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Fish hosts of four species of lampsiline mussels (Mollusca: Unionidae) in Big Moccasin Creek, Virginia

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Collections of stream drift and fishes were made weekly from May to November 1979 and twice monthly from December 1979 to June 1980 to define the periods when glochidia of four mussel species (subfamily Lampsilinae) were in the drift or attached to host fishes. Representatives of all families and most genera of fishes in the stream, including all naturally infected species, were artificially exposed in the laboratory to glochidia of the four species to enable positive identification of host species. The lampsiline mussels displayed a high degree of host specificity. The host fishes were as follows: *Villosa nebulosa*, smallmouth bass (*Micropterus dolomieui*), and rock bass (*Ambloplites rupestris*); *Villosa vanuxemi*, banded sculpin (*Cottus carolinae*); *Medionidus conradicus*, redline darter (*Etheostoma rufilineatum*), and fantail darter (*E. flabellare*); and *Lampsilis fasciola*, smallmouth bass. Periods of natural infestation on fishes corresponded with the occurrence of glochidia in the drift and were different for each mussel species. Duration of the period of attachment on host fishes in the laboratory depended on mussel species, water temperature, and the time when glochidia were obtained from gravid female mussels.

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L'échantillonnage dans un ruisseau, hebdomadaire de mai à novembre 1979 et bimensuel de décembre 1979 à juin 1980, a permis d'établir à quelles périodes les glochidies de quatre espèces de moules (sous-famille des Lampsilinae) se laissent dériver et à quelles périodes elles sont attachées à des poissons hôtes. Des représentants de toutes les familles et de presque tous les genres de poissons du ruisseau, y compris toutes les espèces infectées naturellement, ont été exposées en laboratoire à des glochidies des quatre espèces, afin de déterminer avec certitude l'identité des espèces hôtes. Les moules manifestent une grande spécificité d'hôte: *Villosa nebulosa* s'attache surtout à l'achigan à petite bouche (*Micropterus dolomieui*) et au crapet de roche (*Ambloplites rupestris*), *Villosa vanuxemi*, au cottidé (*Cottus carolinae*), *Medionidus conradicus*, aux dards (*Etheostoma rufilineatum* et *E. flabellare*) et *Lampsilis fasciola*, à l'achigan à petite bouche. Les périodes d'infection naturelle des poissons coïncident avec la présence des glochidies dans la dérive et diffèrent pour chaque espèce de moule. La durée de l'attachement à un poisson hôte en laboratoire dépend de l'espèce, de la température de l'eau et du moment où les glochidies ont été recueillies chez les moules femelles.

[Traduit par le journal]

Introduction

The larvae (glochidia) of freshwater mussels are obligate parasites on the gills or fins of fish. Among members of the subfamily Lampsilinae, the glochidia are discharged into the water through minute pores in the female's marsupial gills and attach primarily to the gills of fish for the parasitic phase. If attachment to the appropriate fish host occurs, the glochidia encyst, metamorphose, and excyst to begin their adult life as free-living juveniles in the substrate. Nearly all freshwater mussels with known life histories exhibit this parasitic phase on fish hosts, although exceptions have been noted (Howard and Anson 1922; Allen 1924; Howard 1951).

The fish hosts for most species of freshwater mussels are unknown. Fuller (1974) summarized the known fish hosts for 46 species, and several additional fish host relationships were elucidated later (Wiles 1975; Weir 1977; Stern and Felder 1978; Tompa 1979). The mussel fauna in the United States has severely declined due to overharvesting, siltation, pollution, channelization, and other human impacts. Attempts to enhance natural recovery are severely hampered by the lack of fish host information. This decline in mussel abundance and diversity is most evident among the unique fauna of the Cumberland Plateau Region, southeastern United States. No results of studies on fish hosts of these species have been published. Our fish host studies were conducted on four lampsiline species of this region that included three Cumberlandian species, *Villosa* (= *Micromya*) *nebulosa*, *V. vanuxemi*, and *Medionidus conradicus*, and the more ubiquitous *Lampsilis fasciola*.

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Study area

Big Moccasin Creek, a third-order tributary of the North Fork of the Holston River, flows through Russell and Scott counties in southwestern Virginia. The study area (latitude 36°47′30″ N, longitude 82°11′50″ W; 616 m elevation above mean sea level; Hansonville, VA, United States Geological Survey quadrangle) encompassed a 400-m section of stream above river kilometre 82, at the intersection of state routes 676 and 677. At this site, termed Owen's farm, the stream runs through open pastureland and averages 7 m in width and 0.2 m in depth. Substrate consists primarily of cobbles and gravel, with some bedrock and silt in localized areas. Water chemistry characteristics during low flow in October were as follows: pH, 8.2; dissolved oxygen, 9.0 mg/L; conductivity, 250 μmhos (1 mho = 15); hardness, 175 mg/L as $CaCO_3$; and total alkalinity, 180 mg/L. Weekly maximum and minimum water temperatures, determined with a 30-day recording thermograph, ranged from 0°C in February to 33.0°C in July (Zale and Neves 1982). The study site supported a large mussel community composed of seven species, with the following relative composition (based on 30 random 0.5-m^2 quadrat samples): *Medionidus conradicus* (68.0%), *Villosa nebulosa* (23.8%), *V. vanuxemi* (6.0%), *Pleurobema oviforme* (1.4%), *Lampsilis fasciola* (0.7%), *Fusconaia barnesiana* (< 0.1%), and *Alasmidonta minor* (< 0.1%).

Materials and methods

Mature glochidia from gravid females of *V. nebulosa*, *V. vanuxemi*, *M. conradicus*, and *L. fasciola* were measured, photographed, and described morphologically to differentiate them from each other and from glochidia of the three other mussel species (subfamilies Unioninae and Anodontinae) in Big Moccasin Creek. Glochidia of the three lampsiline genera were easily identified by their size and distinctive shape, but glochidia of *V. nebulosa* and *V. vanuxemi* could not be readily distinguished from each other (Zale and Neves 1982).

Natural infections

Investigations of glochidial infections on fishes in Big Moccasin Creek were conducted in two phases. In the first phase, from May to September 1979, all species of fish in the study area were examined for lampsiline glochidia. In the second phase, from October 1979 to June 1980, only the fish species found with lampsiline glochidia during the first phase, or implicated as hosts by infections induced in the laboratory, were collected to determine periods of natural infections in the stream. Fish sampling was conducted weekly from May to November 1979 and twice monthly from December 1979 to June 1980. All fish were collected with either back-pack or shore-based engine generator (georator) electrofishing gear.

During the first phase, about 300 fish were collected on each sampling date. We tried to examine individuals of as many species as possible. Captured fish were anaesthetized with tricaine methanesulfonate (MS-222), and their gills were inspected for glochidial infections at streamside. Infected fish were preserved in 10% buffered formalin, and uninfected ones were returned to the stream. Lampsiline infections were later verified by microscopic examination in the laboratory.

On each sampling date during the second phase, we collected and preserved about 30 banded sculpins (*Cottus carolinae*), 30 fantail darters (*Etheostoma flabellare*), and 10 redline darters (*E. rufilineatum*). During this phase all centrarchids captured were anesthetized, inspected, and released. Because infections were readily visible on centrarchids, the sacrifice of fish was unnecessary.

Stream drift

Three 930-cm^2 drift nets (130-μm mesh) were set below the mussel community at the study site during each sampling date to collect glochidia in the drift. The collection period could not be readily standardized because the nets often clogged within 2 h during periodic turbid conditions. Drift samples were washed from the nets into jars and preserved in 10% buffered formalin. In the laboratory, rose bengal was added to facilitate the sorting of glochidia from detritus and sediment. Subsamples of drift were examined in a gridded petri dish with a dissecting microscope (40×). Each glochidium was removed and identified. Lampsiline glochidia were separated into the three genera, and *V. nebulosa* and *V. vanuxemi* were treated together.

Induced infections

The laboratory component of the fish host study involved exposure of 14 fish species to glochidia of all four lampsiline mussel species in Big Moccasin Creek. Representatives of all families and most genera of fishes at the Owen's farm site were tested, including all naturally infected species. Fish to be artificially exposed were collected by electrofishing in streams without mussels to avoid the possibility that the fish were immune as a result of previous infections (Arey 1923). They were inspected for gill parasites or disease, and only healthy fish were retained. Fish were transported to the laboratory in coolers and acclimated to experimental temperatures in Living Streams (Frigid Units Inc., Toledo, OH) for at least 1 week before being exposed to glochidia.

Gravid female mussels were collected from the study site and transported to the laboratory in cloth bags packed in crushed ice. Females were kept in an aerated, chilled recirculating tank (300 L) with stream substrate, in which flow was maintained with a submersible pump. Premature glochidial expulsion was controlled by setting water temperatures at 10°C. Powdered trout food and a commercial invertebrate diet (Hawaiian Marine Imports Inc., Houston, TX) were introduced daily for the mussels.

To obtain infective glochidia, we dissected the marsupial gills of gravid females. The marsupia were excised with forceps and placed in a water-filled glass dish. Glochidia were then teased out by rupturing the ovisacs with a sharp probe, and conglutinates (clumped glochidia) were separated by agitation with a pipette. Activity was tested by manipulating the glochidia with a fine probe or by introducing a weak saline solution to a subsample. Mature, active glochidia rapidly snapped shut when so stimulated.

About 10 fish of each species were used in most trials. Fish were anaesthetized with MS-222 and placed in clean water to rinse away the chemical. Glochidia placed directly into a solution of MS-222 showed no change in activity or responsiveness. Several hundred glochidia were pipetted directly into the right branchial cavity of each immobilized fish, as described by Weir (1977). One-third to one-half of the larvae usually attached to gill lamellae. Small fish were exposed to only half as many glochidia, to avoid lamellar inflammation

TABLE 1. Species composition of the fish population, and incidence of infection by lampsiline glochidia, based on collections from Big Moccasin Creek, May to September 1979

Fish	No. examined	% infected
Catostomidae		
Catostomus commersoni, white sucker	1	0.0
Hypentelium nigricans, northern hogsucker	90	0.0
Moxostoma duquesnei, black redhorse	1	0.0
Centrarchidae*		
Ambloplites rupestris, rock bass	178	31.5
Lepomis auritus, redbreast sunfish	350	4.0
Micropterus dolomieui, smallmouth bass	8	37.5
Cottidae		
Cottus carolinae, banded sculpin	112	0.9
Cyprinidae		
Campostoma anomalum, stoneroller	1281	0.0
Hybopsis amblops, bigeye chub	1	0.0
Nocomis micropogon, river chub	270	0.0
Notropis coccogenis, warpaint shiner	104	0.0
N. cornutus, common shiner	337	0.0
N. galacturus, whitetail shiner	48	0.0
N. leuciodus, Tennessee shiner	27	0.0
N. rubellus, rosyface shiner	177	0.0
N. telescopus, telescope shiner	188	0.0
Pimephales notatus, bluntnose minnow	54	0.0
Rhinichthys atratulus, blacknose dace	2	0.0
Ictaluridae		
Ictalurus natalis, yellow bullhead	27	0.0
Percidae		
Etheostoma blennioides, greenside darter	75	0.0
E. flabellare, fantail darter	423	27.9
E. rufilineatum, redline darter	237	15.6
E. simoterum, Tennessee snubnose darter	82	1.2

*A single uninfected largemouth bass (*Micropterus salmoides*) was taken October 11, 1979.

and subsequent myxobacteriosis. After exposure, the fish were revived and placed in 40-L glass aquaria with aeration, filtration, and temperature controls. Each aquarium contained the individuals of one fish species exposed to glochidia of one species of mussel.

A subsample of fish was checked 2 h after exposure and then daily to determine whether encystment and development were proceeding. Large fish could be inspected with the unaided eye under strong light, but microscopic examination was required for small species such as darters and sculpins. Glochidia were considered sloughed off if their incidence on test fish decreased rapidly during the first few days after exposure. After this period of sloughing, fish were sacrificed and examined microscopically to verify the loss of glochidia. The last day of glochidial attachment on these fish was recorded. If an infection was retained 5 days after exposure to glochidia, daily siphoning of the tank was begun. The bottom of the aquarium was siphoned with a flexible hose (15 mm in diameter) into a 130-μm nylon mesh sieve. We examined the siphoned debris for the presence of juvenile mussels in a gridded petri dish with a dissecting microscope (40×). The number of juveniles recovered daily was recorded and siphoning continued for at least 3 days after the last juveniles were found. Infected fish were then sacrificed and examined for any remaining glochidia. A fish species was considered a host for the glochidia of a mussel species if glochidia attached, encysted, and developed to the juvenile stage. Unsuccessful encystment was verified in many cases by replicate trials, and all tests that yielded juveniles were repeated at least once.

Results

Field collections

Fourteen collections of about 300 fish each were made at Owen's farm during the first stage of the field study, May to September 1979 (Table 1). No largemouth bass (*Micropterus salmoides*) were encountered during the period, but a single uninfected specimen was taken

TABLE 3. Maximum periods of attachment, number of fish exposed (*N*), and mean water temperatures in laboratory trials with glochidia of *Villosa nebulosa*, *V. vanuxemi*, *Medionidus conradicus* and *Lampsilis fasciola* on nonhost fish species

Infected fish species	*V. nebulosa*			*V. vanuxemi*			*M. conradicus*			*L. fasciola*		
	Period (days)	*N*	Temperature (°C)	Period (days)	*N*	Temperature (°C)	Period (days)	*N*	Temperature (°C)	Period (days)	*N*	Temperature (°C)
Hypentelium nigricans	2	6	20.2	3	7	18.2	2	7	21.2	3	13	18.5
Ambloplites rupestris	—	—	—	17	13	17.0	5	11	17.5	10	12	17.7
Lepomis auritus	11	6	17.5	14	9	16.5	9	13	16.5	13	11	16.5
Micropterus dolomieui	—	—	—	17	10	17.7	5	4	18.7	—	—	—
Cottus carolinae	6	6	17.7	—	—	—	3	12	16.5	5	12	16.5
Campostoma anomalum	3	11	15.7	3	14	15.2	3	12	17.0	4	11	16.5
Nocomis micropogon	3	7	18.5	3	7	18.5	4	7	21.0	2	11	18.7
Notropis leuciodus	2	10	20.2	2	10	18.2	2	7	18.5	2	7	18.5
Pimephales notatus	2	7	16.0	2	8	16.2	3	12	18.5	2	12	21.0
Ictalurus natalis	4	2	17.2	4	3	17.0	6	3	15.0	6	2	16.0
Etheostoma blennioides	7	2	18.7	4	2	18.5	9	15	15.7	4	6	18.7
E. flabellare	2	9	16.7	7	9	16.2	—	—	—	5	16	17.0
E. rufilineatum	4	10	17.7	6	12	15.0	—	—	—	5	14	16.5
E. simoterum	6	5	17.5	4	11	17.2	7	14	18.2	5	5	16.2

TABLE 4. Metamorphosis of glochidia of *Villosa vanuxemi* from induced laboratory infections on banded sculpins (*Cottus carolinae*)

Mean temperature (°C)	Period of metamorphosis (days)	No. of fish exposed	No. of juveniles recovered
16.7	28–49	21	817
17.5	28–45	8	546
19.5	18–27	9	408
25.0	8–17	12	321

tached for an extended period on rock bass (10 days) and redbreast sunfish (13 days) prior to sloughing off. All glochidia were lost from other fish species within 6 days (Table 3). The initial trial with glochidia on six smallmouth bass was unsuccessful because all fish died by 27 days postinfection. These fish still retained the glochidia at time of death, indicating that they were probably hosts. A total of 666 juvenile mussels were collected from the single smallmouth bass available for the second trial between 30 and 47 days postinfection at 19.2°C.

Discussion

Results of laboratory and field investigations were in agreement and demonstrated that the four lampsiline species in Big Moccasin Creek exhibited a high degree of fish host specificity. Hosts of *Villosa nebulosa* were limited to two centrarchids, smallmouth bass and rock bass, whereas the only host of *V. vanuxemi* was the banded sculpin. This fish host difference at the family level for two sympatric, congeneric species is noteworthy. Redline and fantail darters served as hosts for *Medionidus conradicus*, but greenside and Tennessee snubnose darters did not. The smallmouth bass was the only host for the glochidia of *Lampsilis fasciola* in Big Moccasin Creek. We acknowledge that other fishes may serve as hosts in other streams and rivers within the geographical range of each mussel species; however, no research on regional differences in fish host specificity has been conducted for any mussel species in North America.

As a consequence of the extended period of release of glochidia of *Medionidus conradicus*, juveniles are recruited throughout the year. Initiation of glochidial release occurred in September when large numbers of young-of-the-year darters were present in the stream. These young darters (total length, 20–25 mm) were large enough to provide sufficient gill surface area for glochidial attachment. The fish host relationship between *M. conradicus* and only two of four darter species in the stream may be a consequence of sympatric habitats. *Medionidus conradicus*, redline darters, and

TABLE 5. Metamorphosis of glochidia of *Medionidus conradicus* from induced laboratory infections on fantail darters (*Etheostoma flabellare*) and redline darters (*E. rufilineatum*)

Infected fish species and mean temperature (°C)	Date* of infection	Period of metamorphosis (days)	No. of fish exposed	No. of juvenile mussels recovered
E. flabellare				
16.5	6/16/79	10–20	11	33
17.7	1/27/80	41–63	13	171
17.5	2/01/80	46–59	11	207
E. rufilineatum				
16.0	6/16/79	10–20	11	16
16.5	2/01/80	50–58	15	32

*Month/day/year.

TABLE 6. Metamorphosis of glochidia of *Lampsilis fasciola* from induced laboratory infections on smallmouth bass (*Micropterus dolomieui*)

Mean temperature (°C)	Period of metamorphosis (days)	No. of fish exposed	No. of juveniles recovered
17.0*	>27	6	—
19.2	30–47	1	666

*All fish died by 27 days postinfection but still possessed glochidia.

fantail darters were typically found in shallow riffle areas with coarse substrate and turbulent flow. Preliminary laboratory observations on the feeding behavior of the four darter species in Big Moccasin Creek have shown that the redline and fantail darters have terminal mouths and feed readily on drift organisms, whereas the nonhost Tennessee snubnose and greenside darters have subterminal mouths and fed exclusively on benthos. Host darters probably became infected by ingesting drifting glochidia. Dartnall and Walkey (1979) noted that the threespine stickleback (*Gasterosteus aculeatus*) actively preyed on glochidia in experimental situations, and their stomachs contained glochidia under natural feeding regimes.

The period of glochidial expulsion by *Villosa vanuxemi* from October to May occurred when banded sculpins were most abundant at the study site. Sculpins were abundant between fall and spring, but were collected infrequently during summer. The glochidia of *V. vanuxemi* were often attached to the thin epithelial tissue on gill arches and gill rakers. Hooked anodontine glochidia have been observed on gill arches (D'Eliscu 1972), but hookless lampsiline glochidia have heretofore been reported only on gill lamellae.

Glochidial release by *Villosa nebulosa* and *Lampsilis fasciola* corresponded with the presence of centrarchids in riffle habitat. Centrarchids remained in deep pools during fall and winter and were rarely collected over mussel beds during these seasons. Prevalence of infection frequencies among rock bass was highest in June, when this species was observed spawning in substrate inhabited by gravid *V. nebulosa*.

Behavioral mechanisms by which female mussels enhance successful attachment of glochidia have been largely unexamined. Female *L. fasciola* have a minnow-like mantle flap that is displayed during the period of glochidial release (Kraemer 1970). This mantle flap may serve to attract the predatory smallmouth bass; an attempted feeding response by this host may result in glochidial expulsion and subsequent infection. An analogy of this fish attraction behavior by *L. fasciola* is hypothesized for *V. nebulosa*. During the period of glochidial release, female *V. nebulosa* were commonly observed completely out of the substrate with valves gaping and foot extended. This behavior may serve to attract potential hosts and result in the release of glochidia when the females are disturbed by these fishes.

The direct relation between duration of the period of metamorphosis and water temperature in the present study corroborated that found in previous studies (Howard and Anson 1922). Metamorphosed juveniles were collected earlier and the drop-off period was shorter at higher temperatures. Duration of the transformation period at a given temperature also appeared distinct for each mussel species, as evidenced by the time difference between *V. vanuxemi* and *V. nebulosa* at 16.7°C.

The season when glochidia are obtained from lampsiline mussels has been suggested as a factor affecting duration of the attachment period. Corwin (1920) noted that glochidia of *Lampsilis luteola*, overwintering in female marsupia, metamorphosed much more rapidly than glochidia that had matured just before the infection

trials. Tedla and Fernando (1969) reported similar results with infections of *Lampsilis radiata* on yellow perch (*Perca flavescens*) at two different times. In our study, glochidia of *Medionidus conradicus* collected in June metamorphosed on darter hosts much sooner than did those collected in January or February. Spawning (gamete release) by *M. conradicus* occurs in early July (Zale and Neves 1982), and glochidia collected in June were therefore much older than those obtained in January or February.

Shedding of glochidia by nonsusceptible fishes was rapid and usually complete within several days. Most glochidia were sloughed off within 24 h of infection, although some remained attached for longer periods in most experiments. The shedding period for glochidia of *V. nebulosa* on redbreast sunfish and *Lampsilis fasciola* on rock bass and redbreast sunfish was inordinately long. This lengthy sloughing period on nonsusceptible centrarchids may be related to specific physiological or biochemical similarities within the Centrarchidae. The lengthy sloughing period for glochidia of *V. vanuxemi* on all three centrarchids may be indicative of the greater susceptibility of centrarchids to glochidial infections or the ontogeny of the *V. vanuxemi* – fish host relationship. The review by Fuller (1974) indicated that centrarchids are hosts of more than half of the mussels with known life histories. Reports of metamorphosis on sculpins and darters are rare by comparison, although several large percids (yellow perch and sauger, *Stizostedion canadense*) have been identified as hosts for a number of mussel species in the Mississippi River drainage.

Changes in the species composition and relative abundance of endemic fish fauna can result in the reproductive failure of mussel populations through loss of required fish hosts. It is evident that maintenance of game and nongame fish populations is critical to prevent further declines in mussel abundance and diversity. Fishing pressure and fishery management practices such as stocking, reclamation, and rough fish control may be having an indirect detrimental impact on mussel populations. River systems inhabited by mussels, particularly endangered species, should therefore be managed to retain their remaining endemic fish fauna, at least until appropriate fish hosts for successful reproduction are identified.

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