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Host Fishes and Host-attracting Behavior of Lampsilis altilis and Villosa vibex (Bivalvia: Unionidae)

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ABSTRACT.—Suitable host fishes were identified for two species of freshwater mussels (Unionidae) from the Coosa River drainage, Mobile Basin: *Lampsilis altilis*, the fine-lined pocketbook and *Villosa vibex*, the southern rainbow. Suitable hosts are defined as fishes that produce juvenile mussels from glochidial infestations in the laboratory. Larvae of both *L. altilis* and *V. vibex* transformed successfully on four species of sunfishes (Centrarchidae): *Lepomis cyanellus, Micropterus coosae, M. punctulatus* and *M. salmoides*. For both mussel species transformation success on *L. cyanellus* was highly variable and generally lower than on *Micropterus* spp. Gravid female *L. altilis* and *V. vibex* display highly modified mantle margin lures in the early spring. In addition to displaying mantle lures, *L. altilis* produce superconglutinates, similar to those recently described for three other species of *Lampsilis* in the southeastern U.S.

INTRODUCTION

The transition from glochidium to juvenile is a critical step in the life history of freshwater bivalves of the family Unionidae. In most species glochidia require a brief period as ectoparasites on the gills or fins of fishes to complete metamorphosis to juvenile mussels. Host specificity varies from generalists, able to complete metamorphosis on a taxonomically wide variety of fishes (Trdan and Hoeh, 1982), to specialists that use only a few, usually closely related, species (Zale and Neves, 1982; Yeager and Saylor, 1995). Freshwater mussels exhibit an array of adaptations that appear to increase the chances of glochidia encountering a fish (Kat, 1984) and these adaptations may target suitable host species, lowering the chances of infesting unsuitable species (Haag and Warren, 1998).

Most species in the closely related genera *Lampsilis* and *Villosa* (Lydeard *et al.*, 1996) for which hosts are known use large predaceous fishes as hosts (Zale and Neves, 1982; Waller and Holland-Bartels, 1988; Haag and Warren, 1997; Keller and Ruessler, 1997). During the period of glochidial release, females in these genera display highly developed mantle margins (Kraemer, 1970; Barnhart and Roberts, 1997) or release larvae in large attached packets (Haag *et al.*, 1995), both of which mimic small fishes or large invertebrates. These displays may elicit attacks from large predaceous fishes, increasing chances of successful infestation. Attempts to better understand this aspect of mussel reproduction are hampered because hosts for many species remain unknown and potential fish-attracting behaviors associated with glochidial release have been described for only a few species.

We determined suitable hosts and describe potential host-attracting behavior for *Lampsilis altilis* and *Villosa vibex*. *Lampsilis altilis* is endemic to the Coosa, Tallapoosa and Cahaba river drainages of the Mobile Basin, in Alabama, Georgia and Tennessee and is listed as threatened by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service, 1994). *Villosa vibex* occurs in Gulf Slope and South Atlantic Slope drainages from the Pearl River, Louisiana and Mississippi, to the Savannah River, Georgia and South Carolina (Clench and Turner, 1956). Hosts were heretofore unknown for both species; Keller and Ruessler (1997) report results of an unsuccessful attempt to determine hosts of *V. vibex*.

METHODS

Host fishes were determined by inducing glochidial infestations on a variety of fishes in laboratory trials and monitoring the rejection of glochidia or production of juvenile mussels. Our methods follow those described in Haag and Warren (1997) and are based on standard host-identification protocols (Zale and Neves, 1982). For both mussel species replicate trials (denoted A and B) were run using glochidia from two different gravid females (mean trial temperature 20 C, range 19–21 C). Fish species were chosen to represent most families, genera and all common species present at sites inhabited by the mussels.

Gravid female mussels were collected from Shoal Creek, Coosa River system, Cleburne County, Alabama, on 11 March 1997; water temperature was 18 C. Mussels were found by searching the stream bottom through a glass-bottomed bucket. When a displaying female was located observations were made on mantle shape, coloration and display behavior before disturbing the mussel. For each species, descriptions of displays are composites based on observations of several individuals in the field and later in the laboratory. We noted some interspecific variation among individuals but made no effort to quantify or characterize this variation. After making display observations, the mussel was removed from the substrate and checked for gravidity by holding the valves slightly open and noting whether or not the gills were charged with glochidia. Gravid mussels were wrapped in moist cloth and transported to the lab in an ice chest. In the laboratory, gravid females were held in aerated aquaria at 8 C to prevent release of glochidia before trials were initiated. Trials were initiated several days to three weeks after collecting mussels. Some females were placed in aquaria at 21 C with gravel and sand substrate for one to two days prior to trials to make further observations on displays. Glochidia were obtained by flushing water through the gills with a hypodermic syringe. All females were returned alive to Shoal Creek after yielding glochidia.

Shell height, length and hinge length of glochidia and transformed juveniles of both species from one female were measured to the nearest 0.01 mm using a binocular microscope and ocular-micrometer. Shell measurements follow the definitions of Clarke (1981) where height is the greatest dimension perpendicular to the hinge from the hinge to the ventral edge of the shell (equal to "depth" sensu Surber, 1912), and length is the greatest dimension across the shell parallel to the hinge line. Representative adult shells of each species are deposited at the Ohio State University Museum of Biological Diversity, Columbus, Ohio, and the Mississippi Museum of Natural History, Jackson, Mississippi. Mussel nomenclature follows Williams *et al.* (1993).

Potential host fishes were collected primarily from Mary's Creek, Coosa River system, in Cleburne County, Alabama. Additional fishes were collected from small streams in the Tallahatchie River system, Lafayette and Panola counties, Mississippi. *Micropterus salmoides* were obtained from hatchery stock. Potential host fishes were collected from streams without mussels or streams with low mussel densities in order to avoid using fish with existing glochidial infestations or acquired immunity to glochidia (Zale and Neves, 1982). Tables of fishes are listed phylogenetically by family (Mayden *et al.*, 1992) and alphabetically within families.

RESULTS

Host fishes.—Glochidia of *Lampsilis altilis* metamorphosed on four species of sunfishes (Centrarchidae): *Lepomis cyanellus, Micropterus coosae, M. punctulatus,* and *M. salmoides* (Table 1). In general, basses (*Micropterus* spp.) gave consistent results among trials and produced high to moderate numbers of juveniles. *Lepomis cyanellus* gave inconsistent results

TABLE 1.—Results of host trials for *Lampsilis altilis*. Letters A and B represent replicate trials using glochidia from two individual mussels. An asterisk (*) denotes that all fish died before termination of trial. A dash (—) denotes that the fish species was not used in the trial. *Lepomis cyanellus* appears under both host and nonhost headings, indicating that some individuals of this species served as host but others did not

	Number tested		Days to transformation (hosts) or rejection (non-hosts)		Mean number juveniles/fish	
Fish species	A	B	A	B	A	B
Hosts						
Lepomis cyanellus	2	5	12*	32	0	<1
Micropterus coosae	2	—	47–55	—	4	—
M. punctulatus	—	1	—	46–97	—	19
M. salmoides	1	2	51–81	41–99	114	297
Nonhosts						
Esox niger	—	1	—	<6		
Campostoma oligolepis	—	3	—	1–6		
Cyprinella callistia	4	—	3	—		
C. trichroistia	1	2	3	<6		
Luxilus chrysocephalus	—	1	—	<6		
Notropis asperifrons	3	—	3	—		
N. xaenocephalus	1	—	3	—		
Semotilus atromaculatus	—	2	—	14–18		
Hypentelium etowanum	2	1	3	2		
Aphredoderus sayanus	—	2	—	2		
Fundulus olivaceus	4	1	20–43	18–41		
F. stellifer	2	—	2	—		
Cottus carolinae	6	1	3	2		
Lepomis auritus	5	—	3	—		
L. cyanellus	2	5	12*	18–41		
L. gulosus	—	1	—	14		
L. macrochirus	—	4	—	6–18		
Etheostoma coosae	3	2	3	<6		
Percina nigrofasciata	5	3	3	2–6		

and produced extremely low numbers of juveniles. In trial B, most *L. cyanellus* individuals rejected all glochidia after 18–41 d, and only one individual produced juveniles. *Fundulus olivaceus* also retained glochidial infestations for extended periods (up to 43 d) but produced no juvenile mussels.

Glochidia of *Villosa vibex* metamorphosed on four species of sunfishes: *Lepomis cyanellus, Micropterus coosae, M. punctulatus* and *M. salmoides* (Table 2). *Micropterus coosae* and *M. punctulatus* produced high numbers of juveniles. *Micropterus salmoides* developed fungal infections during the trial. Two individuals died after carrying glochidia for 13 and 33 d; at the time of death both individuals carried heavy glochidial infestations. The two surviving individuals produced low numbers of juveniles. *Lepomis cyanellus* produced inconsistent results among trials. Individuals produced low to moderate numbers of juveniles in the first trial, but all individuals rejected glochidia in 21–43 d in the second trial. *Fundulus olivaceus, Ambloplites ariommus* and *Lepomis megalotis* also carried glochidial infestations for extended periods but produced no juvenile mussels.

TABLE 2.—Results of host trials for *Villosa vibex*. Letters A and B represent replicate trials using glochidia from two individual mussels. A dash (—) denotes that the fish species was not used in the trial. Not applicable (NA) appears for *Lepomis cyanellus* under both host and non-host headings, indicating that this species produced juveniles in trial A but not in trial B

	Number tested		Days to transformation (hosts) or rejection (non-hosts)		Mean number juveniles/fish	
Fish species	A	B	A	B	A	B
Hosts						
Lepomis cyanellus	2	3	40–44	NA	7	0
Micropterus coosae	1	—	48–88	—	38	—
M. punctulatus	2	—	40–134	—	61	—
M. salmoides	—	4	—	45–79	—	3
Nonhosts						
Esox niger	—	1	—	5		
Cyprinella callistia	3	—	3	—		
C. camura	—	8	—	2		
C. trichoistia	1	—	3	—		
Semotilus atromaculatus	2	2	3–4	2		
Hypentelium etowanum	—	1	—	2		
Noturus leptacanthus	—	2	—	2		
Fundulus olivaceus	2	4	20–48	13–21		
Cottus carolinae	3	1	3	4		
Ambloplites ariommus	2	—	12–42	—		
Lepomis auritus	2	—	12–20	—		
L. cyanellus	2	3	NA	21–43		
L. gulosus	—	2	—	5–13		
L. macrochirus	1	7	<12	5–13		
L. marginatus	—	7	—	5		
L. megalotis	5	—	12–62	—		
Etheostoma coosae	2	—	3–12	—		
E. nigrum	—	2	—	4		
E. raneyi	—	1	—	4		
E. whipplei	3	—	3	—		
Percina nigrofasciata	4	5	4	2		

Glochidia and juveniles of both species were similar to each other in size and shape and resembled other species of *Lampsilis* and *Villosa* (Surber, 1912; Hoggarth, 1988). Shells of newly transformed juveniles of both species were approximately the same size as glochidia. Glochidia of *L. altilis* had a mean height of 0.31 mm, mean length of 0.25 mm and mean hinge length of 0.12 mm (SE < 0.01, n = 8 for all). Newly transformed juveniles of *L. altilis* had a mean height of 0.30 mm, mean length of 0.24 mm and mean hinge length of 0.12 mm (SE < 0.01, n = 6 for all). Glochidia of *Villosa vibex* had a mean height of 0.31 mm, mean length of 0.25 mm and mean hinge length of 0.12 mm (SE < 0.01, n = 8 for all). Newly transformed juveniles of *V. vibex* had a mean height of 0.30 mm, mean length of 0.24 mm and mean hinge length of 0.11 mm (SE < 0.01, n = 3 for all).

Mantle displays.—Six of eight female *Lampsilis altilis* found were displaying mantle flaps on 11 March 1997. All displaying females were either oriented vertically with one half to one third of the shell exposed above the substrate or lay completely exposed on top of the

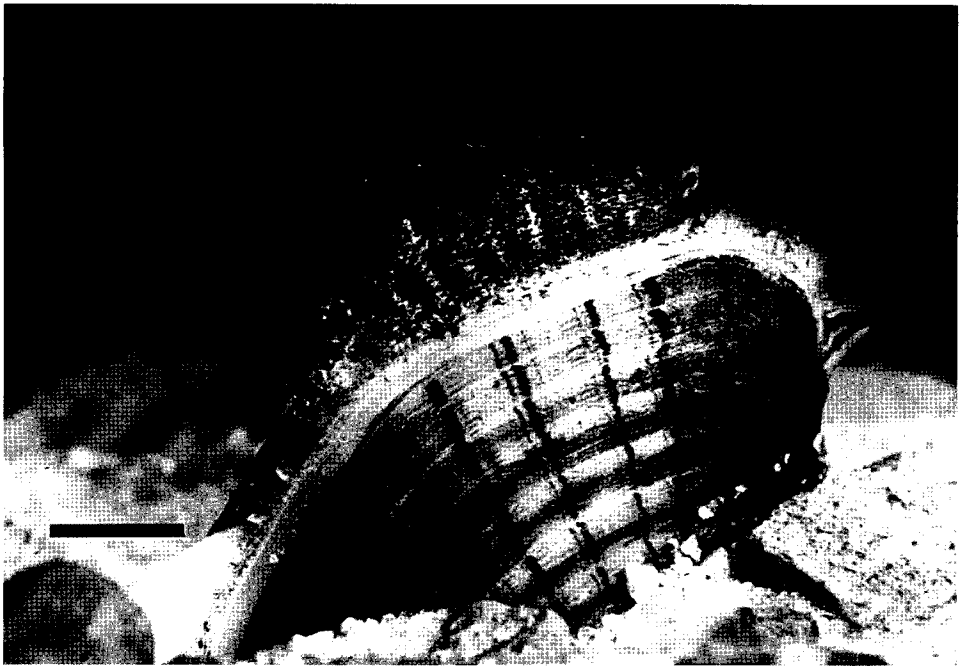

FIG. 1.—Gravid female *L. altilis* displaying mantle flaps in the laboratory. The individual was collected from Shoal Creek, Cleburne Co., Alabama on 11 March 1997. Scale bar = 1 cm

substrate with the ventral margin of the shell facing up. Two males were found, both were buried completely with only the siphons visible in the substrate. Mantle flaps of female *L. altilis* extended from a point immediately anterior to the incurrent siphon to a point ventral and opposite to the posterior end of the hinge ligament (Fig. 1). The margins of the flaps were ornamented with numerous long, fine, branched papillae. The flaps were largest and most highly branched at the anterior-most end, but were not drawn into long terete, free ends as in *L. cardium* (*see* Kraemer, 1970). In general, the shape of the flaps was similar to those figured for *L. fasciola* (Kraemer, 1970). Coloration of the outer surface of the flaps was dusky-gray with numerous fine, black spots and 6–8 distinct white bars oriented perpendicular to the shell margin. A distinct black eye-spot surrounded by a white halo was visible on the posterior-most end of the flap. The inner surface of the flaps was dusky gray with a row of black spots oriented parallel to the shell margin. All displaying females had fully gravid gills visible at, or above, the shell margin. In most individuals, flaps were pulsated rapidly in bursts lasting about 2–4 sec.

One female *Lampsilis altilis* was found producing a superconglutinate, a pair of packets that contains the entire glochidial contents of both gills and is tethered to the female by two hollow mucous strands (Haag *et al.*, 1995). The female was oriented vertically with about half of the shell length exposed above the substrate and was trailing a mucous strand about 40 cm long. The glochidial packets were deposited at the end of the transparent strands which had not yet separated into two strands. The packets were generally fusiform but bluntly rounded at the anterior end and slightly rounded at the posterior end. Coloration was creamy to dirty-white with a dusky stripe dorsally. Eye-spots were lacking on the

FIG. 2.—Gravid female *V. vibex* displaying mantle margins in the laboratory. The individual was collected from Shoal Creek, Cleburne Co., Alabama on 11 March 1997. Scale bar = 1 cm. Photo (©) 1997 Lynda Richardson

packets in contrast to those of *L. perovalis* (Haag *et al.,* 1995). Another female, similarly oriented in the substrate, trailed a short length of mucous strand (about 20 cm); the glochidial packets apparently were torn away, or otherwise detached. Neither female was displaying mantle flaps while producing superconglutinates or mucous strands, but in both, well-developed mantle flaps, similar to those seen in displaying females, were visible lying retracted, anterior to the siphons. Two detached superconglutinates were found snagged on woody debris in the stream, but the females that produced them were not identified.

Thirteen fully gravid female *Villosa vibex* were found on 11 March 1997, ten were displaying mantle lures. Seven of the displaying females lay completely exposed on top of the substrate but were on their sides, in contrast to *Lampsilis altilis.* The other three were also unburied but lying under the edge of large flat rocks. Twenty males were found, one lying on top of the substrate similar to the females, the remaining 19 were buried completely with only the siphons exposed. The modified female mantle extended from a point immediately anterior to the incurrent siphon to a point directly ventral and opposite to the posterior-most end of the hinge ligament (Fig. 2). The mantle margins were ornamented with approximately 15 pairs of unbranched tentacle-like papillae about 15 mm in length that were thick at the base but tapered to a fine point. The papillae were bound along the basal one third of their length by a thin sheath of tissue. Coloration of the papillae was inky black or rusty orange with numerous fine black spots. The outer surface of the sheath varied in color among individuals from inky black to tan with numerous irregular black spots. The inner surface of the sheath was rusty orange with numerous irregular black spots.

All females had fully gravid gills visible just below the shell margin. Papillae were pulsated rapidly and actively similar to the manner of *L. altilis*.

DISCUSSION

Host fish use for both *Lampsilis altilis* and *Villosa vibex* was restricted to fishes of the family Centrarchidae. However, consistent transformation of glochidia occurred only on *Micropterus* spp. Some infestations on sunfishes (*Lepomis* spp.) produced low numbers of transformed juveniles. In most cases, however, glochidia were rejected by *Lepomis* spp. in less than three wk, or glochidial infestations were carried for extended periods but resulted in no transformed juveniles. *Lepomis* may be only marginally suitable as hosts for these mussel species. Exceptions to this pattern of host use in *Lampsilis* and *Villosa* are documented for at least two species (*V. vanuxemensis* using *Cottus* spp., Zale and Neves, 1982; Neves *et al.*, 1985; *L. reeviana* using *Cottus, Micropterus* and *Lepomis,* Barnhart and Roberts, 1997). In general, however, primary host suitability of *Micropterus* spp. and marginal host suitability of *Lepomis* spp. is a trait shared by many species of *Lampsilis* and *Villosa,* including *L. fasciola* (Zale and Neves, 1982), *L. higginsi* (Waller and Holland-Bartels, 1988), *L. perovalis* (Haag and Warren, 1997), *L. rafinesqueana* (Barnhart and Roberts, 1997), *L. siliquoidea* and *L. straminea claibornensis* (Keller and Ruessler, 1997), *V. iris* (Zale and Neves, 1982, as *V. nebulosa*) and *V. nebulosa* (Haag and Warren, 1997).

In addition to sunfishes, topminnows (*Fundulus olivaceus*) may serve as marginal hosts for *Lampsilis altilis* and *Villosa vibex.* Although infestations on topminnows produced no juveniles, glochidial infestations were carried for extended periods in most trials. Several species in the Fundulidae and Poeciliidae serve as marginal hosts for a wide variety of mussel species (reviewed in Haag and Warren, 1997).

Displays of gravid female *Lampsilis* and *Villosa* likely act as lures that attract suitable host species. The modified mantles of females of most species in these genera strongly resemble small fishes, large terrestrial insects, or other large invertebrates, items which comprise the bulk of the diet of centrarchid fishes in streams (Carlander, 1977). Further, these lures may reduce the chances of glochidia infesting a non-suitable fish species. Few other fishes in southeastern streams regularly eat large prey items such as those mimicked by these mussel species, and the few that do may serve as hosts for some species of *Lampsilis* (*e.g.*, Esocidae and large Percidae, Waller and Holland-Bartels, 1988). An extreme example of prey mimicry to attract specific host fishes is found in the production of superconglutinates by some *Lampsilis* species.

Three North American unionid species (*Lampsilis australis, L. perovalis* and *L. subangulata*) have been identified as producing superconglutinates (Haag *et al.*, 1995; O'Brien *et al.*, 1997). We confirm superconglutinate production in another species, *Lampsilis altilis.* This species was suspected to produce superconglutinates because of gravid gill morphology similar to other superconglutinate producers (P. Hartfield, U.S. Fish and Wildlife Service, Jackson, Mississippi, pers. comm.). Our observations bring the total number of known superconglutinate producers to four; two species in the Mobile Basin (*L. altilis* and *L. perovalis*), one in the Escambia, Yellow and Choctawhatchee river systems (*L. australis*) and one in the Apalachicola and Ochlockonee river systems (L. *subangulata*). No other species are known to have gill morphology similar to these species, thus superconglutinate production is apparently a shared unique character within these four taxa.

Lampsilis altilis is unusual in having and displaying a well-developed mantle lure in addition to producing a superconglutinate. Potentially, this species may attract and infest host fishes using both strategies known for *Lampsilis.* Other superconglutinate producers have modified mantle margins that may be rhythmically undulated during the breeding season

(Hartfield and Butler, 1997). However, these mantle flaps are greatly reduced relative to those seen in other, nonsuperconglutinate producing species of *Lampsilis*, and the "display" is inconspicuous and probably does not serve to attract a host fish. The retention of the mantle flap lure in *L. altilis* may be interpreted as a shared primitive attribute among the lampsiline clade (sensu Lydeard *et al.*, 1996). We hypothesize that the reduction of mantle flap lures in the other three species is associated with increased specialization for infecting host fishes via superconglutinates. The function and origin of these modified mantle structures and other apparent mechanisms for infesting host fishes will be better understood when viewed in the context of explicit testable phylogenies.

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