Mussel Propagation, by Experiment and Practice." Pp. 399-402 in Coker, . "The Fairport Fisheries Biological Station . . . ." *Bulletin of the U.S. Bureau of Fisheries* 34 (1914): 383-406.

MUSSEL PROPAGATION, BY EXPERIMENT AND PRACTICE.

ORGANIZATION AND GENERAL PLAN.

In the practical propagation of mussels the Fairport station serves as headquarters for field operations conducted throughout the Mississippi Basin, including the Mississippi River and its various tributaries. There may be in the field at one time from two to six field parties operating near the station or at distances of several hundred miles, and all parties are organized under the superintendent of fish culture.

While the available personnel and means do not permit of covering the extensive field, the present endeavor is to restrict the operations to certain localities favorable for the work and needing of replenishment, and to distribute these localities as widely as practicable through the territory. Hence operations are now conducted in Lake Pepin of Minnesota and Wisconsin, on the Mississippi at Fairport, Iowa, on the Wabash in Indiana, and on the White and Black Rivers of Arkansas.

Each field party is under the direction of a competent head, who may be a permanent or temporary employee, sent out from the Fairport station or from the central office in Washington to work under the direction of the Fairport station. The crews employed in the seining of fishes, inoculating them with glochidia, and liberating them again in the river are made up of local laborers or fishermen temporarily employed.

There is no definite outlay of apparatus required. The chief of the party is provided with a compound microscope or a dissecting microscope, an ordinary Coddington magnifier, the usual dissecting instruments, and a field equipment which may consist of seines, fyke nets, tubs, tanks, buckets, etc. A Government-owned launch and rowboats may be used or launch and rowboats may be employed in the region where the operations are conducted. It is generally convenient to use flat-bottom rowboats of small size, 16 to 24 feet in length, but a launch is also practically necessary in order that more rapid movements can be made from place to place, thus extending the sphere of operations possible for a day's work. In some cases the field parties can find accommodation in towns conveniently situated, but in other cases a house-boat must be rented in order that the fishing party may have a place in which to sleep and board.

The methods of propagation are based upon a peculiar feature of the normal course of development of fresh-water mussels. The very young fresh-water mussels, with rare exception, when first liberated from the incubation pouches of the parent, must become parasitic upon fish in order to pass through the next stage of their existence. To this end, if the chance offers after liberation, the young mussels, or glochidia, as they are called in this stage, attach themselves to the gills, fins, or scales of a fish. The mussels of economic importance attach themselves almost exclusively to the gills. In attaching or biting on the fish a very slight wound seems to be caused, which begins at once to

heal over; but in the process of mending the glochidium is overgrown and thus inclosed within the tissues of the fish. The mussel is now actually an internal parasite, in which condition it remains for a period of two weeks, more or less. It is thus conveyed wherever the fish goes, until, when the proper stage of development is reached, it frees itself from the host and falls to the bottom; if through favorable fortune it finds suitable lodgment, it continues its growth to form an adult mussel.[a]

The glochidia are so small that the infection, if not excessive, has no apparent injurious effect upon the fish that serves as host. Investigations by the station have shown that mussels do not attach to fish indiscriminately, but that for each species of mussel there is a limited number of species of fish which may serve as host. Particular instances are mentioned on a later page.

The task of propagation is to bring together suitable fish and the glochidia of mussels. Careful studies of natural and artificial infections show that a moderate sized fish may successfully carry in parasitism from 1,000 to 2,000 of the microscopic glochidia, but that under the chance operation of nature few of the glochidia find a lodgment upon the proper fish or upon any fish.

During the last fiscal year, in round numbers, 344,000,000 glochidia were liberated in parasitic condition, 208,000 fish being employed in the operations. A considerable proportion of these glochidia undoubtedly fall upon unfavorable ground or from other causes fail of reaching maturity. However, it is the large number which can be infected and liberated at small expense that justifies a confidence in the accomplishment of commensurate benefits. The average cost per 1,000 glochidia artificially infected in the fiscal year 1915 was 2.7 cents, inclusive of overhead expenses.

METHODS OF PROPAGATION.

The operation of infecting the fish with glochidia is a very simple one, though the methods may vary considerably with each party. Essentially the method is as follows:

(1) The first step is to secure a number of gravid mussels in order to obtain a supply of glochidia. Generally this can be accomplished by visiting the beds where mussel fishermen are engaged in work, looking over the catch, and picking out the desired number of gravid females, for which a small sum may be paid.

(2) These mussels are then opened, the marsupial passages are cut out, placed in a pan of water, where they may be opened with scissors or scalpel and the glochidia squeezed out into the water. The glochidia are taken up with a suitable pipette and placed in a small container, such as a glass or can. Usually this operation is delayed until the fish have been obtained.

(3) It is now necessary to secure as many fish as possible by means of seine or nets, and the species of fish must be appropriate for the species of mussel to be propagated. (See pl. LXXIX fig. 8–10.) After the fish are transferred from the seine to tubs or tanks, and when a suitable number of fish are in the tanks, overcrowding being avoided, a lot of glochidia are thrown into the water. (See pl. LXXIX, fig. 11.) There is no definite rule as to the number of glochidia to be used with any number of fish, but the person in charge is guided by his experience with due regard to the temper-

[a] There are one or two species of mussels which need not attach to fish, but these are of no commercial value. There are a few species which during the period of parasitism increase in size manifold, being true parasites; but the greater number of species are between these two extremes, using the fish for conveyance and protection, but certainly deriving no considerable amount of nourishment.

ature of water, the number and size of fish, and the activity of the glochidia. The fish may remain exposed to the glochidia for a period of 5 to 20 minutes. From time to time a specimen of fish is taken by hand, or with a small hand net, and the gills examined to ascertain if a sufficient degree of infection has obtained. When, in the judgment of the operator, the fish show the optimum degree of infection they are ready for liberation.

(4) Using buckets or small nets, the fish are transferred from the tank back into the river or the entire tub may be turned over into the river. This concludes the operation of infection as ordinarily carried on in a practical way.

INVESTIGATIONS RELATING TO PROPAGATION.

A good deal of experimental work is being carried on at the station to determine what species of fish are best suited for certain species of mussels, to ascertain the period of parasitism and the life history of the young mussels after parasitism, and to lead to such improvement of methods as will make the work most productive of practical results.

In addition to the study of special problems of importance, three general lines of investigation have been carried on practically continuously. These are (1) the daily collection of fish from the river for study of the condition of natural infection, (2) experiments in artificial propagation, employing various species of mussels and fish and keeping careful observation of the methods and results, and (3) the study of the habits and distribution of juvenile mussels. The results have been so favorable as to justify the continuance of these studies for a considerable time.

The fishes of the sunfish family, game fishes, such as the bass, crappie, sunfish, etc., are usually used for the mucket (*Lampsilis ligamentina*) and the fat mucket (*Lampsilis luteola*). For a very important mussel, the pimple-back (*Quadrula pustulosa*), the Siluridæ, or catfishes, are found to be best suited. One of the best species of mussel, the "niggerhead" (*Quadrula ebenus*), is known to become parasitic only upon one species of fish, the river herring, *Pomolobus chrysochloris*. This fish is so delicate that it has been impossible to handle it in a practical way, and, therefore, no operations in the propagation of this mussel are yet pursued. Some experiments have been conducted which are promising of success. Examples of the herring found during the breeding season of the "niggerhead" are usually so heavily infected that it may not be necessary to use artificial methods with this mussel, although the abundance of the fish should be promoted. The matter is now under investigation. A very valuable species of mussel, the yellow sand-shell (*Lampsilis anodontoides*), is parasitic upon the several species of gar.

Other investigations are now being conducted with reference to the possibility of rearing young mussels after parasitism in ponds or in floating crates, and the preliminary results are as encouraging as could be expected. It is interesting to note that from glochidia of commercial species of mussels artificially infected upon fish at this station, young mussels have been reared within a period of two years to such a size that it was possible to cut and finish buttons from the shells (pl. LXXX). Some of these were reared in floating crates and some in one of the larger earth ponds. They are not only the first mussels to be reared to such a size from artificial infection, but they are the first commercial forms known to have grown in ponds. The experiments have not yet

advanced to a stage where any definite statements can be made as to the practicability of rearing fresh-water mussels in waters other than the natural mussel streams.

Two years ago an interesting discovery was reported by Lefevre and Curtis, when it was found that some glochidia of the squaw-foot mussel (*Strophitus edentulus*) developed into young mussels without becoming parasitic. Howard, in our laboratory, has since extended these observations by showing that the glochidia of that species will also develop by the customary mode of parasitism and by the discovery that another species, a small "floater" (*Anodonta imbecillis*), will develop without parasitism. Neither of these species, the only ones that have ever been made to develop without the use of a fish as host, is of any commercial importance, but it suggests itself as an important investigation that methods should be sought for causing other and useful species to develop without the fish. Whether the problem should prove simple or difficult, it is worthy of the endeavor.

The interesting and very practical discoveries which have been made, as a result of the close association of practical and investigational work, and the direct bearing of the information gained upon the promotion of the natural resources are held to demonstrate the essential wisdom of Congress in providing at the beginning that the propagation of mussels and the investigation of mussels should go "hand in hand."

The most clearly outstanding feature of our work is the absolute dependence of mussel conservation upon fish conservation in the broadest sense. There can not be abundant mussels if there are not abundant fishes. There can not be varied mussel resources if there are not varied resources in fin fishes. Probably no step for the promotion of the mussel fishery would yield greater benefits to that fishery than effective efforts for the conservation of fin fishes.

The interlocking interests of shell fishers and fin fishers is properly a matter of particular interest and worthy of emphasis, although, of course, the conservation of fishes rests upon a far broader basis than any consideration of value derived from the dependence of shell fisheries.

PROPAGATION AND RECLAMATION OF FISH WITH EXPERIMENTAL AND PRACTICAL ENDS.

The pond-cultural operations are planned to be carried out with particular experimental objects. It is hoped by careful observational and experimental methods to contribute to the improvement of methods of cultivation of pond fishes, especially as relates to the rearing of fish to a size suitable for the table. It is held as a most important responsibility of the station to stimulate and to guide the development of fish farming as a more widespread industry. This function as a fish-cultural experiment station should rightly be regarded as second to none, but its full accomplishment will depend upon the future provision of means proportionate to the labors involved and the far-reaching benefits to be gained.

Meantime the propagation of mussels and of fishes is well carried on hand in hand. While it is not feasible now to rear the quantity of fish requisite for the propagation of mussels, it is attempted by means of the experimental operations of pond culture at the station to obtain a reserve stock of young fish of several species which in the fall are infected with mussels and liberated in the river. A threefold purpose is served in the increase both of the fish and of the mussels in the public waters and in the acquisition of experimental data.

8) Tables 1-4, from Howard, Arthur Day, "Experiments in Propagation of Fresh-Water Mussels of the Quadrula Group." *Report of the U.S. Commissioner of Fisheries* for 1913, Appendix IV.

TABLE 1.—ARTIFICIAL INFECTIONS WITH QUADRULA PUSTULOSA.

Date.	Experiments.	Species of fish.	Number of fish.	Number of glochidia attaching.	Date liberated.	Period on fish.	Development at latest observation.	Average temperature.
								°F.
1912.								
Aug. 21	V-22	Ameiurus melas	6	88	Aug. 27-29	6 to 8 days	Complete	75.1
23	V-26	do	2	230		More than 8 days.	do	75.5
1913.								
June 12	VI-1	Ameiurus melas, nebulosus	7	500	June 27-29	15 to 17 days.	do	72.1
24	VI-4	L. olivaris (wt. ½ lb.)	1	Many		11 days	Advanced.	78.3
24	VI-4	L. olivaris (wt. 2½ lbs.)	1	do		9 days or less.	do	
July 7	VI-10	Ictalurus punctatus	8	do	July 16-18	9 to 11 days.	Complete	78.1
10	VI-12	do	10	do.[a]	July 20-21	10 to 11 days.	do	76.7
10	VI-12	Lepomis pallidus	2	Several.	July 11	1 day	None	
10	VI-12	Pomoxis sparoides	2	Very few	do	do	do	
10	VI-12	Pomoxis annularis	3	do	do	do	do	
10	VI-12	Ictalurus punctatus	1	Many	Aug. 8	10-12 days.	Complete	76.3
29	VI-19	Aplodinotus grunniens.	1	Few	July 29-30	1 day	None	
29	VI-19	Leptops olivaris	1	Several.	Aug. 6-8	8 to 10 days.	Complete	
29	VI-19	Pomoxis sparoides	2	None				
29	VI-19	Micropterus salmoides.	1	Many	July 31	1 day	None	
Aug. 4	VI-20	Ictalurus punctatus	29	do	Aug. 15-16	11 to 12 days.	Complete	75.5
4	VI-20	Leptops olivaris	3	do	Before Aug. 9	Less than 5 days.	?	76

[a] On gills and barbels. All other glochidia were attached to gills only.

TABLE 2.—NATURAL HOST OF FRESH-WATER MUSSEL QUADRULA HEROS.

Name of host.	Date.	Locality.	Number of glochidia.		Development.
			Gill.	Fin.	
Noturus maculosus	Oct. 20	Moline, Ill.	Few.		Not encysted.
Do	do	do	Few.		Do.
Do	Oct. 22	do	Few.		Do.
Dorosoma cepedianum	do	do		25	Do.
Pomoxis annularis	do	do		22	Do.
Dorosoma cepedianum	Oct. 24	do		48	Completely encysted.
Do	do	do		17	Do.
Do	do	do		2	Do.
Pomoxis annularis	do	do		1	Undetermined.
Do	do	do		1	Do.
Roccus chrysops	Oct. 25	Fairport, Iowa	3		Encysted.
Amia calva	Oct. 28	Moline, Ill.	?		Do.
Noturus maculosus	do	do	Many.		Not encysted.
Leptops olivaris	Nov. 7	Hampton, Ill.	2		Deeply encysted.

TABLE 3.—ARTIFICIAL INFECTION OF QUADRULA HEROS SAY.

Date.	Experiments.	Fish.	No. of fish.	Glochidia retained until—	Period on fish.	Encysted.	Position.
Sept. 25	30-34	P. annularis	7	Sept. 26	1 day	No	Gill.
25	30-34	P. sparoides	9	Oct. 1	6 days	Yes	Do.
25	30-34	R. chrysops	4	Oct. 6	5 days	Yes	Do.
Oct. 1	30-34	M. salmoides	4	Oct. 8	11 days	Yes	Do.
Sept. 27	30-34	I. punctatus	7	Feb. 7	4 months 11 days[a]	Yes	Fin.
27	30-32	A. melas	2	Feb. 11	4 months 15 days[a]	Yes	Gill and fin.
27	30-35	L. pallidus	8	Dec. 6 / Feb. 5	2 months 9 days to 4 months 9 days.	Yes	Gill.
25	30-34	S. canadense	5	Oct. 5	10 days	Yes	Do.
25	30-35	A. grunniens	6	Apr. 18	6 months 11 days[a]	Yes	Fin.
Oct. 1	34	C. difformis	1	(Died.)		Yes	Do.

[a] Glochidia remained upon the fish after the date observed.

TABLE 4.—COLLECTION OF JUVENILE QUADRULAS, SEASON OF 1912.

No. of station.	Name.	Date.	Dredge hauls.	Depth.	Bottom.	Q. pustulosa.	Q. pustulata	Q. granifera.	Q. lachrymosa.	Q. metanevra.	Q. ebenus.	Q. solidi.	Q. trigona.	Q. plicata.	Q. heros
1	Iowa Shute	June 20	9	3-6	Sand and gravel	3	...	...	...	...	...	...	3	1	...
2	Smiths Cove to Pine Creek.	June 22	15	4-8	Varied (see hauls)	2	...	...	...	1	...	...	...	...	...
3	Sand bar above Smiths Creek.	June 25	0	.....	Sand silt	0	8	...	...	...	...	...	3	1	...
4	do	June 26 / June 28	0	0-½	do	0	2	...	...	...	...	...	3	2	...
5	Pine Creek	July 10	4	2-8	1, mud; 2, 3, and 4, mud and gravel.	4	...	...	...	1	1	...	4	3	...
6	Pine Creek to Buffalo.	July 12	11	2+	1-6 gravel; 7-11, mud and gravel.	5	1	2	...	1	1	...	17	15	...
7	Montpelier	July 15	5	Varied.	Varied (see hauls)	1	...	1	...	...	...	...	2	...	...
8	Barrs Landing	July 17	2	2-5	Gravel and mud	11	...	...	1	2	...	...	16	6	...
9	Wagglers Landing	July 29	5	3-5	Gravel and sand	12	...	1	...	8	...	...	7	5	[a]1
10	Moline	Sept. 24	4	2-4	Sand and mud	0	...	...	...	...	1	...	1	5	1+[a]3
11	do	Sept. 26	5	2-4	Mud	1	1	...	...	...	1	...	3	10	...
12	Davis Point	Dec. 14 / Dec. 23 / Dec. 24	0	½-4	Pebbles	0	...	...	...	...	...	...	...	...	...
						39	12	4	1	13	4	0	59	48	5

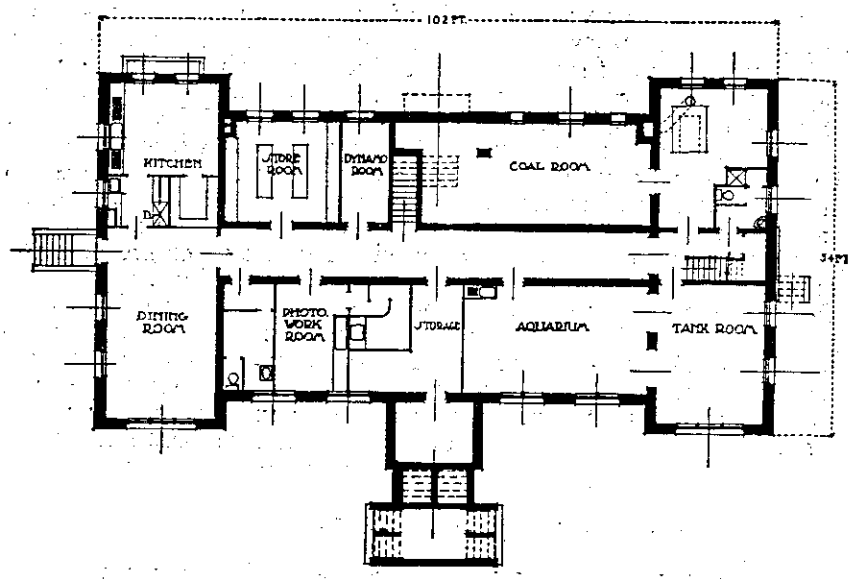

FIG. 1.—The biological laboratory, ground floor plan: D, ice box.

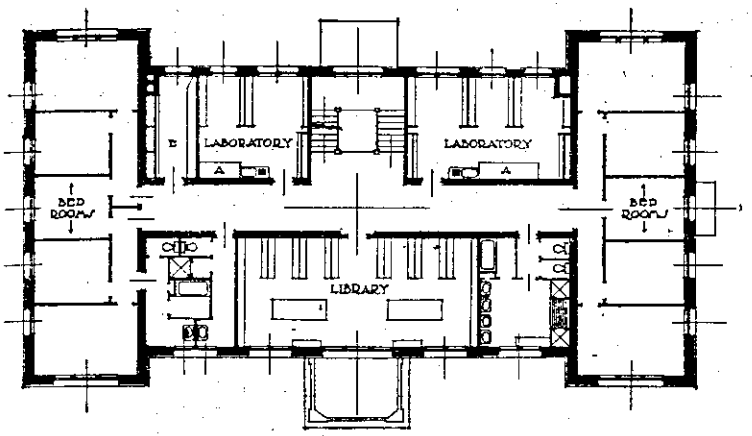

FIG. 3.—The biological laboratory, second floor plan: A, tank table; E, linen closet.

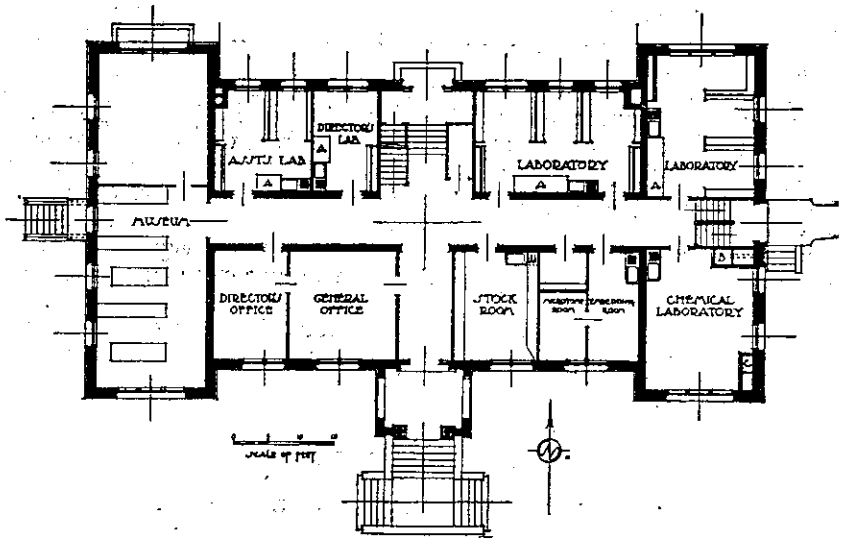

FIG. 2.—The biological laboratory, first floor plan: A, tank table; B, chemical hood; C, balance slab

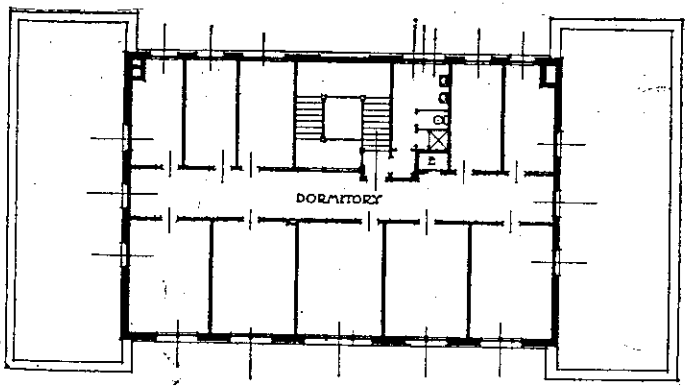

FIG. 4.—The biological laboratory: E, linen closet.

9) Floor Plan for the 1920 Fairport Laboratory. Pp. 6-7 in Coker, R.E. "The Fisheries Biological Station at Fairport, Iowa." Appendix I to the *Report of the U.S. Commissioner of Fisheries for 1920*, 1-12.

10) Coker, R.E., A.F. Shira, H.W. Clark, and A.D. Howard. Table 6, 8, 9, 15, 16; Table 18, Commercial Mussels and Their Hosts; Table 19, Number of Species of Fish Known to Serve as Hosts for Certain Species of Mussels, & Table 20, Number of Species of Commercial Mussels Known to be Carried as Parasites by Certain Fishes, pp. 116, 152-54 in "Natural history and propagation of fresh-water mussels." *Bulletin of the U.S. Bureau of Fisheries* 37 (1922): 75-181.

TABLE 6.—HABITATS OF CERTAIN FRESH-WATER MUSSELS, CLASSIFIED ACCORDING TO CHARACTER OF BOTTOM.

Scientific name.	Common name.	Sand.	Sand and gravel.	Gravel.	Stones and rocks.	Mud and sand.	Mud and gravel.	Soft mud over firm bottom.	Mud.	Deep, soft mud.	Clay and sand.	Clay.
1. Alasmidonta calceola	Slipper-shell		D		G	D		C	A		C	
2. Alasmidonta marginata	Elk-toe	G	DG	BCG				C	A			
3. Anodonta corpulenta	Slop-bucket					F		C	FD	C		
4. Anodonta grandis	Floater					C		C	ABDE	C		
5. Anodonta imbecillis	Paper-shell	E				CF		C	AEF	D	C	
6. Anodonta suborbiculata	do								BE	CD		
7. Anodontoides ferussacianus		G	GD			DGC	G		A		C	
8. Arcidens confragosus	Rock pocketbook			D		C			BD	C		
9. Cyprogenia irrorata	Fan-shell			C								
10. Dromus dromas	Dromedary mussel		C	C								
11. Hemilastena ambigua				BC	ABD				B			C
12. Lampsilis alata	Pink heel-splitter	F				DF		C	ABEF	C	C	G
13. Lampsilis anodontoides	Yellow sand-shell	EGD				DC		C	ABED			
14. Lampsilis capax	Pocketbook	C				D			D			
15. Lampsilis ellipsiformis		G		DG	GD				AE		C	
16. Lampsilis faliaciosa	Slough sand-shell	CF		DF		F		C	DF		C	C
17. Lampsilis glans				C				C				
18. Lampsilis gracilis	Paper-shell	EFG	F	D	D	F			ABDEF	C		G
19. Lampsilis higginsii	Higgin's eye	F	D	F							C	
20. Lampsilis iris	Rainbow-shell	AG	C	C	CG	DG		C	A			
21. Lampsilis lævissima	Paper-shell	EF				F		C	EF	CD		
22. Lampsilis ligamentina	Mucket	DGF	CFGD	CFG	DG		G	C	ABD		C	C
23. Lampsilis ligamentina gibba.	Southern mucket		C									
24. Lampsilis luteola	Fat mucket	CDFG	CF	DF				C	AEFD		C	
25. Lampsilis multiradiata		AC	C						A		C	
26. Lampsilis parva		D		D		D		C	ADEF			
27. Lampsilis purpurata	Purply	F	F			F				E		
28. Lampsilis recta	Black sand-shell	GF	D	EFG		F			AE		C	C
29. Lampsilis subrostrata		C							BED	C		C
30. Lampsilis ventricosa	Pocketbook	CFG	CGF	D	G	DF	G	C	DAE	D	C	
31. Margaritana monodonta	Spectacle-case	D	CD	BC	BD			C	BD			
32. Obliquaria reflexa	Three-horned warty-back.	BDFG	FD	BCDFE	BD	D		C	ABD		C	C
33. Obovaria ellipsis	Hickory-nut	CDFE	CFD	CDF		D	D	C	D		C	
34. Plagiola donaciformis		CFDF	CDF	CDF		D	DF		ADE			
35. Plagiola elegans	Deer-toe	CEGF	CDF	CF	D				ADEF			
36. Plagiola securis	Butterfly	BDEF	F	BDECF		D		C	B		C	
37. Pleurobema æsopus	Bullhead		D					C	D		C	
38. Ptychobranchus phaseolus.	Kidney-shell										C	
39. Quadrula coccinea	Flat niggerhead		CDG	EG	GD	G				A	C	
40. Quadrula cylindracea	Rabbit's foot		C	C								
41. Quadrula ebenus	Niggerhead		DF	FGD	D	D		C				
42. Quadrula granifera	Purple warty-back		F	F				C				
43. Quadrula heros	Washboard		DF			F		C	BDF			C
44. Quadrula lachrymosa	Maple-leaf	AEG	D	E	C	DF		C	ABFE		C	C
45. Quadrula metanevra	Monkey-face		DF	BDCEF	D	D	D	C	BD			
46. Quadrula obliqua	Ohio River pig-toe		C								C	
47. Quadrula plicata	Blue-point	F	DF	F		DF		C	AB	CE		
48. Quadrula pustulata	Pimple-back	CD		C		D		C	BF			
49. Quadrula pustulosa	do	FG	DF	CEF	D	F		C	ABFDE		C	
50. Quadrula rubiginosa		BGG	DG	B	BDG	DE	G	C	ABD		C	
51. Quadrula trapezoides	Bank-climber								FD			
52. Quadrula tuberculata	Purple warty-back	G		BC				C	ABF			
53. Quadrulata undata	Pig-toe	DF	DF	BDF	D	D		C	ABDF		C	
54. Quadrula undulata	Three-ridge	G	CG	G	G	D			AD	CG		G
55. Strophitus edentulus	Squaw-foot	CDG	GDF	CDFG	G	DFG	G	C	ADEF		C	
56. Symphynota complanata	White heel-splitter	F	F	F		F		C	ABDEF	C		
57. Symphynota compressa			G							D	C	
58. Symphynota costata	Fluted shell	GF	CDGF	BCF	D	G			ADF		C	
59. Tritogonia tuberculata	Buckhorn	F	EF	DEF		F		C	BFDE		C	
60. Truncilla sulcata	Cat's paw		C								C	
61. Unio crassidens	Elephant's ear					F		C	BF		C	C
62. Unio gibbosus	Lady-finger	DFG	GF	DFGE	G	F	G		ADEF			

It appears from this and the following table that the preferred bottom for the majority of species is mud (but not deep, soft mud, to which type of bottom few species are adapted) and gravel, including sand and gravel. Sand ranks next and clay last; but few species of mussels exhibit a preference for sand or sandy clay, and only two are

TABLE 8.—CLASSIFICATION OF COMMON FRESH-WATER MUSSELS IN RELATION TO CURRENT.

Scientific name.	Common name.	Little or no current.	Fair or good current.	Strong or swift current.
1. Alasmidonta calceola	Slipper-shell		CG	
2. Alasmidonta marginata	Elk-toe		C	DG
3. Anodonta corpulenta	Slop-bucket	CDF	CF	
4. Anodonta grandis	Floater	CDF	CG	
5. Anodonta imbecillis	Paper-shell	CDF	CF	
6. Anodonta suborbiculata	do	CD		
7. Anodontoides ferussacianus		CG	CG	G
8. Arcidens confragosus	Rock pocketbook	CDF		
9. Cyprogenia irrorata	Fan-shell			C
10. Dromus dromas	Dromedary mussel			C
11. Hemilastena ambigua		D	CD	
12. Lampsilis alata	Pink heel-splitter	CDFG	CF	
13. Lampsilis anodontoides	Yellow sand-shell	D	CDF	
14. Lampsilis capax	Fat pocketbook	CD	C	
15. Lampsilis ellipsiformis		CG	CG	D
16. Lampsilis fallaciosa	Slough sand-shell	DF	CF	
17. Lampsilis glans		C	C	
18. Lampsilis gracilis	Paper-shell	CDFG	CDF	
19. Lampsilis higginsii	Higgin's eye		CDF	
20. Lampsilis iris	Rainbow-shell	CGD	CG	
21. Lampsilis lævissima	Paper-shell	CDF	F	
22. Lampsilis ligamentina	Mucket		CF	DG
23. Lampsilis ligamentina gibba	Southern mucket		C	C
24. Lampsilis luteola	Fat mucket	CDFG	CFG	
25. Lampsilis multiradiata			C	C
26. Lampsilis parva		CDF		
27. Lampsilis purpurata	Purply	CF	CF	
28. Lampsilis recta	Black sand-shell	F	CDFG	G
29. Lampsilis subrostrata		CD	C	
30. Lampsilis ventricosa	Pocketbook	CFGD	CDFG	G
31. Margaritana monodonta	Spectacle-case		CD	
32. Obliquaria reflexa	Three-horned warty-back	DF	CFGD	D
33. Obovaria ellipsis	Hickory-nut		CDFG	
34. Plagiola donaciformis		DF	CDF	
35. Plagiola elegans	Deer-toe	F	CFG	D
36. Plagiola securis	Butterfly	D	CDF	
37. Pleurobema æsopus	Bullhead		CDF	
38. Ptychobranchus phaseolus	Kidney-shell		C	
39. Quadrula coccinea	Flat niggerhead		CDG	DG
40. Quadrula cylindrica	Rabbit's-foot		CF	
41. Quadrula ebenus	Niggerhead		CFD	D
42. Quadrula granifera	Purple warty-back		CD	D
43. Quadrula heros	Washboard	DF	CDF	
44. Quadrula lachrymosa	Maple-leaf	DF	CFG	
45. Quadrula metanevra	Monkey-face	F	CDF	D
46. Quadrula obliqua	Ohio River pig-toe		C	
47. Quadrula plicata	Blue-point	CDF	CDF	
48. Quadrula pustulata	Pimple-back	CD	CDF	C
49. Quadrula pustulosa	do		CFGD	D
50. Quadrula rubiginosa		CG	CDG	DG
51. Quadrula trapezoides	Bank-climber	CF	CF	
52. Quadrula tuberculata	Purple warty-back		CG	CG
53. Quadrula undata	Pig-toe	DF	CFD	
54. Quadrula undulata	Three-ridge	CGD	CFGD	C
55. Strophitus edentulus	Squaw-foot	CGDF	CDG	
56. Symphynota complanata	White heel-splitter	CFG	CDF	
57. Symphynota compressa			G	G
58. Symphynota costata	Fluted shell		CF	D
59. Tritogonia tuberculata	Buckhorn	DFG	CFD	DG
60. Truncilla sulcata	Cat's paw		C	
61. Unio crassidens	Elephant's ear		CDF	
62. Unio gibbosus	Lady-finger	CDGF	CDG	DG

EXPLANATION OF TABLE 8.

The symbols are those used in Table 6, C representing Clark; D, Howard; F, Shira; and G, Coker. The large capital denotes preference in the opinion of the observer, for a particular condition of current. The small capital denotes that the condition is favorable but not, so far as is known, preferred to other conditions. When no large capital occurs on a line, no preference is indicated; and when a particular letter appears in small capital throughout a line, the observer denoted by the letter has no evidence upon which to base an opinion of discrimination on the part of the particular mussel between the different conditions of current regarded as favorable.

TABLE 9.—CONTENTS OF WATERS OF CERTAIN PRODUCTIVE MUSSEL STREAMS AND OTHER NONPRODUCTIVE STREAMS.[a]

	Turbidity.	Suspended matter.	Coefficient of fineness.	Total iron (Fe).	Silica (SiO_2).	Iron (Fe).	Calcium (Ca).	Magnesium (Mg).
PRODUCTIVE RIVERS.								
Wabash, Vincennes, Ind	172	193	1.20	.....	13.0	0.24	61.0	22.0
Illinois, La Salle, Ill	159	136	.80	.....	12.0	.21	50.0	22.0
Illinois, Kampsville, Ill	188	145	.80	.....	12.0	.27	47.0	20.0
Fox, Ottawa, Ill	94	87	1.20	.....	11.0	.20	60.0	32.0
Sangamon, Springfield, Ill	74	39	.80	.....	16.0	.32	52.0	24.0
Cumberland, Nashville, Tenn	126	94	.74	.....	20.0	.42	26.0	3.6
Cumberland, Kuttawa, Ky	176	165	.92	.....	18.0	.30	28.0	4.3
Des Moines, Keosauqua, Iowa	542	642	1.09	.....	22.0	.36	58.0	21.0
Grand, Grand Rapids, Mich	37	43	1.61	1.1	14.0	.07	56.0	19.0
Cedar, Cedar Rapids, Iowa	64	61	.97	.....	14.0	.09	48.0	16.0
Maumee, Toledo, Ohio	143	112	.95	3.4	17.0	.27	57.0	16.0
Mississippi, Moline, Ill	117	106	.9	.....	16.0	.39	33.0	13.0
Mississippi, Quincy, Ill	173	119	.8	.....	18.0	.46	36.0	16.0
NONPRODUCTIVE RIVERS.								
James, Richmond, Va	90	71	.96	3.9	18.0	.5	14.0	3.0
Potomac, Cumberland, Md	28	29	1.59	3.0	8.2	.14	24.0	4.6
Wateree, Camden, S. C	259	214	.79	.....	25.0	.28	6.3	1.8
Shenandoah, Millville, W. Va	31	39	1.64	.9	15.0	.08	32.0	8.2
Mississippi, Chester, Ill	858	634	.....	.8	22.0	.39	44.0	16.0
Mississippi, Memphis, Tenn	556	519	.97	.....	24.0	.61	36.0	12.0
Red, Shreveport, La	790	870	1.11	.....	30.0	1.1	74.0	17.0
Missouri, Ruegg, Mo	1,931	1,890	1.02	.....	29.0	.51	52.0	16.0
Savannah, Augusta, Ga	172	142	.77	.....	23.0	.44	5.7	.8
Hudson, Hudson, N. Y	13	16	1.26	.7	11.0	.15	21.0	3.8
Cape Fear, Wilmington, N. C	73	21	.92	1.3	9.9	.78	5.0	1.5

	Sodium and potassium (Na+K).	Carbonate radicle (CO_3).	Bicarbonate radicle (HCO_3).	Sulphate radicle (SO_4).	Nitrate radicle (NO_3).	Chlorine (Cl).	Total dissolved solids.
PRODUCTIVE RIVERS.							
Wabash, Vincennes, Ind	25.0	0.0	230	55.0	6.4	36.0	336
Illinois, La Salle, Ill	16.0	.....	203	50.0	6.6	13.0	278
Illinois, Kampsville, Ill	18.0	.....	202	42.0	4.3	15.0	267
Fox, Ottawa, Ill	14.0	.....	275	61.0	4.9	7.9	335
Sangamon, Springfield, Ill	16.0	.....	247	37.0	3.4	7.5	276
Cumberland, Nashville, Tenn	9.6	.0	92	14.0	1.2	2.1	119
Cumberland, Kuttawa, Ky	7.8	.9	100	9.7	1.8	3.0	124
Des Moines, Keosauqua, Iowa	17.0	.0	216	71.0	3.3	4.8	312
Grand, Grand Rapids, Mich	10.0	8.5	214	33.0	2.3	7.7	258
Cedar, Cedar Rapids, Iowa	12.0	.0	209	30.0	3.1	3.4	228
Maumee, Toledo, Ohio	24.0	2.5	173	48.0	4.5	40.0	298
Mississippi, Moline, Ill	10.0	.....	152	24.0	1.8	3.7	179
Mississippi, Quincy, Ill	11.0	.....	175	25.0	2.2	4.4	203
NONPRODUCTIVE RIVERS.							
James, Richmond, Va	6.7	.0	60	7.1	.3	2.3	89
Potomac, Cumberland, Md	9.0	.0	36	58.0	.9	6.4	130
Wateree, Camden, S. C	8.4	0	34	4.2	.4	2.8	73
Shenandoah, Millville, W. Va	6.7	3	132	6.2	2.6	3.0	140
Mississippi, Chester, Ill	21.0	.....	174	56.0	2.7	9.8	269
Mississippi, Memphis, Tenn	19.0	.0	129	43.0	1.7	8.6	202
Red, Shreveport, La	90.0	4.6	135	140.0	.4	121.0	561
Missouri, Ruegg, Mo	36.0	.0	178	104.0	2.9	12.0	346
Savannah, Augusta, Ga	12.0	.0	30	6.0	.6	2.1	60
Hudson, Hudson, N. Y	7.9	.0	73	16.0	.8	4.0	108
Cape Fear, Wilmington, N. C	7.2	0	25	3.2	.2	5.8	57

[a] After U. S. Geological Survey.

TABLE 15.—THE MORE IMPORTANT COMMERCIAL MUSSELS, WITH INDICATION OF MONTHS DURING WHICH FEMALES HAVE BEEN FOUND WITH MATURE GLOCHIDIA.

Scientific name.	Common name.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Cyprogenia irrorata	Fan-shell	....	....	....	....	....	....	....	....	....	(?)	×	....
Dromus dromas	Dromedary mussel	....	....	....	....	....	....	....	....	....	×	×	....
Lampsilis anodontoides	Yellow sand-shell	×	×	×	×	×	×	×	×	×	×	×	×
Lampsilis fallaciosa	Slough sand-shell	....	....	....	×	×	×	×	×	×	×	×	×
Lampsilis higginsii	Higgin's eye	....	....	....	....	×	....	....	....	×	....	....	....
Lampsilis ligamentina	Mucket	....	×	×	×	×	×	×	×	×	×	×	×
Lampsilis luteola	Fat mucket	×	×	×	×	×	×	×	×	×	×	×	×
Lampsilis recta	Black sand-shell	....	....	×	×	×	×	×	×	×	×	×	×
Lampsilis ventricosa	Pocketbook	×	×	×	×	×	×	×	×	×	×	×	×
Obliquaria reflexa	Three-horned warty-back	....	....	....	×	×	×	×	×	....	....	....	....
Obovaria ellipsis	Hickory-nut	....	×	....	×	×	×	....	×	×	×	×	×
Plagiola securis	Butterfly	....	×	....	....	×	×	×	×	×	×	×	....
Pleurobema æsopus	Bullhead	....	....	....	....	×	×	×	....	....	....	....	....
Ptychobranchus phaseolus	Kidney-shell	....	....	....	....	....	....	....	×	×	×	×	....
Quadrula cylindrica	Rabbit's foot	....	....	....	....	....	×	×	....	....	....	....	....
Quadrula ebenus	Niggerhead	....	....	....	×	×	×	×	×	×	....	....	....
Quadrula heros	Washboard	×	×	×	....	....	....	....	....	×	×	×	×
Quadrula lachrymosa	Maple-leaf	....	....	....	×	×	×	×	×	....	....	....	....
Quadrula metanevra	Monkey-face	....	....	....	×	×	×	×	....	....	....	....	....
Quadrula obliqua	Ohio River pig-toe	....	....	....	×	×	×	×	×	....	....	....	....
Quadrula perplicata	Round Lake	....	....	....	....	×	×	×	....	....	....	....	....
Quadrula plicata	Blue-point	....	....	....	....	×	×	×	×	....	....	....	....
Quadrula pustulata	Pimple-back	....	....	....	....	....	×	×	....	....	....	....	....
Quadrula pustulosa	....do	....	....	....	....	....	×	×	×	....	....	....	....
Quadrula rubiginosa		....	....	....	....	×	×	×	×	....	....	....	....
Quadrula solida		....	....	....	....	×	×	....	....	....	....	....	....
Quadrula undata	Pig-toe	....	....	....	....	....	×	×	×	×	....	....	....
Quadrula undulata	Three-ridge	....	....	....	....	×	×	×	....	....	....	....	....
Symphynota complanata	White heel-splitter	×	....	×	×	×	×	....	....	×	×	×	×
Tritogonia tuberculata	Buckhorn	....	....	....	×	×	×	....	....	....	....	....	....
Unio crassidens	Elephant's ear	....	....	....	×	×	×	....	....	....	....	....	....
Unio gibbosus	Lady-finger	....	....	....	....	×	×	×	×	....	....	....	....

75412°—22——10

TABLE 16.—SOME NONCOMMERCIAL MUSSELS, WITH INDICATION OF MONTHS DURING WHICH FEMALES HAVE BEEN FOUND WITH GLOCHIDIA.

Scientific name.	Common name.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Alasmidonta marginata	Elk-toe	....	....	....	....	....	....	....	....	×	....	....	....
Anodonta cataracta		....	....	....	....	....	....	....	....	....	....	×	....
Anodonta corpulenta	Slop-bucket	×	....	....	×	....	....	....	....	....	×	×	....
Anodonta grandis	Floater	×	×	×	....	....	....	....	....	(?)	....	....	×
Anodonta imbecillis	Paper-shell	×	×	×	....	×	×	×	×	×	×	×	×
Anodonta implicata		....	....	....	....	....	....	....	....	×	×	....	....
Anodonta stewartiana		....	....	....	....	....	....	....	....	....	....	×	....
Anodonta suborbiculata	Paper-shell	×	×	....	....	....	....	....	....	....	....	....	×
Arcidens confragosus	Rock pocketbook	×	....	....	....	....	....	....	....	×	....	×	....
Gonidea angulata		....	....	....	....	....	×	....	....	....	....	....	....
Hemilastena ambigua		....	....	....	....	....	....	....	....	×	×	....	....
Lampsilis alata	Pink heel-splitter	×	×	×	....	×	×	×	×	×	×	×	....
Lampsilis borealis		....	....	....	....	....	....	....	....	×	....	....	....
Lampsilis capax	Pocketbook	....	....	....	....	....	×	×	×	×	....	....	....
Lampsilis gracilis	Paper-shell	×	×	....	×	×	×	×	×	....	×	×	×
Lampsilis iris	Rainbow-shell	....	....	....	....	....	×	....	....	....	....	....	....
Lampsilis ellipsiformis		....	....	....	....	×	×	....	....	....	....	....	....
Lampsilis lævissima	Paper-shell	×	....	×	×	....	×	×	×	×	....	×	....
Lampsilis lienosa		....	....	....	....	×	....	....	....	×	....	....	....
Lampsilis parva		....	....	....	....	....	×	....	....	....	....	....	....
Lampsilis subrostrata		....	....	....	....	....	×	....	....	×	....	....	....
Lampsilis texasensis		....	....	....	....	×	....	....	....	....	....	....	....
Lampsilis ventricosa satura		....	....	....	....	×	×	....	....	....	....	....	....
Plagiola donaciformis		....	....	....	....	×	....	×	....	....	....	....	....
Plagiola elegans	Deer-toe	....	....	....	....	×	....	×	....	....	....	....	....
Ptychobranchus phaseolus	Kidney-shell	....	....	....	....	....	....	....	×	....	....	....	....
Quadrula cooperiana		....	....	....	....	....	×	×	×	....	....	....	....
Quadrula granifera	Purple warty-back	....	....	....	....	....	....	×	....	....	....	....	....
Strophitus edentulus	Squaw-foot	....	....	×	×	×	×	....	×	×	×	×	....
Symphynota costata	Fluted shell	....	....	....	....	....	....	....	....	×	×	....	....
Symphynota compressa		....	....	....	....	....	....	....	....	×	....	....	....
Truncilla arcæformis	Sugar-spoon	....	....	....	....	....	....	....	....	....	×	....	....
Truncilla capsæformis	Oyster mussel	....	....	....	....	....	....	....	....	....	×	....	....
Unio tetralasmus		....	....	....	....	×	....	....	....	....	....	....	....

The experimental method is simpler in some respects. It consists in submitting various species of fish to infection with the glochidia of a given species of mussel and observing whether or not the glochidia attach. Since glochidia will sometimes attach to fish which are not their natural hosts, it is necessary to hold the fish under observation until the mussels have completed the metamorphosis and dropped off. It is, however, impracticable to have on hand all the species of fish at the particular time when the glochidia of a given species of mussel may be available. Furthermore, the failure of an artificial infection to go through successfully on fish held in confinement may be due, not to the want of a natural affinity between mussel and fish, but to the fact that the fish does not retain its full vitality in close confinement, or to some other defect in the experimental conditions. Neither of the two methods for the study of infections may, then, be relied upon exclusively for the determination of the natural hosts of fresh-water mussels. On the contrary, it has been found necessary to carry on the two lines of study hand in hand, according to the plan which was adopted at the beginning of the scientific work of the station. In this way, though our knowledge of the hosts of mussels is as yet incomplete, there has been obtained a considerable body of information most of which is summarized in the following table (18),[a] listing 17 species of mussel and 30 hosts (29 fishes and 1 amphibian), and indicating those which serve as hosts for each species of mussel.

EXPLANATION OF TABLE 18.

N. Found on the gills in natural infection.
Nf. Found on the fins in natural infection.
n. Record of natural infection but of doubtful significance.
A. Carried through on gills after artificial infection.
Af. Carried through on fins after artificial infection.
a. Results of artificial infection unsatisfactory or not uniform.
o. Tested and found unsuitable.
T. Tested; development occurred; host perhaps suitable, but experiment not carried to conclusion.

TABLE 18.—COMMERCIAL MUSSELS AND THEIR HOSTS.

Mussels.		A. melas, bullhead.	A. nebulosus, bullhead.	A. calvus, bowfin.	A. chrysypa, eel.	A. gruniens, sheepshead.	D. cepedianum, gizzard shad.	E. lucius, pike.	E. gibbosus, red-ear sunfish.	H. tergisus, mooneye.	I. punctatus, spotted cat.	L. osseus, long-nosed gar.	L. platostomus, short-nosed gar.	L. tristœchus, alligator gar.	L. cyanellus, blue-spotted sunfish.	L. euryorus, sunfish.
Scientific name.	Common name.															
Lampsilis anodontoides	Yellow sand-shell	o	o	a		o					o	AN	A	A	no	
Lampsilis fallaciosa	Slough sand-shell										o		NA			o
Lampsilis higginsii	Higgin's eye					n										
Lampsilis ligamentina	Mucket	o	o	o	n	o		a			o		a		N	
Lampsilis luteola	Fat mucket	o	o			o				o	o		o			
Lampsilis recta	Black sand-shell				n						o				a	
Lampsilis ventricosa	Pocketbook															
Obovaria ellipsis	Missouri niggerhead					o					o					
Plagiola securis	Butterfly					NA									n	
Quadrula ebenus	Niggerhead	o	o	o		o	a			o	o				o	
Quadrula heros	Washboard	A	A		N	ANf	Nf				Af				A	
Quadrula metanevra	Monkey-face														N	
Quadrula plicata	Blue-point	a	a					N	N		o		A			A
Quadrula pustulata	Warty-back										N					
Quadrula pustulosa	do	NA	A								AN		o			
Quadrula solida																
Quadrula undata	Pig-toe															

[a] A great many data regarding the hosts of noncommercial species of mussels had been accumulated, but unfortunately most of the records applying to such species were destroyed with the burning of the laboratory in December, 1917.

TABLE 18.—COMMERCIAL MUSSELS AND THEIR HOSTS—Continued.

Mussels.		L. humilis, orange-spotted sunfish.	L. pallidus, bluegill.	L. olivaris, yellow cat.	M. dolomieu, small-mouth black bass.	M. salmoides, large-mouth black bass.	N. maculosus, mud puppy.	P. chrysocloris, river herring.	P. flavescens, yellow perch.	P. annularis, white crappie.	P. sparoides, black crappie.	R. chrysops, striped bass.	S. platorhynchus, sand sturgeon.	S. gyrinus, mad Tom.	S. canadense, sauger.	S. vitreum, walleye.
Scientific name.	Common name.															
Lampsilis anodontoides	Yellow sand-shell	n	o	.....	.....	na	.....	.....	o	no	no	a	o	.....	o	.....
Lampsilis fallaciosa	Slough sand-shell	.....	.....	o	.....	o	.....	.....	.....	n	o	.....	n	.....	.....	.....
Lampsilis higginsii	Higgin's eye	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	N	.....
Lampsilis ligamentina	Mucket	.....	aN	.....	N	AN	.....	.....	AN	NA	A	AN	o	n	A	.....
Lampsilis luteola	Fat mucket	.....	NA	o	A	A	.....	.....	AN	A	A	A	o	n	A	NA
Lampsilis recta	Black sand-shell	.....	aN	.....	.....	.....	.....	.....	.....	N	.....	.....	.....	.....	.....	.....
Lampsilis ventricosa	Pocketbook	.....	A-	.....	A	A	.....	.....	A	AN	.....	.....	.....	.....	N	.....
Obovaria ellipsis	Missouri niggerhead	.....	o	.....	.....	o	.....	.....	o	o	o	.....	NA	.....	.....	.....
Plagiola securis	Butterfly	.....	o	.....	.....	o	.....	.....	.....	o	o	.....	.....	.....	.....	.....
Quadrula ebenus	Niggerhead	.....	o	o	.....	o	.....	TN	o	o	o	.....	o	.....	.....	.....
Quadrula heros	Washboard	.....	NA	AN	.....	o	n	n	.....	NA	A	N	.....	Nf	.....	.....
Quadrula metanevra	Monkey-face	.....	on	.....	.....	o	.....	.....	.....	.....	.....	.....	.....	.....	N	.....
Quadrula plicata	Blue-point	.....	a	o	...	AN	.....	.....	A	Nf AN	A	n	.....	.....	N	.....
Quadrula pustulata	Warty-back	.....	.....	n	.....	.....	.....	.....	.....	n	.....	.....	.....	.....	.....	.....
Quadrula pustulosa	.....do	.....	o	an	.....	o	.....	.....	.....	on	o	.....	n	.....	.....	.....
Quadrula solida		.....	N	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Quadrula undata	Pig-toe	.....	.....	.....	.....	.....	.....	.....	.....	n	n	.....	.....	.....	.....	.....

It will be observed that the number of hosts corresponding to a particular species of mussel (as so far determined) varies from one to thirteen. It is of interest to give the number of known hosts for each species of fresh-water mussel, as determined both by observation of natural infections and by the experimental method, and this is done in Table 19.

TABLE 19.—NUMBER OF SPECIES OF FISH KNOWN TO SERVE AS HOSTS FOR CERTAIN SPECIES OF MUSSELS.

Mussels.		Natural infection.	Artificial infection.	Common.	Total.
Scientific name.	Common name.				
Lampsilis anodontoides	Yellow sand-shell	1	3	1	3
Lampsilis fallaciosa	Slough sand-shell	1	1	1	1
Lampsilis higginsii	Higgin's eye	1	0	0	1
Lampsilis ligamentina	Mucket	7	6	4	9
Lampsilis luteola	Fat mucket	3	9	3	9
Lampsilis recta	Black sand-shell	2	0	0	2
Lampsilis ventricosa	Pocketbook	2	5	1	6
Obovaria ellipsis	Missouri niggerhead	1	1	1	1
Plagiola securis	Butterfly	1	1	1	1
Quadrula ebenus	Niggerhead	1	1	1	1
Quadrula heros	Washboard	8	9	4	13
Quadrula metanevra	Monkey-face	2	0	0	2
Quadrula plicata	Blue-point	5	6	2	9
Quadrula pustulata	Warty-back	1	0	0	1
Quadrula pustulosa	.....do	2	3	2	3
Quadrula solida		1	0	0	1
Quadrula undata	Pig-toe	(?)	0	0	(?)

Table 20 lists the common species of fish showing the number of species of mussels which each fish has been observed to carry as parasites. The greatest number is six, for the bluegill, *Lepomis pallidus*, the white crappie, *Pomoxis annularis*, and the sauger, *Stizostedion canadense*.

TABLE 20.—NUMBER OF SPECIES OF COMMERCIAL MUSSELS KNOWN TO BE CARRIED AS PARASITES BY CERTAIN FISHES.

Fishes.		Natural infection.	Artificial infection.	Common.	Total.
Scientific name.	Common name.				
Ameiurus melas	Bullhead	1	2	1	2
Ameiurus nebulosus	do	0	2	0	2
Anguilla chrysypa	Eel	1	0	0	1
Aplodinotus grunniens	Sheepshead	2	2	2	2
Dorosoma cepedianum	Gizzard shad	1	0	0	1
Esox lucius	Pike	1	0	0	1
Eupomotis gibbosus	Red-ear sunfish	1	0	0	1
Ictalurus punctatus	Spotted cat	2	2	1	3
Lepisosteus osseus	Long-nosed gar	1	1	1	1
Lepisosteus platostomus	Short-nosed gar	1	3	1	3
Lepisosteus tristœchus	Alligator gar	0	1	0	1
Lepomis cyanellus	Blue-spotted sunfish	2	1	0	3
Lepomis euryorus	Sunfish	0	1	0	1
Lepomis humilis	Orange-spotted sunfish	(?)	0	0	(?)
Lepomis pallidus	Bluegill	5	3	2	6
Leptops olivaris	Yellow cat	1	1	1	1
Micropterus dolomieu	Smallmouth black bass	1	2	0	3
Micropterus salmoides	Largemouth black bass	2	4	2	4
Necturus maculosus [a]	Mud puppy	(?)	0	0	(?)
Pomolobus chrysochloris	River herring	1	1	1	1
Perca flavescens	Yellow perch	2	4	2	4
Pomoxis annularis	White crappie	5	5	4	6
Pomoxis sparoides	Black crappie	0	4	0	4
Roccus chrysops	Striped bass	2	2	1	3
Scaphirhynchus platorhynchus	Sand sturgeon	1	1	1	1
Schilbeodes gyrinus	Mad Tom	1	0	0	1
Stizostedion canadense	Sauger	4	2	0	6
Stizostedion vitreum	Wall-eye	1	1	1	1

[a] An amphibian.

It is necessary to point to some significant practical conclusions from the data presented. Since mussels are "choice" as to their hosts, the chances for the successful attachment of glochidia in nature are greatly diminished. The glochidia when discharged from a parent mussel are lost if no fish are at hand to receive them or if the fish that pass are not of one of the very limited number of species which are useful to the glochidia of that particular mussel.

There must necessarily be some definite ecologic relation between the mussel and the fish. The bottom that is inhabited by the hickory-nut mussel must be one that is frequented by the sand sturgeon during the breeding season of that mussel. Again, if one were looking for the river herring, it would be reasonable to expect to find them, during June at least, in places where niggerhead beds are known to exist. It is evident that no species of mussel could exist unless its host were of such habit as to be at the right places at the right times in a sufficient number of cases to permit first, of the infection occurring, and second, of the young dropping where they can survive.

What the factors are that bring mussels and fish into proper association we can not say. In the case of one species of mussel (the pocketbook) at least, it is known that the gravid mussel protrudes from its shell a portion of its mantle as a long brightly marked flap that waves in the water, assuming the appearance of an insect larva or other attractive bait (p. 85). Again we have the sheepshead fish (fresh-water drum) which is known to feed upon small mollusks, mussels, and the sphæriids and univalves that live on mussel beds, and which thus exposes itself to easy infection; sheepshead, indeed, are almost invariably found to be loaded with glochidia. The behavior of the pocketbook is believed to be exceptional, and the sheepshead is one of a very few species of fish

11) Coker, R.E., A.F. Shira, H.W. Clark, and A.D. Howard. "Artificial Propagation," pp. 160-66, in "Natural history and propagation of fresh-water mussels." *Bulletin of the U.S. Bureau of Fisheries* 37 (1922): 75-181.

ARTIFICIAL PROPAGATION.

PRINCIPLE OF OPERATION.

As the previous account of the life history of fresh-water mussels has shown, the mussel not only deposits great numbers of eggs but nurtures them in brood pouches within the protection of her shell. There is not, as in fish, a great wastage of eggs and larvæ in the very earliest stage of development. There exists, therefore, no necessity for artificial aid to effect fertilization; that is, to bring the male and female reproductive elements together. Nature's own provisions have adequately provided for the bringing of enormous numbers of each generation of offspring to the glochidium stage. It is after this stage is attained that the greatest mortality occurs; the great abundance of glochidia produced by each female is, indeed, evidence that enormous losses are to occur subsequently, and observation indicates that the critical stages are, first, when the glochidia are liberated from the parent to await a host, and, second, when the juvenile mussels are dropped from the fish that serves as host.

The artificial propagation of mussels as now practiced aims to carry the young mussels through the first great crisis. Its object is to insure to a large number of glochidia the opportunity to effect attachment to a suitable fish. Under present conditions the operations can be conducted extensively and economically only in the field. The procedure in brief is to take fish in the immediate vicinity of the places to be stocked, infect them with glochidia of the desired species of mussels, and liberate them immediately. Artificial propagation, then, as applied to fresh-water mussels, is a very different sort of operation from that employed in the propagation of fish, although it is no less directly adapted to the conditions and needs of the objects to be propagated.

METHODS.

In each field the operations are conducted under the immediate direction of a qualified person who may be either a permanent or temporary employee of the Bureau working under the Fairport station. The fishing crew is comprised of three or four local fishermen, or laborers, temporarily employed.

The equipment for seining and handling the fish consists of a motor boat, one or two flat-bottomed rowboats, seines or other nets, including small dip nets, tanks, buckets, etc. The motor boat is used to cover the various fishing grounds as rapidly as possible to distribute the infected fishes, and to move the outfit from place to place as it becomes advisable or necessary to extend the field of operations. The rowboat is employed in the actual work of seining and handling the fish. If the fish are taken in very large numbers it is convenient to have one or two tanks, similar to the ordinary 4-foot galvanized stock tanks and equipped with handles. Under ordinary conditions, tubs serve very well, especially if the fish have to be transported by hand for some distance, as is the case when the fish are taken in rescue work from land-locked ponds or lakes. At times, when the field of operations is at some distance from a place where living and sleeping accommodations can be secured, a camping outfit, or a house boat, is used for quartering the crew. The head of the party must be provided with a dissecting microscope, a magnifying hand lens, and simple dissecting instruments.

Before an infection can be made, it is first necessary to obtain a supply of glochidia of the desired species of mussels. In localities where commercial shelling is actively practiced this can be done by visiting the shellers' boats and examining the catch for freshly-taken gravid mussels. If it is desired to use the glochidia at once, the brood pouches are immediately cut from the females and placed in water; but if it is desired to use them over a period of several days, the gravid shells are purchased and the glochidia removed as needed. In locations where shells are scarce, or where little or no commercial shelling is done, it is sometimes necessary to hire a sheller to procure the mussels.

The fish are next sought by means of seines or nets, and when secured are sorted and transferred to the tanks or tubs; the fish that are not required for purposes of mussel propagation are immediately liberated in suitable waters. When the containers are comfortably filled with fish, overcrowding being avoided, the brood pouches of one or more mussels, as necessary, are cut out and opened with scissors or scalpel and the glochidia are teased out in a small pail or other container from which they are poured into the tanks with the fish. Figures 1 to 4, Plate XVIII, show the seining and infection operations in the field.

The experienced operator can usually tell at a glance whether or not the glochidia are sufficiently ripe for infection. If they freely separate when removed from the brood pouches and placed in a dish of water, it is usually a sign that a sufficient degree of ripeness has been obtained. If, however, they adhere in a conglutinate mass and can be separated only with difficulty, it is certain indication that they are unsuitable for infection; examination with a hand lens in such case will show also that the glochidia are still inclosed in the egg membrane, thus revealing their immaturity. If the glochidia are fully developed, one can readily determine if they are alive and active by dropping a few particles of salt or a couple of drops of fish blood into a small dish containing some of the glochidia. It is a sign of maturity and vitality if the valves begin to snap together as the salt or blood diffuses through the water.

After being removed from the brood pouches the life of the glochidia is usually rather short, but it is possible to keep them alive a day or two if the water in which they are retained is changed at frequent intervals and not permitted to become too warm.

The operator is guided by his experience as to the quantity of glochidia to be placed with a given lot of fish and as to the length of the infection period. The water may be

stirred from time to time in order to keep the glochidia in somewhat even suspension, but in most cases the movements of the fish themselves insure a circulation of the water and a general distribution of the glochidia. At intervals individual fish are taken by hand or small dip net, and the gills examined with a lens; when, in the opinion of the operator, a sufficient degree of infection has occurred, the fish are placed at once in open waters, or transferred to other containers for conveyance to a place suitable for their liberation. The rapidity with which infection takes place depends upon a variety of conditions, such as temperatures of water, kind and size of fish, and activity of glochidia. Ordinarily a period of from 5 to 25 minutes is sufficient to insure an optimum infection. The infection time is usually shorter in warm water than in cold. As basis for approximate computation of the number of glochidia planted, several average-sized specimens of each species of fish infected are killed and the gills removed for subsequent counts of the glochidia attached. The counting is done by the foreman with the aid of a microscope and usually in the evening after the close of the field operations of the day. The number of glochidia per fish of each species having been determined by the count of representative examples, and the numbers of fish of the species being known, the entire number of glochidia planted on a given lot of fish is easily computed. The data in detail are promptly recorded on form cards provided for the purpose. The count of total glochidia planted is of course only approximate, but the method of count and computation described is as accurate as the conditions of operation permit, and it is as precise as the methods of count generally practiced in fish-cultural operations. In the long run, the actual errors on one side and the other must approximately balance.

That degree of infection which employs the fish to best advantage in mussel propagation, without doing appreciable injury to the host, is termed the "optimum infection." It varies with the species of mussel and with the kind and the size of the fish. Table 23 gives illustrative instances.

TABLE 23.—OPTIMUM INFECTION FOR CERTAIN SPECIES OF MUSSEL ON SEVERAL SPECIES OF FISH.

Species of mussel.		Fish host.		Number of glochidia on fish.
Scientific name.	Common name.	Species.	Size in inches.	
Lampsilis luteola	Lake Pepin mucket	Black bass	8	2,000
Do	do	White bass	8	2,000
Do	do	Wall-eyed pike	8	2,500
Do	do	Bluegill	5	500
Do	do	Crappie	5	400
Do	do	Yellow perch	6	1,500
Lampsilis anodontoides	Yellow sand-shell	Gar	16	2,000
Lampsilis ligamentina	Mucket	Black bass	8	2,000
Lampsilis pustulosa	Pimple-back	Channel catfish	14	1,200

Incidental to the field work in mussel propagation, valuable results are frequently gained in the reclamation of fish from the overflowed lands bordering the various rivers. All fishes rescued in connection with propagation work, whether suitable or unsuitable for infection, are liberated in the open waters, and under such circumstances the value of the fish thus saved in large measure recompenses for the cost of the mussel propagation work.

The operations of mussel propagation as just described serve to carry the young mussels through the most critical stage of the life history—to give to thousands the

chance of life that would ordinarily fall only to dozens. As previously pointed out (p. 151), an extensive series of observations of fish reveals the fact that but few are naturally infected with mussels and these usually in slight degree. The chance that a large proportion of the glochidia discharged by any mussel will become attached to a proper host is slight, and it is only because nature is prodigal in the production of glochidia that the various species of mussels can maintain their numbers under natural conditions. With the disturbance of natural conditions by the active pursuit of a commercial shell fishery, nature's fair balance is destroyed, and some compensatory artificial aid to the propagation of mussels is rendered necessary.

It is not presumed that all the vicissitudes of mussel life are removed by the bringing together of fish and mussel. Nature undoubtedly exacts heavy tolls at other stages. Many of the young mussels on being liberated from the fish will fall in unfavorable environments and meet an early death, while those that survive the earliest stage of independent life may still be subjected to numerous enemies throughout the juvenile period at least. Nevertheless, glochidia of certain species can be planted in such large numbers and at such slight cost that, after making due allowance for an extraordinary subsequent loss, substantial returns can be expected. That such results do obtain is indicated both by experiments to be later described (p. 166) and by common experience

MUSSEL CULTURE.

The rearing of young mussels in tanks, in ponds, or (if under conditions of control) in the river, may properly be termed "mussel culture," as distinguished from "mussel propagation," which, as we have seen, consists in bringing about the attachment of glochidia to fish and liberating the fish in public waters. For several years experiments in mussel culture have been carried on by the Bureau of Fisheries at Fairport and elsewhere, with a view both to securing information regarding the life history of mussels and to testing experimentally the possibilities of culture as a public measure of conservation or as a field for private enterprise. At first little success attended these efforts. It was found that the mussels could readily be carried through the parasitic stage, but that soon after leaving the fish hosts they perished. Apparently there was something inimical to the young mussels in the artificial conditions of aquaria, tanks, or ponds, although these might be supplied with running water derived from the natural habitat of mussels.

The first reported rearing of mussels under control was accomplished with the Lake Pepin mucket in a crate floating in the Mississippi River (Howard, 1915). Experiments initiated by the senior author in the ponds at Fairport, Iowa, about the same time were also successful with the same species. Subsequently broods of the Lake Pepin mucket have been reared from year to year by various methods. Less consistent results have been obtained with the following river mussels: The pocketbook, *Lampsilis ventricosa*, the pimple-back, *Quadrula pustulosa*, and until recently the yellow sand-shell, *Lampsilis anodontoides*, and the mucket, *Lampsilis ligamentina*. Apparently the conditions required for rearing the Lake Pepin mucket are less difficult to meet under control than is the case with the other species mentioned. The reason is, doubtless, that *Lampsilis luteola*, being a lake-dwelling species as well as an inhabitant of rivers, is adapted to more varied conditions.

The methods employed in rearing mussels may be designated as follows: (1) The floating crate with closed bottom (chiefly used in rivers); (2) the floating crate with open

bottom (chiefly used in ponds); (3) the bottom crate; (4) pen with wooden or box bottom; (5) concrete ponds; (6) earth ponds; (7) troughs of sheet metal, wood, or concrete tanks, and aquaria.

(1) The floating crate with closed bottom was devised to meet the special conditions of a large river where the level is subject to considerable change, where excessive turbidity frequently prevails, and where there is a decided current. To prevent the washing away of the microscopic mussels, while permitting the passage of water and food through the crate, the crates are constructed of fine-meshed (100 mesh to the inch) wire cloth on a wooden frame. The form of the crates and the manner of using them may be understood from the illustrations (Pl. XIX, figs. 1 and 2). They are described in more detail in a forthcoming paper by A. D. Howard. A plant of young mussels is obtained by placing infected fish in the crate and removing them after they are freed of the mussels. The results with the floating crate have been quite satisfactory with the Lake Pepin mucket, and a few yellow sand-shells have also been obtained in them. Other river mussels have failed to develop beyond early stages. Good results with river mussels would be expected, but it is found that even with the crate floating in the river, the conditions within it are not those of the natural habitat of the mussel on the clean current-swept bottom of the river. No one has yet devised a container to employ under such conditions that would fully answer the requirements.

(2) The floating crate with open bottom has been used in artificial earth ponds. The bottom is actually closed to fish, though open to juvenile mussels, since it is made of coarse-mesh wire cloth (1½-inch mesh). The infected fish are kept inclosed until freed of glochidia, which fall through the wire to the bottom of the pond. To obtain the mussels when developed, the water is temporarily drawn from the pond. Good results have been obtained with the Lake Pepin mucket only.

(3) The bottom crate has been used in studies of growth of larger mussels, by Lefevre and Curtis (1912, p. 180), Coker, and others, and in experiments in pearl culture by Herrick (Coker, 1913). It has recently been adapted for the purpose of retaining infected fish and securing plants of early postparasitic stages of mussels. The crate rests on the bottom of the pond. It may have either a solid bottom or one of screen wire which, of course, sinks a little way into the mud covering the bottom of the pond.

(4) The pen of galvanized netting with wooden floor is adapted to quiet water without current. The pen, having walls of wire cloth that extend from the bottom to a safe distance above the surface of the water, allows the fish to seek their own range of depth and permits the mussels that fall from the fish to remain close to the bottom of the pond or lake, as is natural for them. The mussels are collected by raising the wooden bottom at the end of the growing season. Excellent results have been obtained in Lake Pepin with the Lake Pepin mucket. In the most successful experiment more than 11,000 living young were secured in one crop in a pen 12 feet square. These were liberated from 79 fish which had been artificially infected (Corwin, 1920).

(5) Concrete ponds having vertical sides have been planted in the usual way and the fish removed with a seine after the mussels have been shed. Some 50 examples of a river-inhabiting species, the pimple-back, *Quadrula pustulosa*, were reared to the age of 4 years in one experiment, but other trials with this species have failed. The usual consistent results have been secured with the Lake Pepin mucket.

(6) Earth ponds with devices for control of depth and water supply have been stocked with mussels by introducing infected fish. As a rule the fish are not removed

until the end of the season when the pond is drawn. The Lake Pepin mucket in considerable numbers have been reared in earth ponds. A few pocketbook mussels, *L. ventricosa*, were obtained after a recorded plant in a pond of modified type, having earth bottom but wooden sides. Mussels of several other species have been found in ponds from accidental plantings. The sporadic occurrences of young mussels in the first ponds and in the reservoir constructed at the Biological Station at Fairport, Iowa, are of interest as showing how, through parasitism upon fish, many species of mussel will quickly invade new waters. It is significant that none of the species which have introduced themselves abundantly into these ponds are commercially valuable. Apparently the commercially useless mussels are more easily and abundantly distributed by natural means than the useful ones. A list of the species noted, with additional data, is comprised in the following table (cf. Pl. XX):

TABLE 24.—MUSSELS RECORDED FROM PONDS AT THE FAIRPORT STATION.

Scientific name.	Common name.	Number or frequency.	Length in millimeters.
Anodonta corpulenta Cooper	Floater	Abundant	60–90
Anodonta suborbiculata Say [a]	Paper-shell	3	67.4
Anodonta imbecillis Say	do	Abundant	2–48
Arcidens confragosus Say [a]	Rock pocketbook	7	39–49
Lampsilis ligamentina Lam	Mucket	7	6–20
Lampsilis (Proptera) alata Say	Pink heel-splitter	2	69.5
Lampsilis (Proptera) capax Green	Pocketbook	2	49.5
Lampsilis (Proptera) lævissima Lea	Paper-shell	Abundant	27–90
Lampsilis subrostrata Say [a]		do	8.48
Lampsilis gracilis Barnes	Paper-shell	do	9.1–71
Lampsilis parva Barnes [a]		do	5.7–27
Obliquaria reflexa Rafinesque	Three-horned warty-back	1	16
Plagiola donaciformis Lea	Deer-toe	Abundant	2.6–20
Quadrula plicata Say	Blue-point	1	13.5
Quadrula undata Barnes	Pig-toe	1	15.8
Strophitus edentulus Say [a]	Squaw-foot	1	62.1
Symphynota complanata Barnes	White heel-splitter	26	64–91
Obovaria ellipsis Lea	Hickory-nut	1	11.4

[a] Uncommon in the river.

(7) Experiments have also been made with various containers of small dimensions which are usually supplied with running water. Such are the glass aquarium and the tank or trough which may be made of wood, concrete, or sheet metal. Of these the one most used for experimental rearing of mussels at Fairport, Iowa, has been the trough of sheet metal painted with asphaltum. A special arrangement for water supply is employed. The water is not taken directly from the main reservoir, but is drawn from the surface of a pond containing vegetation; in some cases it is also strained through cloth. In this way water is obtained that is very clear and probably free to a large extent from such small animals of the bottom as would prey upon the young mussels. The Lake Pepin mucket, the river mucket, and the yellow sand-shell have been reared through the first year in such troughs. The experiments are of such importance as to merit detailed description. The following account is based upon a report of F. H. Reuling, who first assisted in the experiments and later was charged with their conduct. (See also Reuling, 1919.)

The experiments were conducted in a series of eight galvanized iron troughs, placed at a sufficiently low level to receive a gravity supply of water from pond 1D. This pond was supplied by gravity from the reservoir which received its supply direct from the Mississippi River through the pumping plant. The water in pond 1D remained comparatively clear throughout the season, and this was one of the primary considerations

in locating the troughs. The troughs were 12 feet long, 1 foot wide, and 8 inches deep, painted with asphaltum, and each had its independent inflow from a common screened supply pipe in the pond. The bottom of each trough was covered with fine sand to a depth of about one-half inch.

Records were kept of the progress of the larval mussels through the process of development, and when they had reached that stage when they were ready to drop from the fish, counts on the fish gave a close approximation of the number dropped in the trough.

The results of the experiments the first season were quite meager, as only 7 young of the Lake Pepin mucket, *Lampsilis luteola*, varying from 6 mm. to 17.8 mm. in length, and 4 of the mucket, *L. ligamentina*, with an average length of 2.6 mm., were reared. However, in case of the mucket the results were very encouraging, as it marked the first instance of juveniles of this species being artificially reared to this size.

During the season of 1918 greater results were obtained with the Lake Pepin mucket, the young mussels being successfully reared in four troughs. In one trough a count of 746 was obtained. The experiments with *ligamentina* yielded negative results, though a lack of glochidia for infection greatly handicapped the work with this species.

The results in 1919 were still more gratifying. Young Lake Pepin muckets were obtained in each of five troughs planted with this species. In one trough 2,008 were counted at the end of the season, these little mussels varying in length from 9 mm. to 17.5 mm., the growth comparing very favorably with that made by the young of this species in their natural habitat. In a trough devoted to the river mucket, *L. ligamentina*, a total of 565 were reared. These little mussels varied in length from 5 mm. to 8.5 mm. In a trough planted with the yellow sand-shell a count of 2,006 was obtained at the end of the season, the young mussels varying in length from 5.5 mm. to 12 mm. The result of this experiment is highly interesting, in that it is the first record of the artificial rearing of this very valuable species in any quantity.

The 746 young *luteola* reared during the summer of 1918 were carried over the winter in a shallow crate bottom 5 feet square and 8 inches deep, submerged in one of the earth ponds. During the summer of 1919 an inventory of the crate bottom gave a count of 238 young mussels, a survival percentage of about 32 per cent.

The method of artificial rearing of young mussels, as detailed above, denotes a distinct departure from the methods previously used and gives the operator complete control of conditions throughout. The results of the experiments have been such as to justify the employment of the method on a much larger scale in future, and plans are under way for materially increasing the facilities and equipment. Certain phases of the work need further study and amplification. Additional information on the possible enemies of the young mussels in the troughs is needed; a study of their food should be made; it should be learned if artificial feeding is practicable; and further experiments should be made to determine the most favorable bottom material for the troughs, whether fine sand alone, or sand with a slight admixture of silt, etc. The present indications are that fine sand is the most desirable bottom material.

In summary of the topic of the culture of fresh-water mussels, it may be stated that the results of many experiments conducted under diverse conditions demonstrate that the valuable Lake Pepin mucket can be reared in quantities, under conditions of control. Sufficient success has been attained with other species to warrant confidence that, with them also, methods of securing constant results will be found.

12) M.M. Ellis and M.D. Ellis, "Growth and Transformation of Parasitic Glochidia in Physiological Nutrient Solutions," *Science* 64 (No. 1667, December 10, 1926): 579-80.

SPECIAL ARTICLES

GROWTH AND TRANSFORMATION OF PARASITIC GLOCHIDIA IN PHYSIOLOGICAL NUTRIENT SOLUTIONS

In experiments completed at the U. S. Bureau of Fisheries Biological Station at Fairport, Iowa, by us this summer, artificial nutrient solutions were prepared in which the glochidia of the freshwater mussel, *Lampsilis fallaciosa* Smith (known as the Creeper or Slough Sand-shell), were carried through their various developmental stages from glochidium to the free-living juvenile mussel. The glochidia of this species of freshwater mussel are parasitic on the gills of the short-nosed gar, *Lepisosteus platostomus* Rafinesque, for a period varying from two to several weeks, during which time the glochidia undergo marked internal changes and differentiations and emerge from their cysts at the end of this sojourn on the fish as free-living juvenile mussels. The nutrient fluid was perfected so that this period of parasitic life on the fish could be replaced by a period *in vitro*, during which the growth and differentiations ordinarily made by the glochidium in the cyst could be studied and controlled.

The glochidia used in these first series of experiments were dissected out of their cysts on the gills of artificially infected gar, eighteen and ninety-six hours after encystment was begun. The freed glochidia were transferred at once to the solutions in which their development was to be followed. Glochidia removed from the cyst eighteen hours after attachment to the fish gill differed little if at all in appearance from ripe glochidia in the maternal marsupium. Glochidia removed at the end of ninety-six hours showed considerable development of the organ anlagen, although the glochidia were still in a very embryonic stage, as was evidenced by the presence of a large portion of the larval mantle cell mass. In the most favorable solution tested the glochidia were carried through the twelfth day in the solution, at which time their development equalled that of control glochidia which had been carried on the fish and were just ready to emerge from their cysts. When this stage was reached by the glochidia *in vitro* they were transferred from the nutrient solution to river water in which they made their final transformation in less than a half hour. In actual time the transformation stage was reached by the glochidia *in vitro* more quickly than by the glochidia on the fish, but there may be several factors involved in this comparison. Certainly, however, the growth and development of the glochidia *in vitro* was not delayed.

Juvenile mussels which transformed in these artificial nutrient solutions were kept in river water for three weeks after transformation without the loss of a single individual, the juvenile mussels making excellent growth of both shell and soft parts during that time and seeming in every way to be very vigorous. This was a bit surprising, as there is known to be a rather high mortality, on the contrary, among mussels during the first few days after leaving the fish following the natural parasitic cycle.

The several series of glochidia carried in the various nutrient solutions *in vitro* showed that parasitic life on the fish is not essential to development and transformation if the proper food substances be supplied in the proper environment; that the glochidium receives by its encystment a much-needed protection against certain bacterial and protozoan enemies; and that the glochidium is a true parasite while on the fish, receiving essential food substances from the host fish. This last statement was repeatedly tested in a variety of experiments and the so-called protective physiological solutions containing only inorganic salts were neither adequate to produce growth and differentiation nor to maintain glochidia already well started on their way to transformation.

The successful solutions contained sodium chlorid, potassium chlorid, calcium chlorid, sodium bicarbonate, dextrose and a mixture of amino-acids, together with small quantities of phosphates and traces of magnesium salts. Detailed data of these experiments as well as experiments on glochidia taken directly from the maternal marsupium are to be published.

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13) Isom, Billy G., and Robert G. Hudson, "In Vitro Culture of Parasitic Freshwater Mussel Glochidia," *The Nautilus* 96 (No. 4, 1982): 147-51.

IN VITRO CULTURE OF PARASITIC FRESHWATER MUSSEL GLOCHIDIA

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ABSTRACT

Ellis and Ellis (1926 and 1930) reported transformation of freshwater mussel glochidia in vitro culture. However, their methodology was never published. This report gives a new method for the in vitro culture of mussel glochidia to juveniles rather than by their natural fish host encystment. The medium consists of physiological salts, amino acids, glucose, vitamins, antibiotics, and a nonspecific component of fish blood plasma. The relative concentration of fish plasma required for optimum results was 33 percent. In vitro culture may prove very beneficial in reestablishing the populations of endangered mussels, management of species used by the pearl culture industry, and culturing of stocks for bioassays, genetic studies, or other uses.

Application of in vitro culture for the purpose of sustaining endangered mussels of commercial importance is obvious, since usually an unknown fish host is required for larval development in nature. The female mussel has her eggs fertilized by sperm cells which are released into the water by a male mussel and travel into the female with water taken in during filter feeding. The fertilized eggs, contained in the female's gills, develop into simple glochidia, or larvae, consisting primarily of two shells, mantle cells, and one adductor muscle. The glochidia are released and encyst in a specific fish tissue, usually the gills. Development of glochidia into juveniles (transformation) in an artificial medium would help endangered mussels, since the fish host required for most of these species is unknown and would be difficult to determine. The fish host of some species may even be extirpated. Use of in vitro culture could sustain a species until its fish host could be found or the absence of a host availability determined. Even mussels with a known fish host could be reared for commercial or scientific purposes.

Freshwater mussels have been used commercially for manufacturing buttons and presently as nuclei for cultured marine pearls. They are also currently being used for the culture of freshwater pearls in the United States. Overharvesting as a result of demand for shells has contributed significantly to the decline of freshwater mussel resources in the United States over the past three decades. Historically, over 500 of the more than 1000 world species of freshwater mussels occurred in the United

FIG. 1. *Glochidial shell of the freshwater mussel* Ligumia recta *(length 260 μm).*

States. Many species are now thought to be extinct; others are listed as threatened or endangered by individual states or the United States Government.

Ellis and Ellis reported in 1926 that they had successfully obtained transformation of parasitic glochidia of freshwater mussels in physiological nutrient solutions. However, neither the composition of the media nor the process used was ever published. In addition, unlike the present study, Ellis and Ellis excised the glochidia they used from a known fish host, an action which undoubtedly contributed to their reported success.

Composition of our artificial medium include salts which are modified from the "unionid Ringers" solution proposed by Ellis et al. (1930) and are shown in Table 1. The essential modification of the solution includes the deletion of K_2HPO_4 and the addition of 2.2 gm $NaHCO_3$ per 1000 milliliters of solution. The $NaHCO_3$ was required in order to regulate the pH with varying atmospheric CO_2 concentrations.

TABLE 1. *Salts contained in stock artificial glochidial medium.*

Compound	*Concentration (mg/L)*
$CaCl_2$	1200
$MgCl_2.6H_2O$	1000
NaCl	1530
KCl	99
$NaHCO_3$	2200

The amino acids in the artificial medium are the same as those used by Eagle (1959) for cell and tissue cultures with the exception of the addition of taurine and ornithine which are constituents of fish blood. The essential amino acids are shown in Table 2, the nonessential amino acids in Table 3.

The vitamins present in the complex artificial growth medium, the same as those used by Eagle (1959) for cell and tissue cultures, are shown below in Table 4. The antibiotics and antimycotic used in the artificial medium are listed in Table 5; other compounds are shown in Table 6.

Plasma was obtained from fish blood which

TABLE 2. *Essential amino acids contained in stock artificial glochidial medium.*

Compound	*Concentration (mg/L)*
L - arginine	105
L cystine	24
L - histidine	31
L - isoleucine	52
L - leucine	52
L lysine	58
L - methionine	15
L - phenylalanine	32
L - threonine	48
L - tryptophane	10
L - tyrosine	36
L - valine	46

TABLE 3. *Nonessential amino acids contained in stock artificial glochidial medium.*

Compound	*Concentration (mg/L)*
L - alanine	8.9
L - asparagine	13.2
L - aspartic acid	13.3
glycine	7.5
L - glutamic acid	14.7
L - proline	11.5
L - serine	10.5
taurine	31.0
L - ornithine	10.0

TABLE 4. *Vitamins contained in stock artificial glochidial medium.*

Compound	*Concentration (mg/L)*
choline chloride	1.0
folic acid	1.0
inositol	2.0
nicotinamide	1.0
calcium pantohthenate	1.0
pyridoxal	1.0
riboflavin	0.1
thiamine	1.0

was removed from the fish by heart puncture with a sterile heparinized syringe (the syringe chamber was coated with a sodium heparin solu-

TABLE 5. *The antibiotics and antimycotic contained in stock artificial glochidial medium.*

Compound	*Concentration*
Antibiotics	
Carbenicillin	100 μg/ml
Gentamicin sulfate	100 μg/ml
Rifampin	100 μg/ml
Antimycotic	
Amphotericin B	5 μg/ml

TABLE 6. *Other compounds contained in stock artificial glochidial medium.*

Compound	*Concentration (mg/L)*
Glucose	1000.0
Phenol red (optional)	10.0

tion of 1000 U/ml) having an 18 gauge needle. The blood was centrifuged at 1000 rpm in a refrigerated centrifuge for 10 minutes followed by 3000 rpm for 10 minutes, decanted into sterile centrifuge tubes, and centrifuged for another 10 minutes. The plasma was removed by aspiration, then frozen and subsequently sterile filtered. The antibiotics and antimycotic were added to the plasma in the same concentration as shown in Table 5, at time of use.

Glochidia from gravid female mussels were obtained by utilizing sterile surgical instruments to remove the gills containing glochidia, then the gills were placed in sterile deionized water. The glochidia were excised from the gills by sectioning and then swirling the gills in the deionized water.

The glochidia were washed several times with deionized water by decanting or aspirating the water following swirling of the beaker contents. The healthy glochidia settled, allowing the removal of tissue debris, dead glochidia, bacteria, and protozoa. The glochidia were left in the last rinse water until they were removed with a Pasteur pipette and placed in the growth medium. A representative scanning electron photomicrograph of a glochidium of *Ligumia recta* (Lamarck, 1819) is shown in Figure 1.

Different components and concentrations of the growth medium were tested to determine which combination would stimulate and best

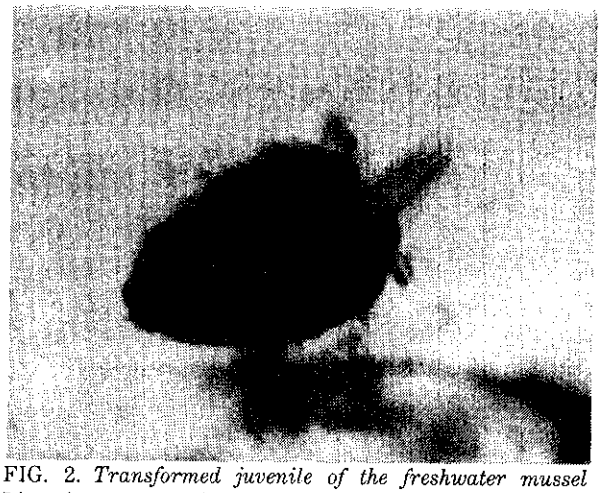

FIG. 2. *Transformed juvenile of the freshwater mussel* Ligumia recta, *89 days old, in lake water. Note the protruding ciliated foot.*

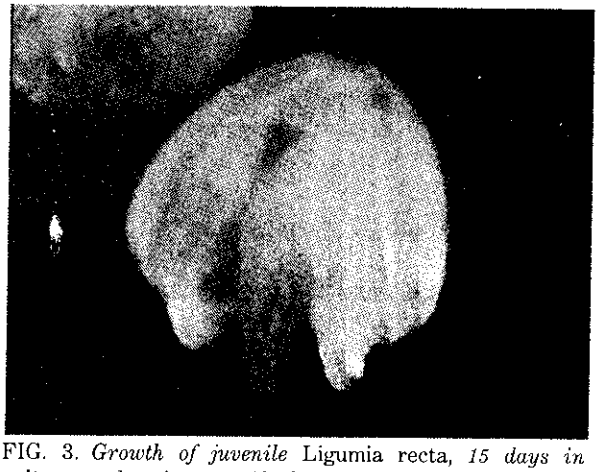

FIG. 3. *Growth of juvenile* Ligumia recta, *15 days in culture, 13 days in water (dark field), a total of 28 days. End view showing protruding foot in center.*

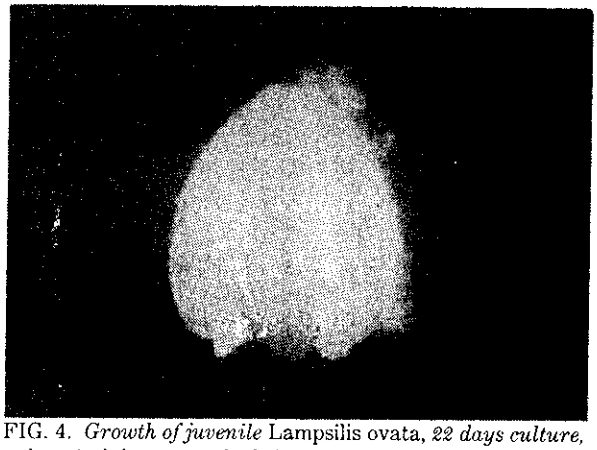

FIG. 4. *Growth of juvenile* Lampsilis ovata, *22 days culture, 9 days in lake water (dark field), a total of 31 days old.*

support glochidial transformation. Numerical comparisons of different cultures were difficult to evaluate because the varying stages of development in, as well as the number of, glochidia. The presence of bacteria in initial cultures in 1981 further confounded the accuracy of numerical culture evaluations. Many cultures failed to yield fully transformed glochidia because of bacterial infections, even though most glochidia had good initial development prior to their contamination. Experiments in 1982 with the new antibiotics shown in Table 5 have been much more successful.

Only two different salt solutions, unionid Ringers (Table 1) and Earles' balanced salt solution (Earle, 1943), were compared in experiments. Glochidia transformed in both salts, even though the amino acids used in conjunction with each varied slightly. Because parasitic glochidia are surrounded by fish cells, and since Earles' is the salt solution most commonly used in fish cell culture medium (Wolf and Quimby, 1969), glochidal adaptation for life in Earles' salt concentrations as well as in unionid Ringers would be expected.

Different groups of amino acids were tested in cultures to get transformation, but elimination of nonessential, single, amino acids has not been attempted to date. In earlier experiments with the medium being 20 percent artificial, the amino acid content seemed less important, probably because the 80 percent plasma had the necessary concentrations of amino acids. The artificial growth medium was formulated to include all free amino acids which had been found in three species of catfish (*Ictalurus furcat s. I. punctatus,* and *Pylodictis olivaris*) (Johnson, 1971). All of the amino acids which had been found in fish blood could also be found in equal or higher concentrations in Eagles' essential and nonessential amino acids if taurine and L-ornithine were added. The only amino acid found in Eagles' amino acid group which was not found in the catfish blood was L-tryptophane. Since Eagles' amino acids could be purchased premixed, this combination was used along with taurine and L-ornithine in the successful in vitro medium. Medium 199, which also has 21 amino acids (Morgan et al., 1950), was sufficient for glochidial transformation. Medium 199 has the same 12 essential amino acids as Eagles' medium; however, medium 199 is lacking 4 of the 9 nonessential amino acids which had been used. This would indicate that these four (L-alanine, L-asparagine, L-ornithine, and taurine) were not necessary for glochidial development. Even though development occurred in both media, the development rate was faster in Eagles' amino acids with taurine and L-ornithine than in medium 199.

Fish blood plasma was found to be necessary to stimulate development in all mussel species tested. Other massive protein components, specifically fetal bovine serum, bovine serum, and lobster hemolymph, were tested and found unsuccessful. Although earlier tests indicated a positive correlation between percent transformation and percent fish blood plasma in the medium, 33-1/3 percent blood plasma was adopted in our standard medium as producing satisfactory yields at a more economical level.

Earlier cultures of *Legumia recta* were placed in unfiltered plasma which contained several blood cells. First observations seemed to indicate that development was enhanced by the presence of these cells. The glochidia were held in a matrix of cells and fibrin on the dish and developed rapidly. Subsequent media changes were made using filtered plasma to prevent a buildup of cells in the culture. Conversely, later cultures with *Fusconaia ebena* (Lea, 1831) did not show any indication of enhancement by the presence of these cells. In fact, cultures with unfiltered plasma suffered a higher rate of contamination which resulted in a lower yield. More work is needed in this area, but the presence of the fish cells does not appear to be necessary for glochidial development.

The pH of the medium varied from ca. 7.3 to 8.1; however, the lower pH promoted best transformation in at least one species. Cultures of *Fusconaia ebena* developed much better in a pH range of 7.3 to 7.4 rather than 7.8 to 8.0. For example, in eight different cultures of *F. ebena*, 16 of 26 culture dishes contained transformed juveniles after 18 days at a pH of ca. 7.3, whereas none of an identical set of 26 cultures were alive at 11 days when cultured at a pH of ca. 7.9.

Bacterial infection was present in cultures at both pH levels and was responsible for much of this loss; however, many of the higher pH cultures died even when bacterial action was minimal, while infections in the lower pH cultures did not result in death of the entire culture. The lower pH level appeared to either make it easier to control bacterial contamination or minimize the detrimental effects of the bacteria. Subsequent experiments have corroborated that a pH of 7.3 is optimum.

The use of antibiotics and their concentrations varied with the presence or absence of bacteria in the medium. Carbenicillin, usually added to yield 100 μg/ml, can be increased to as high as 500 μg/ml without apparent inhibition to the glochidial development. Gentamicin sulfate and Rifampin can also be increased from 100 μg/ml to 500 μg/ml safely, and the antimycotic, Amphotericin B (Fungizone) from 5 to 25 μg/ml. These antibiotics and antimycotic, along with rinsing and changing infected glochidia to new media and dishes, usually would control contamination successfully. Older glochidia could withstand infection much longer than younger glochidia.

The medium was kept at 23°C but cultures were successful, to a lesser extent, even at 28°C. Higher temperature did reduce the yield, as shown by the comparison of glochidia of *Ligumia recta* which developed in 23°C and 28°C. Using six culture dishes grown in 60 percent plasma, three grown in 23°C had an average yield of advanced glochidial development equal to 48.8 percent ($S\bar{x} = 8.7$), while those grown at 28°C averaged 18.8 percent ($S\bar{x} = 3.3$). A transformed glochidium of *Ligumia recta* is shown in Figure 2.

During the spawning season of 1982, these variables have been refined to a greater degree, resulting in successful mass culturing of glochidia (some cultures averaging as high as 80 percent transformation). These successes will provide opportunity for conservation of many mussel species including endangered species, and the management of others. Efficacy of the process to date includes transformation of glochidia of six genera and species representing two subfamilies of Unionidae, the Unioninae and Lampsilinae.

A growth stage of a juvenile *Ligmia recta* is shown in Figure 3 and that of a *Lampsilis ovata* in Figure 4.

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Recent Deaths

We regret to announce the death of our dear friend, Katherine Van Winkle Palmer, former Director of the Paleontological Research Institution, of Sept. 12, 1982, at the age of 87. Contributions to her memorial fund for P.R.I. may be sent to Dr. Raymond Van Houtte, Tompkins County Trust Co., Ithaca, NY 14850. An obituary is in prepartion.

Meeting

The Eighth International Malacological Congress, sponsored by the Unitas Malacologica, will be held in Budapest, Hungary, in 1983, from August 29 - September 3. Further information may be obtained by writing Dr. László Pintér, Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary.