J. N. Am. Benthol. Soc., 2003, 22(1):78–91

Host fishes and infection strategies of freshwater mussels in large Mobile Basin streams, USA

WENDELL R. HAAG[1] AND MELVIN L. WARREN, JR.

USDA Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research,
1000 Front Street, Oxford, Mississippi 38655 USA

Abstract. We investigated host fishes, timing and modes of glochidial release, and host-attraction strategies for 7 species of freshwater mussels from the Buttahatchee and Sipsey rivers (Mobile Basin), Alabama and Mississippi, USA. We determined hosts as fish species that produced juvenile mussels from laboratory-induced glochidial infections. We established the following primary mussel/host relationships: *Elliptio arca* with *Etheostoma artesiae* and *Percina nigrofasciata*; *Fusconaia cerina* with 6 species of minnows (Cyprinidae); *Lampsilis ornata* with *Micropterus salmoides*; *Medionidus acutissimus* with 8 species of darters (Percidae); *Obovaria unicolor* with *Ammocrypta beani*, *A. meridiana*, and *Etheostoma artesiae*; *Pleurobema decisum* with *Cyprinella venusta*; and *Quadrula asperata* with *Ictalurus punctatus*. For most mussel species, host use was similar to that of closely related species, indicating that, in general, this trait is highly conserved at the generic level. Four mussel species used host-attraction strategies that targeted their specific host fish. *Fusconaia cerina* and *P. decisum* released glochidia in conglutinates that elicited feeding responses from fishes in the field and in the laboratory. Gravid female *Lampsilis ornata* and *M. acutissimus* displayed mantle lures. Host-attraction strategies were less apparent for *E. arca* and *Q. asperata*, but these species released glochidia in association with copious mucous secretions, which may serve to entangle fishes, facilitating host infection. No host-attraction strategy was apparent for *O. unicolor*.

Key words: host-parasite relationship, life history, Unionidae, Bivalvia, mussels, glochidia, Mobile Basin.

The southeastern United States supports the most diverse freshwater mussel fauna on earth. This fauna also is distinguished as one of the most endangered groups of organisms in North America (Neves et al. 1997). The basic life histories of many southeastern mussel species are poorly known. To complete development, larvae (glochidia) of most mussel species must undergo a brief period as ectoparasites on the gills or fins of fishes. Host specificity ranges from generalists, able to parasitize a wide variety of fishes, to specialists, whose glochidia can develop on only a few, usually closely related fish species (Haag and Warren 1997). Larvae encountering an unsuitable host are rejected by the fish immune system (O'Connell and Neves 1999). Many species display remarkable adaptations to facilitate transmission of glochidia to hosts, including display of lures and release of glochidia in packets that mimic food items of host fishes (e.g., Barnhart and Roberts 1997, Haag and Warren 1999, Watters 1999, Jones and Neves 2002). Knowledge of host fishes, host-attraction strategies, and other aspects of reproductive biology is lacking or incomplete for many North American mussel species. This lack of knowledge hampers conservation efforts and limits our understanding of the ecology of these animals.

The Mobile Basin of Alabama, Georgia, Mississippi, and Tennessee is home to a unique, highly endangered mussel fauna including a large number of endemic species (Stansbery 1976, Lydeard and Mayden 1995). The Buttahatchee and Sipsey rivers support the best remaining examples of large-stream Mobile Basin mussel communities. Host information exists for a number of headwater species in the Mobile Basin (Haag and Warren 1997, Haag et al. 1999), but hosts are unknown for most large-stream species in the basin.

We investigated host fishes, timing and modes of glochidial release, and host-attraction strategies for 7 species of mussels from the Buttahatchee and Sipsey rivers: Alabama spike (*Elliptio arca*), Gulf pigtoe (*Fusconaia cerina*), southern pocketbook (*Lampsilis ornata*), Alabama moccasinshell (*Medionidus acutissimus*), Alabama hickorynut (*Obovaria unicolor*), southern clubshell (*Pleurobema decisum*), and Alabama orb (*Quadrula asperata*). With the exception of *F. cerina* and *L. ornata*, all of these species are endemic

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[1] E-mail address: whaag@fs.fed.us

to the Mobile Basin. *Fusconaia cerina* also occurs in the Amite, Pearl, and Pascagoula rivers (Williams and Fradkin 1999), and *L. ornata* is endemic to Gulf of Mexico drainages from the Amite River east to the Escambia River (Williams and Butler 1994). The US Fish and Wildlife Service recognizes *P. decisum* and *M. acutissimus* as endangered and threatened, respectively. The American Fisheries Society considers *E. arca* threatened, and *L. ornata, O. unicolor,* and *Q. asperata* species of special concern (Williams et al. 1993). Along with 2 other species not studied here (*Quadrula rumphiana* and *Tritogonia verrucosa*), these 7 species dominate mussel communities in the Buttahatchee and Sipsey rivers (WRH and MLW, unpublished data).

Methods

We determined host fishes by inducing glochidial infestations in laboratory trials and monitoring the rejection of glochidia or production of juvenile mussels. Our methods were described by Haag and Warren (1997) and are based on a standard host-identification protocol (Zale and Neves 1982). We identified primary host-fish species as those that consistently produced live juvenile mussels. We identified unsuitable host-fish species as those in which all mussel glochidia were rejected from all individual fishes without producing juvenile mussels. In some cases, some individuals of a particular fish species rejected all glochidia, but others produced juvenile mussels. Because of inconsistent glochidial transformation, we regarded these fish species as marginal hosts. For each mussel species, we ran 2 to 4 replicate trials (20–22°C), using glochidia from a different female in each trial. We exposed glochidia from each mussel species to 15 to 34 fish species (l-10 individuals of each). We chose fish species to represent most families and genera and all common species present at study sites (Boschung 1989).

We collected gravid female mussels from the Buttahatchee River, Monroe Co., Mississippi and the Sipsey River, Pickens/Greene Co., Alabama in June and July 1998 and 2001. Both streams are large tributaries of the Tombigbee River (Mobile Basin). Water temperature at the time of collection was 22 to 30°C. We collected mussels by diving and, in shallow areas, by searching the stream bottom using a glass-bottomed bucket. We assessed reproductive status of each individual by gently prying apart the valves and examining the gills. We recognized gravid females by the presence of distended gills. We immediately returned male and non-gravid specimens to the stream. We brought gravid mussels into the laboratory and placed them into individual, aerated beakers at room temperature (21–25°C). Most individuals of *E. arca, F. cerina, P. decisum,* and *Q. asperata* released glochidia into the beakers within 24 to 48 h; we used these glochidia in host trials immediately upon release. *Lampsilis ornata, M. acutissimus,* and *O. unicolor* did not release glochidia in the laboratory. With the exception of *P. decisum* and *M. acutissimus,* we harvested glochidia from individuals that did not release in the laboratory by sacrificing the animal and dissecting the gills. Wc harvested glochidia from *M. acutissimus* by flushing the contents of the gills into a beaker using a hypodermic syringe and aged tap water. Because of their federal conservation status, *M. acutissimus* and *P. decisum* were released alive where they were collected within 7 d of collection. We worked with these 2 species under US Fish and Wildlife Service Endangered Species Subpermitee Authorization Number SA-98-06, Mississippi Department of Wildlife, Fisheries, and Parks Scientific Collecting Permit, and Alabama Department of Conservation Scientific Collecting Permit Number 182.

We based descriptions of gravid periods on a composite of field observations from 1996, 1998, 2000, and 2001; we based descriptions of host-attraction strategies and glochidial release on field and laboratory observations from the same period. We classified species into 1 of 2 categories, short-term or long-term brooders, based on the duration and timing of the gravid period (Kat 1984). We used glochidia from gravid female mussels from the following localities and dates in host-identification trials (trials are identified as A, B, C, or D): Alabama-Sipsey River, Pickens-Greene Co.: *E. arca,* A, 6 July 1998, B, 27 June 2001; *F. cerina,* A, 10 June 1998, B, 8 July 1998, C, 29 July 1998; *L. ornata,* A and B, 6 July 1998; *O. unicolor,* A, 17 June 1998, B, 26 June 1998, C and D, 27 June 2001; *P. decisum,* A, 14 July 1998, B, 29 July 1998, D, 3 July 2001; *Q. asperata,* A, 26 June 1998, B, 14 July 1998; Mississippi-Buttahatchee River, Monroe Co.: *F. cerina,* D, 22 June 2001; *L. ornata,* C and D, 28 June 2001; *M. acutissimus,* A, 21 June 2001, B, 28 June 2001; *Q. asperata,* C, 22 June 2001. We de-

TABLE 1. Results of host trials for *Elliptio arca.* Letters A and B represent replicate trials using glochidia from 2 different female mussels. Sample size (*n*) is either the number of fish that produced juvenile mussels or the number of fish that rejected all glochidia and produced no juvenile mussels. = the fish species was not used in the trial. na = not applicable.

	Mean no. juveniles/fish (II)			
	Days to transformation		Days to rejection (n)	
Fishes'	A	B	A	B
Hosts				
Percina nigrofasciata	8 (3) 19–29	9 (3) 22-35	na (0)	na (0)
Etheostoma artesiae	5 (2) 15–19	—	na (0)	—
Marginal hosts				
Ammocrypta meridiana	—	3 (1) 33	—	4 (1)

Fish species (number of trials, mean number of fish per trial, range of days to rejection) that did not produce juvenile mussels: *Campostoma oligolepis* (1, 3, 2), *Cyprinella venusta* (2, 4.5, 2–20), *Luxilus chrysocephalus* (1, 4, 2–7), *Lythrurus bellus* (1, 4, 4), *L. umbratilis* (1, 2, 2), *Notemigonus crysoleucas* (2, 3, 2–7), *Notropis ammophilus* (2, 3.5, 2–4), *N. atherinoides* (1, 2, 2–20), *N. baileyi* (1, 2, 2–7), *N. stilbius* (1, 3, 4), *N. volucellus* (1, 2, 2), *Pimephales notatus* (1, 4, 2), *Ictiobus bubalus* (1, 2, 2), *Ictalurus punctatus* (2, 2, 2–5), *Noturus leptacanthus* (1, 2, 2–14), *Lepomis cyanellus* (2, 2, 5-14), *L. macrochirus* (1, 2, 7–14), *L. megalotis* (2, 2.5, 2–7), *Micropterus salmoides* (2, 3, 7–19), *Ammocrypta beani* (1, 2, 4), *Etheostoma rupestre* (2, 2, 2–4), *E. stigmaeum* (1, 3, 4–19)

posited voucher specimens of all species at the Mississippi Museum of Natural Science (MMNS), Jackson, Mississippi and the Illinois Natural History Survey, Champaign, Illinois.

We collected most potential host fishes from the following streams in the western Mobile Basin: **Alabama-Clear** Creek (Black Warrior River system), Winston **Co.; Mississippi-Bull** Mountain Creek (Tombigbee River system), Itawamba Co.; Noxubee River (Tombigbee River system), Winston Co.; Hashaqua Creek (Tombigbee River system), Noxubee Co. We augmented fish collections with specimens from the following streams: **Alabama-Cedar Creek** (Tennesee River system), Franklin **Co.; Mississippi-Goodwin** Creek (Yazoo River system), Panola Co.; Lee Creek (Yazoo River system), Lafayette Co.; and Little Tallahatchie River (Yazoo River system), Lafayette Co. We collected all fishes from stream sites without mussels or with low mussel densities to avoid using fish with pre-existing glochidial infestations or acquired immunity to glochidia (Zale and Neves 1982). We obtained *Ictalurus punctatus, Micropterus salmoides,* and *Notemigonus crysoleucas* from hatchery stock. We maintained all fishes in aerated aquaria in the laboratory and fed them bloodworms (minnows, darters, madtoms), earthworms and minnows (sunfishes), and pelletized fish food (channel catfish).

Results

Elliptio arca

Elliptio arca is a short-term brooder and was gravid from late spring to early summer. We observed gravid female E. *arca* from 28 May to 28 July and mature glochidia from 27 June to 28 July. In the laboratory, mature glochidia were released freely and were not contained in conglutinates. Some glochidia were released in small clusters that disassociated quickly after release. Copious mucus was released with mature glochidia, and many glochidia were bound in this mucus. Long strands of mucus often issued from the excurrent siphon of releasing females. Immature glochidia and eggs were released in irregular clusters, which conformed loosely to the shape of the gill water tubes. These clusters resembled true conglutinates (see *F. cerina*) but lacked a regular, cohesive shape, and never contained mature glochidia.

Glochidia of E. *arca* transformed consistently on only 2 darter species (Percidae): *Etheostoma artesiae* and *Percina nigrofasciata* (Table 1). Glo-

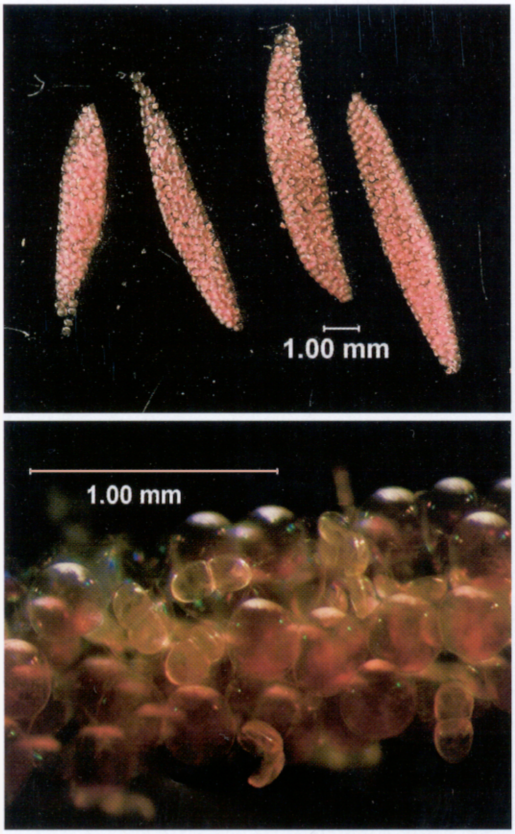

FIG. 1. Conglutinates of *Fusconaia cerina* from the Buttahatchee River, Monroe Co., Mississippi. Conglutinates in the top panel contain developing embryos. The bottom panel shows detail of a conglutinate with mature glochidia. Round bodies are undeveloped eggs.

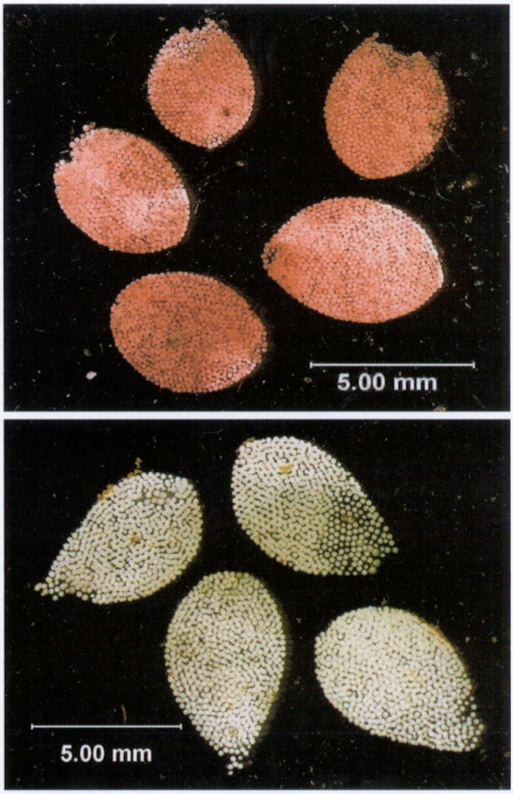

FIG. 2. Conglutinates of *Pleurobema decisum* from 2 different females from the Buttahatchee River, Monroe Co., Mississippi, showing color variation.

chidia transformed inconsistently on *Ammocrypta meridiana*. Three darter species were unsuitable hosts. Nineteen other fish species, representing the families Catostomidae, Centrarchidae, Cyprinidae, and Ictaluridae, were unsuitable hosts for *E. arca* (Table 1).

Fusconaia cerina

Fusconaia cerina is a short-term brooder and was gravid from late spring to early summer. We observed gravid female *F. cerina* from 28 May to 28 July and mature glochidia from 8 June to 28 July. In the laboratory, both immature and mature glochidia were released in well-formed conglutinates of consistent shape (Fig. 1, top panel). Conglutinate shape was maintained by strong cohesion among undeveloped eggs, which constituted a large portion of each conglutinate; developing propagules were scattered throughout the resulting matrix (Fig. 1, bottom panel). Egg membranes of developing glochidia degenerated upon maturity and, when slight pressure was exerted on the conglutinate with forceps, mature glochidia were propelled readily from the conglutinate matrix. Conglutinate color varied among, but not within, individuals and was pink, orange, or white.

In the field, we frequently observed gravid female *F. cerina* releasing conglutinates. Releasing females were buried just under the surface of gravel substrates with only the siphons visible. Conglutinates were forcibly ejected by the female in groups of 10 to 20 and were propelled upward ~15 to 20 cm into the water column, where they drifted with the current, well above the bottom. We commonly saw drifting conglutinates in the mid-water column and observed schools of blacktail shiners, *Cyprinella venusta,* repeatedly approaching drifting conglutinates. Because of the fishes' rapid movements, we could not discern whether shiners ingested conglutinates; in most cases, the fishes approached conglutinates very closely and then veered off just before, or at, the moment of contact. If shiners did ingest conglutinates, contact was brief, and conglutinates were expelled quickly. In the laboratory, we presented conglutinates to minnows *(C. venusta, Nocomis leptocephalus,* and *Notropis ammophilus),* darters *(Etkeostoma rupestre* and *Percina sciera),* and sunfish (*Lepomis macrochirus*). All fish species responded to the presence of conglutinates by repeatedly approaching them closely as observed in the field, but again, in most cases, we could not discern if individuals ingested conglutinates. We observed an individual of *E. rupestre* ingest and expel a conglutinate 3 times in rapid succession.

Glochidia of *F. cerina* transformed on a wide variety of minnow species (Cyprinidae) (Table 2). Glochidia transformed consistently on 6 minnow species and inconsistently on 6 additional minnow species. Five minnow species were unsuitable hosts. Fourteen other fish species, representing the families Catostomidae, Centrarchidae, Ictaluridae, and Percidae, were unsuitable hosts for *F. cerina* (Table 2).

Lampsilis ornata

Lampsilis ornata is a long-term brooder and was gravid from late summer to late spring of the following year. We found gravid individuals throughout most of the year with the exception of July to September when most females were spent. *Lampsilis ornata* did not release glochidia in the laboratory. Gravid females displayed a large mantle lure that we observed in the laboratory and in the field. The lure consisted of a pair of elongated flaps ~50 to 75 mm long, which protruded beyond the shell margin, with the gravid gills visible between the flaps. Each flap was cream colored with a distinct eyespot and a dark, lateral stripe, and flaps were pulsated vigorously during display. The lure and display behavior closely resembled that described for *L. cardium* (Kraemer 1970, Haag and Warren 1999).

Glochidia of *L. ornata* transformed only on largemouth bass, *Micropterus salmoides* (Centrarchidae) (Table 3). Four centrarchid species were unsuitable hosts. Ten other fish species, representing the families Catostomidae, Cyprinidae, Esocidae, Ictaluridae, and Percidae, were unsuitable hosts for *L. ornata* (Table 3).

Medionidus acutissimus

Medionidus acutissimus is a long-term brooder and was gravid from approximately October to June of the following year. By late May, gills of most females had only 2 to 3 gravid water tubes (fully charged gills have -3040 gravid water tubes). Most females were spent from early June to October. Females did not release glochidia in the laboratory. We observed several gravid females in the Sipsey and Buttahatchee rivers displaying small, black modified mantle margins. When displaying, females were widely agape and completely unburied but were often lying within the interstices of coarse gravel or cobble substrates in swift currents. Females usually were tethered to a pebble by a byssal thread. We observed displaying individuals in a variety of orientations with the dorsal margin facing up, the ventral margin facing up, or lying on their side. The modified portion of the mantle extended along the ventral margin of the shell from the posterior tip to slightly anterior of the midpoint of the shell. The modified mantle was matte, inky black with a small (-2 mm^2), white patch located at about the midpoint of the shell, near the anterior-most portion of the modified mantle margin. The white patch flickered rapidly at -1 s intervals; the motion was similar to the flickering of a television screen. With the exception of the flickering mantle patch, displaying females appeared moribund and showed little response to handling. Females remained widely agape when removed from the water, and did not attempt to close the shell or retract the mantle margins. The flickering motion of the white patch often continued for 15 s or more after being removed from the water. These behaviors were not observed in the laboratory.

Glochidia of *M. acutissimus* transformed on a wide variety of darter species (Percidae) (Table 4). Glochidia transformed consistently on 8 darter species. Another darter species, *E. rupestre,* was a marginal host. No darter species were identified as unsuitable hosts. Seven fish species, representing the families Centrarchidae, Cyprinidae, and Ictaluridae, were unsuitable hosts for *M. acutissimus* (Table 4).

TABLE 2. Results of host trials for *Fusconaia cerina.* Letters A to D represent replicate trials using glochidia from 4 different female mussels. Sample size (*n*) is either the number of fish that produced juvenile mussels, or the number of fish that rejected all glochidia and produced no juvenile mussels. * = all fish died before completion of the trial. — = the fish species was not used in the trial. na = not applicable.

	Mean no. juveniles/fish (*n*)							
	Days to transformation				Days to rejection (I)			
Fishes’	A	B	C	D	A	B	C	D
Hosts								
Cyprinella callistia		2 (1) 15	—	6 (4) 24-32	—	na (0)	—	na (0)
C. venusta	*	2 (2) 19-21	15 (7) 19-26	22 (1) 24	*	na (0)	na (0)	na (0)
Hybopsis winchelli				1 (1) 20				na (0)
Luxilus chrysocephalus	*	1 (3) 19-21	0* (3) 15	3 (3) 24-31	*	na (0)	na (0)	na (0)
Lythrurus bellus	—	—	—	2 (3) 27-31	*		—	na (0)
Notemigonus crysoleucas	*		2 (4) 14-21	1 (1) 18-27	*		na (0)	na (0)
Marginal hosts								
Campostoma oligolepis	*	0 (0) na	2 (3) 14–16	1 (4) 18-27	*	2 (4)	5-7 (2)	3 (1)
Nocomis leptocephalus	0 (0) na	0 (0) na	1* (1) 14	2 (1) 18	2-5 (l)	5 (2)	na (0)	3 (1)
Notropis ammophilus	0 (0) na	0 (0) na	4 (3) 14–19	1 (2) 20-24	2 (2)	2-14 (3)	13 (1)	3 (1)
N. atherinoides	—	1 (1) 21		0 (0) na	—	2 (2)		3 (1)
N. stilbius				2 (3) 18-26		—	—	3-6 (2)
Pimephales notatus	*	0 (0) na	1* (3) 14	—	*	2-20 (3)	12 (1)	

Fish species (number of trials, mean number of fish per trial, range of days to rejection) that did not produce juvenile mussels: *Hybognathus nuchalis* (2, 1, 5–18), *Notropis baileyi* (2, 4.5, 1–12), *N. texanus* (1, 5, 2), *N. volucellus* (2, 3, 2–3), *Pimephales vigilax* (7, 3, 3), *Ictiobus bubalus* (1, 2, 2), *Ameiurus natalis* (1, 2, 5), *Ictalurus punctatus* (2, 3, 3–5), *Noturus leptacanthus* (1, 3, 5), *Lepomis cyanellus* (1, 3, 2–5), *L. macrochirus* (2, 2.5, 2–12), *L. megalotis* (3, 2.3, 2-3), *Micropterus salmoides* (3, 2.5, 2–7), *Pomoxis annularis* (1, 1, 5), *Etheostoma artesiae* (2, 3, 5–7), *E. rupestre* (3, 4.3, 1–7), *E. stigmaeum* (1, 3, 3), *Percina nigrofasciata* (2, 3.5, 2–18), *P. sciera* (1, 2, 2-7)

Obovaria unicolor

Obovaria unicolor is a long-term brooder and was gravid from approximately August to June of the following year. Glochidial release took place from April to June. We observed fully gravid and partially spent females from April to early June. After 8 June, we found only partially spent individuals and, after 26 June, all females were completely spent. By late August, we found gravid females that were brooding embryos. We observed gravid females with mature glochidia by November. Females did not release glochidia in the laboratory, and we observed no mantle displays in the field or laboratory.

Glochidia of O. *unicolor* transformed consistently on 3 darter species (Percidae) and inconsistently on 4 additional darter species (Table 5). Six darter species were unsuitable hosts. Twenty other fish species, representing the families Catostomidae, Centrarchidae, Cyprinidae, Esocidae, and Ictaluridae, were unsuitable hosts for *O. unicolor* (Table 5).

TABLE 3. Results of host trials for *Lampsilis ornata.* Letters A to D represent replicate trials using glochidia from 4 different female mussels. Sample size (M) is either the number of fish that produced juvenile mussels, or the number of fish that rejected all glochidia and produced no juvenile mussels. * = all fish died before completion of the trial. na = not applicable.

	Mean no. juveniles/fish (*n*)							
	Days to transformation				Days to rejection (I)			
Fishes’	A	B	C	D	A	B	C	D
Host								
Micropterus salmoides	3 (3) 39–57*	2 (3) 54*	12 (4) 42-81	6 (4) 39–94	na (0)	na (0)	na (0)	na (0)

Fish species (number of trials, mean number of fish per trial, range of days to rejection) that did not produce juvenile mussels: Esox *americanus (1,* 1, 2), *Campostoma oligolepis* (2, 2, 2), *Cyprinella venusta (2, 3,* 2), *Notemigonus crysoleucas* (2, 3, 2), *Notropis ammophilus (2,* 3, 2), *Pimephales notatus (2, 3,* 2), *Ictiobus bubalus (1, 2,* 2), *Ictalurus punctatus (2, 2,* 2), *Ambloplites ariommus* (1, 2, 2-l 4), *Lepomis cyanellus* (3, 1.6, 2–14), *L. macrochirus* (4, 3, 2–22), *L. megalotis* (4, 3.3, 2–15), *Etheostoma rupestre* (2, 3, 2), *Percina nigrofasciata* (2, 2, *2)*

TABLE 4. Results of host trials for *Medionidus acutissimus.* Letters A and B represent replicate trials using glochidia from 2 different female mussels. Sample size (M) is either the number of fish that produced juvenile mussels, or the number of fish that rejected all glochidia and produced no juvenile mussels. * = all fish died before completion of the trial. = the fish species was not used in the trial. na = not applicable.

	Mean no. juveniles/fish (M)			
	Days to transformation		Days to rejection (n)	
Fishes’	A	B	A	B
Hosts				
Ammocrypta beani	13 (2) 28-51	0 (4) 25*	na (0)	na (0)
A. meridiana	4 (2) 32–38*		na (0)	
Etheostoma nigrum	3 (2) 32–34*		na (0)	–
E. stigmaeum	2 (5) 32-45	0 (3) 35*	na (0)	na (0)
E. swaini	19 (1) 32-51	2 (2) 52	na (0)	na (0)
E. artesiae	20 (1) 3842	–	na (0)	
Percina nigrofasciata	9 (3) 2545	2 (5) *31”*	na (0)	na (0)
P. vigil	36 (1) 38–65	–	na (0)	
Marginal hosts				
Etheostoma rupestre	2 (1) 25-38	0 (1) 31*	7 (2)	4 (2)

Fish species (number of trials, mean number of fish per trial, range of days to rejection) that did not produce juvenile mussels: *Cyprinella venusta* (7, 4, 2–4), *Notemigonus crysoleucas* (1, 2, 4), *Ictalurus punctatus (1, 4,* 4), *Lepomis cyanellus (2, 1,* 4–7), *L. macrochirus (2, 2, 4-1* 1), *L. megalotis (2, 1,* 4–11), *Micropterus salmoides (1, 3, 7)*

TABLE 5. Results of host trials for *Obovaria unicolor.* Letters A to D represent replicate trials using glochidia from 4 different female mussels. Sample size (n) is either the number of fish that produced juvenile mussels, or the number of fish that rejected all glochidia and produced no juvenile mussels. * = all fish died before completion of the trial. = the fish species was not used in the trial. na = not applicable.

	Mean no. juveniles/fish (n)							
	Days to transformation				Days to rejection (I)			
Fishes'	A	B	C	D	A	B	C	D
Hosts								
Ammocrypta beani			2 (3) 21–53*	3 (6) 20–24*	—	—	na (0)	na (0)
A. meridiana	—	—	***2 (3)*** ***21-37"***	0 (5) 11*	—		na (0)	na (0)
Etheostoma artesiae	3 (2) 18-22	10 (3) 2141	3 (1) 18-26	—	na (0)	na (0)	na (0)	—
Marginal hosts								
Etheostoma nigrum	—		0 (25)* na	0 (0)			na (0)	11 (1)
E. swaini		0 (0) na	0 (0) na	1 (1) 24	—	6 (1)	11 (2)	11 (1)
I? nigrofasciata	1 (1) 22	0 (0) na	8 (1) 26-28	2 (1) 24	11-19 (6)	6-14 (3)	9-11 (3)	11-18 (7)
P. sciera	0 (0) na	1 (1) 23	0 (0) na	—	19-22 (3)	23 (1)	11 (1)	—

[1] Fish species (number of trials, mean number of fish per trial, range of days to rejection) that did not produce juvenile mussels: *Esox americanus (1,* 1, 4), *Campostoma oligolepis* (2,3,2), *Cyprinella venusta (2,* 3, 2), *Luxilus chrysocephalus* (2, 2.5, 2), *Notemigonus crysoleucas (1, 3,* 2), *Notropis ammophilus* (3, 4, 2–5), *N. atkerinoides* (1, 2, 2), N. *stilbius* (2, 2, 4–5), *N. texanus* (1, 2, 2), N. *volucellus* (I, 2, 2), *Pimephales notatus* (2, 4.5, 2), I? *vigilax* (1, 1, 2), *Ictiobus bubalus* (1, *3,* 2), *Ameiurus natalis* (1, 1, 2), *Ictalurus punctatus (2, 7.5,* 2), *Noturus leptacanthus* (1, 2, 2), *Lepomis cyanellus* (1, *2,* 11), *L. macrochirus (3,* 2.6, 2–11), *L. megalotis* (3, 2.6, 2–11), *Micropterus salmoides* (3, 2.6, 6–11), *Etheostoma caeruleum* **(1,** 1, 2), **E.** *ruflineatum* **(1, 2,** 2), **E.** *rupestre* (3,3.3, 2–6), **E.** *stigmaeum* ***(4, 2.7,*** 2-1 1), *Percina kathae* (2, 1.5, 2), *P.* vigil (1, 1, 2)

Pleurobema decisum

Pleurobema decisum is a short-term brooder and was gravid from late spring to early summer. We observed gravid females from 28 May to 28 July and found mature glochidia from 8 June to 28 July. In the laboratory, both immature and mature glochidia were released in well-formed conglutinates similar in structure, but different in shape, to those described for *F. cerina* (Fig. 2). Conglutinate color varied among, but not within, individuals and was either orange or white. In the field, we observed gravid female *P. decisum* releasing conglutinates in a manner similar to *F. cerina* and commonly observed drifting conglutinates in the water column. In the field, we observed schools of blacktail shiners, *Cyprinella venusta,* interacting with conglutinates as described for *F. cerina.* In the laboratory, we presented conglutinates to minnows *(Campostoma oligolepis, Cyprinella venusta, Luxilus ckrysocepkalus, Lytkrurus bellus, Nocomis leptocepkalus, Notropis atkerinoides,* and *N. baileyi),* and darters *(Percina scicra).* All fish species responded to the presence of conglutinates by repeatedly approaching them closely, but we could not ascertain whether fishes ingested conglutinates.

Glochidia of *P. decisum* transformed consistently only on C. *venusfa* (Cyprinidae) (Table 6) and inconsistently on an additional minnow species, *L. ckrysocepkalus.* Fourteen minnow species were unsuitable hosts. Nine other fish species, representing the families Centrarchidae, Ictaluridae, and Percidae, were unsuitable hosts for *P. decisum* (Table 6).

Quadrula asperata

Quadrula asperata is a short-term brooder and was gravid from spring to early summer. We

TABLE 6. Results of host trials for *Pleurobema decisum.* Letters A to D represent replicate trials using glochidia from 4 different female mussels. Sample size (*n*) is either the number of fish that produced juvenile mussels, or the number of fish that rejected all glochidia and produced no juvenile mussels. * = all fish died before completion of the trial. — = the fish species was not used in the trial. na = not applicable.

	Mean no. juveniles/fish (n)							
	Days to transformation				Days to rejection (M)			
Fishes’	A	B	C	D	A	B	C	D
Hosts								
Cyprinella venusta	*2 (3)* *24*	2 (10) *16-22*	0 (5) *5”*	*2 (5)* *23-37*	na (0)	na (0)	na (0)	na (0)
Marginal hosts								
Luxilus chrysocephalus	0 *(3)* *23”*	0 (0) na	2 (5) 17–21	1 (1) *17*	na (0)	2-13 (4)	na (0)	10 (2)

Fish species (number of trials, mean number of fish per trial, range of days to rejection) that did not produce juvenile mussels: *Campostoma oligolepis (3, 3.6, 2-Y), Cyprinella callistia (4, 2.2,* 2–17), *Hybopsis winchelli* (1, 1, 2), *Lythrurus bellus (4, 3,* 2–6), *Nocomis leptocephalus (3, 3.6,* 2–10), *Notemigonus crysoleucas (3, 3.6,* 2–15), *Notropis ammophilus* (2, 3.5, 2–3), *N. atherinoides* (3, 2.3, 2–3), *N. baileyi* (3, 3, 2–3), *N. stilbius (3,* 3.6, 2–3), *N. texanus* (3, 2, 2–3), *N. volucellus* (3, 3, 2–3), *Pimephales notatus* (3, 1.6, 2–3), *P. vigilax* (1, 1, 2), *Noturus leptacanthus* (1, 2, 2), *Lepomis cyanellus (1, 3,* 6), *L. macrochirus (1,* 2, 2), *I.. megalotis (2,* 1.5, 2), *Micropterus salmoides (2,* 3.5, 2–15), *Etheostoma artesiae* (2, 2.5, 2–15), *E. rupestre* (2, 4.5, 2), *Percina nigrofasciata* (1, 1, 3), *P. sciera* (1, 2, 2)

observed gravid females from 17 April to 28 July and found mature glochidia from 17 June to 28 July. In the laboratory, mature glochidia were released freely and were not contained in conglutinates. Copious mucus was released with mature glochidia, and many glochidia were bound in this mucus. In dissected individuals, mucus was also associated with glochidia inside the gills. Long strands of mucus often issued from the excurrent siphon of releasing females, simi-

TABLE 7. Results of host trials for *Quadrula asperata.* Letters A to C represent replicate trials using glochidia from 3 different female mussels. Sample size (n) is either the number of fish that produced juvenile mussels, or the number of fish that rejected all glochidia and produced no juvenile mussels. * = all fish died before completion of the trial. — = the fish species was not used in the trial. na = not applicable.

	Mean no. juveniles/fish (M)					
	Days to transformation			Days to rejection (*n*)		
Fishes’	A	B	C	A	B	C
Hosts						
Ictalurus punctatus	*4* (6) *25-27*	*o* (3)* 22*	*2 (5)* *17-34*	na *(0)*	na (0)	na (0)
Marginal hosts						
Noturus leptacanthus	0 (0) na	0 (0) na	1 (1) 31	3 (2)	2 (2)	*26 (1)*

[1] Fish species (number of trials, mean number of fish per trial, range of days to rejection) that did not produce juvenile mussels: *Campostoma oligolepis* (1, 4, 3), *Cyprinella callistia* (1, 2, 3), C. *camura* (I, 3, 2), C. *venusta* (3, 3.3, 2–6), *Luxilus chrysocephalus (I, 4,* 3), *Lythrurus bellus (1, 2,* 3), *Nocomis leptocephalus* (1, 2, 3), *Notemigonus crysoleucas (3, 3,* 2–7), *Notropis ammophilus (1, 4,* 3), *N. atherinoides (2, 2.5,* 2–3), *N. baileyi (2, 2.5,* 2–6), *N. stilbius* (1, 1, 3), N. *texanus* (1, 2, 3), N. *volucellus* (2, 2.5, 2–3), *Pimephales notatus* (1, 4, 3), *Ictiobus bubalus (2, 3.5,* 2–6), *Moxostoma poecilurum (1,* 1, 3), *Ameiurus natalis (2, 2.5,* 4–18), *Fundulus olivaceus* (1, 1, 18), *Lepomis cyanellus (2, 2,* 3–4), *L. macrochirus (2, 2,* 2–3), *L. megalotis (3, 2,* 2–4), *Micropterus salmoides (3, 2.6,* 2–4), *Pomoxis annularis (1, 2,* 3), *Ammocrypta meridiana* (1, 2, 4), *Etheostoma rupestre (2, 3.5,* 2–6), *Percina nigrofasciata (2, 2.5,* 3–4), *P. sciera (1, 2, 3-6)*

lar to *Elliptio arca.* Immature glochidia and eggs were released in irregular clusters, as described for *E. nrca.*

Glochidia of Q. *asperata* transformed consistently on channel catfish, *Ictalurus punctatus* (Ictaluridae) (Table 7). One additional catfish species, *Noturus leptacanthus,* was a marginal host. One catfish species, *Ameiurus natalis, was* an unsuitable host. Twenty-seven other fish species, representing the families Catostomidae, Cyprinidae, Centrarchidae, Fundulidae, and Percidae, were unsuitable hosts for Q. *asperata* (Table 7).

Discussion

Host use

All 7 mussel species in our study were host specialists, with host use restricted to a single family or genus of fishes. Host use for most species was concordant with host information obtained by laboratory infection trials for closely related species. For example, primary host use of *Elliptio dilatata* is limited to darters and sculpins (Luo 1993), similar to E. *arca,* which uses only darters; sculpins do not occur in the Sipsey and Buttahatchee rivers (Boschung 1989). Hosts for *Fusconaia* COY and *F. cuneolus* include a wide variety of minnows (Neves 1991, Bruendcrman and Neves 1993, respectively), and are similar to *F. cerina.* Host use of *Medionidus conradicus, M. penicillatus,* and a small-stream population of *M. acutissimus* is restricted to darters (Zale and Neves 1982, O'Brien and Williams 2002, and Haag and Warren 1997, respectively) and is similar to large-stream populations of *M. acutissimus.* Host use of *Lampsilis ornata* is restricted to *Micropterus* spp., similar to a large number of other species of *Lampsilis* (reviewed in Haag et al. 1999). Host use of *Pleurobema decision* is similar to 7 other species of *Pleurobema* (*P. clava, P. coccineum, P. collina, P. cordatum, P. furvum, P. oviforme,* and *P. pyriforme*), for which host use is restricted mostly to minnows (O'Dee and Watters 2000, Hove et al. 1997, Hove and Neves 1994, Yokcly 1972, Haag and Warren 1997, Weaver et al. '1991, O'Brien and Williams 2002, respectively). Host information based on laboratory trials for close relatives of *Quadrula asperata* is available only for *Q. nobilis* and Q. *pustulosa,* for which host use is similar (catfishes: Howclls 1997, Coker et al. 1921, respectively). The similarity of host use among congeneric mussel species indicates that this trait is highly conserved at lower taxonomic levels and may be highly predictable among closely related mussel species.

Apparent departures from patterns of host use among ostensibly closely related mussel species may reflect incomplete understanding of phylogenetic relationships within these groups. Host use of *Quadrula cylindrica* and *Q. intermedia* is restricted to 3 minnow genera (Yeager and Neves 1986, Yeager and Saylor 1995, respectively), departing widely from host-use patterns of other species of *Quadrula.* However, recent work showed that these 2 species are members of a monophyletic clade distinct from other members of the genus (Serb et al. 2003). Similarly, host use of *Fusconaia ebena* (restricted to skipjack herring, *Alosa chrysochloris,* Cokcr et al. 1921) differs from other species of *Fusconaia* but, as currently recognized, this genus is polyphyletic and *F. ebena* is not closely related to other members of the genus (Lydeard et al. 2000). *Elliptio* is a large genus with most species occurring in coastal streams on the Atlantic slope or eastern Gulf of Mexico (Davis et al. 1981); species from these drainages use sunfishes (Centrarchidae) or yellow perch (*Perca flavescens*) as hosts (E. *complanata,* Matteson 1948; *E. buckleyi* and *E. icterina,* Keller and Ruessler 1997), in contrast to *E. arca* and *E. dilatata* from interior streams in the Mobile and Mississippi basins, respectively. Differences in host use between these species groups provide evidence for divergent phylogenetic lines within *Elliptio.*

Other apparent departures from well-established phylogenetic patterns of host use are likely a result of differences in host-identification methods among studies. Many host relationships reported in the early literature were based on observations of natural infestations only and were not confirmed by laboratory transformation experiments. Most glochidia attach readily to nonhost-fish species but are later rejected, so such observations potentially result in erroneous host relationships. Furthermore, in some cases, these relationships are based on probable misidentifications of encysted glochidia (see account for *Elliptio crassidens* in Brim Box and Williams 2000). Host information based on a wide variety of methods has been summarized in several reviews (Fuller 1974, Hoggarth 1992, Watters 1994). Despite cautionary statements by these authors, circumstantial or potentially erroneous host relationships reported in these reviews have been widely and uncritically cited (e.g., Parmalee and Bogan 1998). We stress the need to critically examine original sources of host information and methods of study before making and reporting conclusions about mussel host use.

Host-attraction strategies

The mussel species in this study used a diverse array of strategies for infecting host fishes with glochidia. Two previously described host strategies, lure-displaying host-specialists and conglutinate-producing host-specialists (Haag and Warren 1998), are represented in this group of species but, for 3 species, the method of host infection was unclear.

Lure-displaying host-specialists were represented by *Medionidus acutissimus* and *Larnpsilis ornata.* In this strategy, gravid females display lures that elicit attacks from host fishes, resulting in host infection (Haag and Warren 1999). Lures of this type have been described for several other species of *Lampsilis* (Kraemer 1970, Barnhart and Roberts 1997, Haag et al. 1999). Modified mantles similar to those described here for *M. acutissimus* have been reported for *M. penicillatus* (Brim Box and Williams 2000), and similar displays in the wild have been observed for *M. conradicus* (S. Ahlstedt, US Geological Survey, Knoxville, Tennessee, personal communication). In *Lampsilis,* large mantle lures selectively target suitable host fishes by mimicking prey items of these fishes, reducing the probability of infection of unsuitable fish species (Haag and Warren 2000). The modified mantle of *Medionidus* likely has a similar function, although interactions with fishes have not been observed. Because of the small size of the lure and the location of displaying females within the interstices of coarse substrates, the lure may be inconspicuous to most fishes except darters (the sole host for *Medionidus*), many species of which typically feed among gravel and cobble substrates (Page 1983).

Conglutinate-producing host-specialists were represented by *Fusconaia cerina* and *Pleurobema decisum.* In this strategy, females release glochidia in small packets, which resemble food items of small, predaceous fishes such as darters and minnows. This strategy is known for several other species of *Fusconaia* and *Pleurobema* (Bruenderman and Neves 1993, Hove and Neves 1994, Haag and Warren 1997). It is hypothesized that this strategy facilitates host infection through the ingestion of conglutinates by small fishes, but observations of conglutinate release and interactions with fishes in the wild are rare (but see Jones et al. 1986). In the laboratory, we observed a large number of fish species, including many unsuitable hosts, feeding on or otherwise interacting with conglutinates in ways that could result in glochidial transmission. In contrast, in the field, we observed interactions of conglutinates of both mussel species only with the blacktail shiner, *Cyprinella venusta,* a primary host for both species. *Cyprinella venusta* occurs most commonly in the mid-water column in moderate to swift riffles (Baker and Ross 1981), and most food items are taken from the drift (Ross 2001). Based on the prevalence of infestations of wild fishes, Bruenderman and Neves (1993) hypothesized that drift-feeding minnows were the primary hosts of *F. cuneolus* and *P. oviforme* in Virginia. The conglutinate-release behavior we observed for *F. cerina* and *P. decisum* resulted in conglutinates being suspended in the mid-water column where they were vulnerable to C. *venusta* and other drift-feeding minnows, but less vulnerable to unsuitable hosts such as darters and other benthic-feeding fishes.

Elliptio arca and *Quadrula asperata* displayed no modified mantle lures and did not release mature glochidia in conglutinates. During handling, both species, as well as other short-term brooders (Yeager and Neves 1986), often abort immature glochidia or eggs in structures resembling conglutinates, but this behavior does not represent a strategy for host attraction. Rather, transmission of glochidia to hosts may be facilitated by entanglement of fishes in mucous threads, which are released in association with and contain mature glochidia. Release of mucus or other web-like structures in association with glochidia has been observed in host-specialists (Matteson 1948, Yokely 1972, Woody and Holland-Bartels 1993) and host-generalists (Lefevre and Curtis 1910, Wood 1974, Haag and Warren 1997). Such a strategy would be effective for generalists because a wide variety of fishes likely would be infected indiscriminately. For host-specialists, such a strategy seems maladaptive because the likelihood of infection of nonhost fishes and subsequent loss of these offspring would be high. Our observations of glochidial release by *E. arca* and Q. *asperata* were made only in the laboratory and may not be representative of release behaviors in the wild. Field observations are needed to fully elucidate host-attraction strategies for these species.

We made no observations of *Obovaria unicolor* in the field or laboratory that suggested potential host-attraction strategies for this species. Animals did not display mantle lures, did not produce conglutinates, and did not release mucus in association with glochidia. Glochidia were brooded only in the posterior portion of the outer gills and were not associated with mucus or any conglutinate structure. These brooding traits are shared with the genera *Epioblasma, Medionidus, Lampsilis, Ligumia, Toxolasma,* and *Villosa,* all of which display lures. It is therefore possible that *O. unicolor* possesses a lure that we did not observe. However, in lure-displaying species, modified mantle margins that compose the lures are visible even when the lure is not displayed (Haag et al. 1999); such a structure was not evident in *O. unicolor. Obovaria unicolor* was found in close association with its primary fish host; both *O. unicolor* and sand darters (*Ammocrypta* spp.) occur most frequently in clean or silty sand in low-flow areas (Ross 2001, WRH and MLW, unpublished data). Sand darters feed mostly on midge larvae (Diptera), but also ingest other small prey, including larval Asian clams (*Corbicula fluminea*) (Ross 2001). Glochidia broadcast in this habitat may have a high likelihood of being encountered and ingested by foraging sand darters. However, no North American mussel species are currently known to broadcast glochidia and rely on passive infection of host fishes; rather, all well-studied species exhibit some type of strategy to facilitate host infection. Further field and laboratory observations are needed to determine the host-infection mode for this species.

Implications for conservation

Mussel populations in the Mobile Basin, as in most of North America, have declined over the last 30 y (Neves et al. 1997). In some rivers, declines in mussel populations are attributed to disappearance or declines of host fishes, resulting in reduced mussel reproductive success (Smith 1985, Khym and Layzer 2000). This mechanism is insufficient to explain declines of the 7 mussel species in this study because all species use common, widespread fishes as hosts. *Pleurobema decisurn,* a federally endangered species, consistently used only one fish species, *Cyprinella venusta,* as host. Although in some cases, use of only one fish species may be considered a conservation liability, *C. venusta* is one of the most widespread and abundant fishes in the western Mobile Basin (Boschung 1989, Ross 2001). Furthermore, *C. venusta* is tolerant of highly degraded habitats including impounded and channelized streams (Mettee et al. 1996, Ross *2001). Medionidus acutissimus,* a federally threatened species, uses many darter species as hosts, including abundant and widespread species such as *Percina nigrofasciata. Obovaria unicolor* has experienced a dramatic recent decline in the Buttahatchee River (Hartfield and Jones 1990, Jones 1991). We have no data on current population levels of sand darters and *Etheostoma artesiae* (hosts for *0. unicolor)* in the Buttahatchee River, but these fishes are currently widespread and common in other tributaries of the Tombigbee River in Alabama and Mississippi (Mettee et al. 1996, Ross 2001, MLW and WRH, unpublished data). Clearly, factors other than loss of fish hosts (e.g., altered flows, habitat loss, water-quality degradation) are responsible for declines of these and other freshwater mussels in the Mobile Basin.

Acknowledgements

We thank J. G. McWhirter, A. Greer, J. L. Staton, T. Fletcher, T. Slack, T. Mann, I? Hartfield, A. Sheldon, J. Layzer, C. Lydeard, D. Carlson, C. Jenkins, and F. McEwen for their various contributions to this study. This study was supported by the Mississippi Wildlife Heritage Fund and the Southern Research Station, US Department of Agriculture, Forest Service.

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Received: 10 July 2002
Accepted: 10 December 2002