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HOST FISHES FOR FOUR FEDERALLY ENDANGERED FRESHWATER MUSSELS (UNIONIDAE) IN THE APALACHICOLA-CHATTAHOOCHEE-FLINT BASIN

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ABSTRACT

We determined host use and glochidial metamorphosis success of four federally endangered mussel species from the Apalachicola-Chattahoochee-Flint River Basin. Fishes of 19-27 species in a total of 14 families were tested as potential hosts for each mussel species. Metamorphosis of *Pleurobema pyriforme* was observed only on six minnow species (Cyprinidae): *Cyprinella venusta, Nocomis leptocephalus, Notropis amplamala, N. lutipinnis, Pimephales promelas* and *Semotilus atromaculatus*, and metamorphosis success was >27% for all six species. Metamorphosis of *Medionidus penicillatus* was observed only on four darter species (Percidae): *Etheostoma inscriptum, E. swaini, Percina crypta,* and *P. nigrofasciata*, but metamorphosis success varied among species and was highest on *E. inscriptum* (40%) and *P. nigrofasciata* (39%). Metamorphosis of *Hamiota subangulata* was observed only on three species of black basses (Centrarchidae): *Micropterus cataractae, M. coosae,* and *M. salmoides*, and metamorphosis success was >78% on all three species. Metamorphosis of *Amblema neislerii* was observed on 23 species in seven families, indicating that this species is a host generalist, but metamorphosis success varied widely among species. These data augment existing host information for these species and provide a clearer picture of host breadth and the relative suitability of host species.

KEY WORDS *Amblema neislerii, Pleurobema pyriforme, Hamiota subangulata, Medionidus penicillatus,* life history, glochidia

INTRODUCTION

The Apalachicola-Chattahoochee-Flint Basin (ACF) in eastern Alabama, northwestern Florida, and western Georgia has a diverse mussel fauna of 32 species, including eight endemic species (Brim Box & Williams, 2000; Williams et al., 2008). Dams, water pollution, and more recently, heavy and contentious water withdrawal (Pierce et al., 1984; Ruhl, 2005) all have contributed to declines in the mussel fauna, and six species in the basin are listed as federally endangered or threatened. Life history information is needed for the conservation of these species.

Metamorphosis of mussel larvae (glochidia) to juvenile mussels usually requires parasitism on fishes, but host use varies from generalists that can use multiple fish species, to specialists that can metamorphose on only one or a few species (Kat, 1984; Barnhart et al., 2008; Haag, 2012). Despite the recent proliferation of host studies, host information remains lacking for many species and much available information is incomplete or potentially inaccurate (Haag & Warren, 2003). Accurate and comprehensive knowledge of host fishes is necessary for mussel recovery because suitable hosts must be available in sufficient numbers and at the appropriate time, and captive propagation programs also depend on this information (NNMCC, 1998; Haag & Williams, 2014). Host information exists for five of the federally listed ACF mussel species (O'Brien & Brim Box, 1999; O'Brien & Williams, 2002; Fritts et al., 2012a), but for most, only a limited number of potential hosts were tested and quantitative assessment of host suitability was not conducted. The objective of this study was to provide more comprehensive host information and measures of metamorphosis success on fishes for *Hamiota subangulata, Medionidus penicillatus, Pleurobema pyriforme,* and *Amblema neislerii.*

METHODS

Adult female mussels were collected from the ACF Basin from October 2010 to May 2012 (Tables 1-4). We inspected the gills of each mussel by slightly opening the valves with either an oyster knife for *A. neislerii* or with our thumbnail for *H. subangulata, P. pyriforme,* and *M. penicillatus*. Gravid females were identified by the presence of swollen gills. We collected five gravid mussels of a particular species on each sampling date and transported them in river water in aerated coolers to the Aquatic Science Laboratory at the University of Georgia (UGA) where they were held in dechlorinated municipal water at 17-20º C. Female *P. pyriforme* and *A. neislerii* released glochidia spontaneously in the laboratory within two days, and we extracted glochidia from *H. subangulata* and *M. penicillatus* within seven days of the original collection by flushing the gills with water through a syringe. We returned all females to their collection site within 28 days after collection.

Host suitability trials were conducted following Neves et al. (1985) and Fritts et al. (2012a). For each mussel species we tested the suitability of 19-27 fish species representing a total of 14 families (Tables 1-4). Most fishes were collected from rivers and ponds throughout Georgia using a nylon seine and backpack electrofisher, but some species were obtained from federal, state, or private hatcheries. Collections of wild fish focused on locations where mussels were not present to avoid potential acquired immunity from previous glochidial exposures (Dodd et al., 2006). Fish were transported to UGA in aerated coolers or hauling tanks and held in dechlorinated tap water until the experiments began. Fish nomenclature follows Page et al. (2013).

Glochidia viability for each female was quantified prior to host trials by adding a saturated sodium chloride (NaCl) solution to a subsample of glochidia and counting the number of glochidia that closed their shells in response (Lefevre & Curtis, 1912; Fritts et al., 2014). If viability was less than 90%, glochidia from that female were not used in the experiment. Glochidial viability was >90% for all five individuals of *H. subangulata, M. penicillatus,* and *P. pyriforme* but for only three individuals of *A. neislerii*. For each species, glochidia were pooled from all females with >90% viability then enumerated by placing them in a known volume of water, counting the number of viable glochidia in ten 200-µl subsamples, and extrapolating the total number of viable glochidia from the mean subsample count. A standardized inoculation suspension was then made by diluting to a concentration of 4000 viable glochidia L-1.

Potential hosts were exposed to glochidia by allowing the fish to swim for 15 min in the inoculation suspension. Glochidia were kept in suspension with vigorous aeration and a large-bulb pipette. Following exposure, fish were removed from the inoculation suspension, rinsed with fresh water to remove unattached or loosely attached glochidia that might influence estimates of metamorphosis success (see subsequent), and placed in holding chambers. All fishes were held in individual tanks (one fish per tank) in a modified recirculating aquaculture system (AHAB®; Aquatic Habitats Inc., Apopka, Florida, USA), except for Threadfin Shad (*Dorosoma petenense*). Threadfin Shad are difficult to hold in captivity, and all individuals of this species were held in a single 800-L round, communal tank to increase survival. Static water changes (50% renewal) were conducted daily after siphoning the bottom of the tanks (see subsequent).

The outflow from each AHAB tank was equipped with a 100-µm mesh filter cup to recover sloughed glochidia or metamorphosed juveniles released from the fish. Contents of the filter cups were examined one day after inoculation and every second day thereafter. Immediately prior to examining filter cups, water velocity in the tanks was increased for 15 min to flush glochidia and juveniles from the bottom of the tanks into the cups. The bottom of the large communal Threadfin Shad tank was siphoned daily through a large filter (20-cm diameter) equipped with 100-µm mesh to recover sloughed glochidia or metamorphosed juveniles. Contents of the filters were then rinsed into Bogorov trays and glochidia and juveniles were counted under a stereomicroscope. An individual fish was removed from a trial if three consecutive observations revealed no glochidia or juveniles, but prior to removal, the individual's gills were examined to insure that no encysted glochidia remained. The number of glochidia that attached to each fish during inoculation was estimated as the sum of sloughed glochidia and metamorphosed juveniles recovered throughout the duration of each trial. Percent metamorphosis (%M) for each individual fish was calculated by dividing the number of juveniles by the sum of glochidia and juveniles recovered from that fish.

Water temperature, dissolved oxygen (DO), and pH in the holding systems were measured daily with a Hydrolab Quanta (Hach Hydromet, Loveland, Colorado). Ammonia concentrations were monitored weekly using a LaMotte colorimeter (LaMotte Co., Chestertown, Maryland). Water chemistry parameters were maintained within suitable levels for aquatic organisms throughout all trials (DO=7.6-8.4 mg L^{-1}, pH=6.8-7.8, total ammonia= <0.1 mg L^{-1}). All fishes survived the host trials for all four mussel species.

RESULTS

Nineteen fish species in five families were tested as potential hosts for *P. pyriforme*. Metamorphosis was observed on six minnow species (Cyprinidae): *Cyprinella venusta, Nocomis leptocephalus, Notropis amplamala, N. lutipinnis, Pimephales promelas* and *Semotilus atromaculatus* (Table 1). *Cyprinella venusta* and *Semotilus atromaculatus* had the highest metamorphosis success at 58.3% and 52.7%, respectively, but metamorphosis was relatively high on all suitable hosts and confidence intervals overlapped broadly among species. The only minnow species that produced no juvenile metamorphosis was *Notropis texanus*. The glochidia of *P. pyriforme* were released as fragile pink conglutinates, similar to those described for other *Pleurobema* (e.g., Hove & Neves, 1994; Haag & Warren, 1997).

Twenty-four fish species in seven families were tested as potential hosts for *M. penicillatus*. Metamorphosis was observed on all four darter species (Perci-

TABLE 1

Fish species tested as potential hosts for *Pleurobema pyriforme*. HR denotes hatchery reared species; all other species were field collected. %M is the mean percent metamorphosis across all individual fishes of a species (N). Female mussels were collected from Sawhatchee Creek, Early County, Georgia, May 2011. Water temperature ranged from 22-23° C during the trial. The dashed line (–) indicates a non-host species (i.e., metamorphosis = 0%).

Fish species	N	Days to metamorphosis (hosts) or rejection (non-hosts)	%M ± 95% CI
Cyprinidae			
Cyprinella venusta	5	11-21	58.3 ± 13.2
Nocomis leptocephalus	5	11-21	38.0 ± 11.7
Notropis amplamala	4	13-24	38.5 ± 22.1
Notropis lutipinnis	5	11-21	27.7 ± 21.6
Notropis texanus	1	5	–
Pimephales promelas (HR)	2	11-21	38.5 ± 7.8
Semotilus atromaculatus	1	13-21	52.7
Catostomidae			
Hypentelium nigricans	1	3	–
Ictaluridae			
Ameiurus brunneus	1	3	–
Ameiurus natalis	1	3	–
Ictalurus punctatus	4	3	–
Centrarchidae			
Lepomis auritus	1	3	–
Lepomis cyanellus	4	3	–
Lepomis macrochirus	4	3	–
Lepomis punctatus	2	3	–
Micropterus salmoides (HR)	5	3	–
Percidae			
Etheostoma inscriptum	6	3	–
Percina crypta	2	3	–
Percina nigrofasciata	3	3	–

dae) tested: *Etheostoma inscriptum, E. swaini, Percina crypta,* and *P. nigrofasciata* (Table 2) Metamorphosis success was highly variable among darter species and between the two trials. Mean metamorphosis success on *Percina nigrofasciata* was only 19.7% in trial A (female mussels collected in May 2011) but 58.5% in trial B (female mussels collected in January 2012). Overall, metamorphosis success was highest on *Percina nigrofasciata* (39.1%; mean of both trials) and *Etheostoma inscriptum* (39.9%), and it was low on the other two darter species (mean metamorphosis: 2.5-7.9%). Two *Ichthyomyzon gagei* carried glochidia for 12 days after inoculation but no juveniles were recovered.

TABLE 2

Fish species tested as potential hosts for *Medionidus penicillatus*. HR denotes hatchery reared species; all other species were field collected. %M is the mean percent metamorphosis across all individual fishes of a species (N). Female mussels were collected from Sawhatchee Creek, Early County, Georgia, May 2011 (Trial A), and January 2012 (Trial B). Water temperature ranged from 19-20° C during Trial A, and 22-23° C during Trial B.

	N		Days to metamorphosis (hosts) or rejection (non-hosts)		%M ± 95% CI	
Fish species	A	B	A	B	A	B
Petromyzontidae						
Ichthyomyzon gagei	—	2	—	12		
Anguillidae						
Anguilla rostrata	—	1	—	1		
Cyprinidae						
Cyprinella trichroistia	—	4	—	9		
Cyprinella venusta	4	—	3	—		
Nocomis leptocephalus	4	—	3	—		
Notropis amplamala	—	4	—	5		
Notropis chalybaeus	—	4	—	3		
Notropis lutipinnis	4	—	3	—		
Pimephales promelas (HR)	2	—	3	—		
Semotilus atromaculatus	2	—	3	—		
Ictaluridae						
Ameiurus brunneus	1	—	3	—		
Ameiurus natalis	2	—	3	—		
Ictalurus punctatus	4	—	3	—		
Noturus leptacanthus	—	2	—	3		
Aphredoderidae						
Aphredoderus sayanus	—	3	—	6		
Centrarchidae						
Lepomis auritus	3	—	5	—		
Lepomis cyanellus	4	—	3	—		
Lepomis macrochirus	4	—	5	—		
Lepomis punctatus	2	—	3	—		
Micropterus salmoides (HR)	4	—	5	—		
Percidae						
Etheostoma inscriptum	4	—	20-30	—	39.9 ± 5.7	—
Etheostoma swaini	—	3	—	15-24	—	2.5 ± 4.9
Percina crypta	5	—	23-30	—	7.9 ± 12.8	—
Percina nigrofasciata	3	5	20-28	13-29	19.7 ± 16.4	58.5 ± 7.8

Twenty-six fish species in eight families were tested as potential hosts for *H. subangulata*. Metamorphosis was observed on all three species of black bass (Centrachidae) tested: *Micropterus cataractae, M. coosae,* and *M. salmoides* (Table 3). Metamorphosis success was consistently high on all three species (78-88%). *Lepomis cyanellus* and *L. gulosus* carried glochidia for 12 days after inoculation but no juveniles were recovered from either species.

Twenty-seven fish species in nine families were tested as potential hosts for *A. neislerii*. Metamorphosis

TABLE 3

Fish species tested as potential hosts for *Hamiota subangulata*. HR denotes hatchery reared species; all other species were field collected. %M is the mean percent metamorphosis across all individual fishes of a species (N). Female mussels were collected from Spring Creek, Miller County, Georgia, October 2010 (Trial A), and May 2011 (Trial B). Water temperature ranged from 19-21° C for both trials.

Fish species	N		Days to metamorphosis (hosts) or rejection (non-hosts)		%M ± 95% CI	
	A	B	A	B	A	B
Acipenseridae						
Acipenser brevirostrum (HR)	2	–	3	–		
Acipenser fulvescens (HR)	2	–	3	–		
Acipenser oxyrinchus	2	–	3	–		
Esocidae						
Esox niger	–	1	–	3		
Cyprinidae						
Cyprinella venusta	4	–	3	–		
Hybopsis rubrifrons	2	–	1	–		
Nocomis leptocephalus	4	–	1	–		
Notropis lutipinnis	4	–	3	–		
Pimephales promelas (HR)	4	–	3	–		
Semotilus atromaculatus	4	–	5	–		
Catostomidae						
Hypentelium nigricans	2	–	3	–		
Minytrema melanops	–	1	–	3		
Ictaluridae						
Ameiurus brunneus	2	–	3	–		
Ameiurus natalis	2	–	3	–		
Ictalurus punctatus	6	–	3	–		
Noturus leptacanthus	2	–	1	–		
Aphredoderus sayanus	–	3	–	3		
Centrarchidae						
Lepomis auritus	9	–	5	–		
Lepomis cyanellus	6	–	12	–		
Lepomis gulosus	–	5	–	12		
Lepomis macrochirus	7	–	8	–		
Micropterus cataractae	–	2	–	17-35	–	82.7 ± 3.3
Micropterus coosae	–	4	–	12-21	–	87.7 ± 3.2
Micropterus salmoides (HR)	9	1	16-30	19-35	78.2 ± 4.6	85.6
Percidae						
Etheostoma inscriptum	4	–	3	–		
Percina nigrofasciata	2	–	3	–		

was observed on 23 species in seven families (Table 4). Metamorphosis success was variable both among and within families. Metamorphosis success was consistently high only on darters (*Etheostoma fusiforme, E.*

TABLE 4

Fish species tested as potential hosts for *Amblema neislerii*. HR denotes hatchery reared species; all other species were field collected. %M is the mean percent metamorphosis across all individual fishes of a species (N). Females were collected from the Apalachicola River, Gulf County, Florida, May 2012. Water temperature ranged from 22-23° C during the trial. The dashed line (—) indicates a non-host species (i.e., metamorphosis = 0%). The asterisk (*) indicates that fish were held in a communal tank rather than individually, which precludes estimation of individual variability in metamorphosis.

Fish species	N	Days to metamorphosis (hosts) or rejection (non-hosts)	%M ± 95% CI
Clupeidae			
Dorosoma petenense	12	13-18	6.6*
Cyprinidae			
Nocomis leptocephalus	7	10-15	6.7 ± 3.7
Notropis amplamala	4	10-15	2.6 ± 0.7
Notropis lutipinnis	2	10-18	25.3 ± 46.7
Notropis texanus	3	10	—
Pimephales promelas (HR)	8	10-15	12.6 ± 12.3
Pteronotropis grandipinnis	3	10-18	46.2 ± 15.2
Ictaluridae			
Ameiurus brunneus	4	10-13	1.3 ± 2.3
Ameiurus melas	1	10-13	1.9
Ameiurus natalis	2	10-13	1.9 ± 1.2
Ictalurus punctatus	1	13-18	0.2
Noturus leptacanthus	1	3	—
Aphredoderidae			
Aphredoderus sayanus	1	5	—
Poeciliidae			
Gambusia holbrooki	1	10-13	8.3
Moronidae			
Morone saxatilis	9	10-18	28.0 ± 7.6
Centrarchidae			
Lepomis auritus	3	10-15	6.2 ± 3.5
Lepomis cyanellus	6	10-18	58.0 ± 7.4
Lepomis gulosus	6	10-18	12.0 ± 7.4
Lepomis macrochirus	2	10-15	9.3 ± 1.9
Lepomis marginatus	1	10-13	7.3
Lepomis megalotis	3	10-18	18.2 ± 23.8
Lepomis punctatus	1	10-13	3.4
Micropterus salmoides (HR)	6	10-15	8.1 ± 3.0
Percidae			
Etheostoma fusiforme	2	10-15	42.6 ± 9.1
Etheostoma inscriptum	5	10-18	56.5 ± 9.5
Etheostoma olmstedi	3	10-18	56.1 ± 4.1
Elassomatidae			
Elassoma zonatum	1	5	—

inscriptum, E. olmstedi; 43-57%). Similarly high metamorphosis was observed on a minnow (*Pteronotropis grandipinnis*, 46%) and a sunfish (*Lepomis cyanellus*, 58%), but metamorphosis success varied widely on other species in these families. Metamorphosis was consistently weak on catfishes (Ictaluridae, 0.2-1.9%), and no juveniles were recovered from a madtom (*Noturus leptacanthus*). Only four out of 27 fish species produced no juveniles. The mature glochidia of *A. neislerii* were released in a loose mucous matrix similar to that reported by O'Brien and Williams (2002).

DISCUSSION

Three of the mussel species in our study appear to be host specialists, and patterns of host use in these species were in close agreement with previous information about these species or related species. A single minnow species (*Pteronotropis hypselopterus*) was previously identified as a suitable host for *P. pyriforme*, but four additional minnow species were unsuitable (O'Brien and Williams, 2002). All other species of *Pleurobema* for which host use is known are specialists on minnows to varying extents (e.g., Yokley, 1972; Weaver et al., 1991; Hove & Neves, 1994; Hove et al., 1997; Haag & Warren, 1997, 2003; Layzer et al., 2003; White et al., 2008; Culp et al., 2009). However, specialists on minnows may use either a broad array of minnow species (e.g., *Fusconaia cerina, Pleurobema collina, P. oviforme, Theliderma metanevra*; Weaver et al., 1991; Hove & Neves, 1994; Haag & Warren, 2003; Fritts et al., 2012b) or only one or a few closely related species (e.g., *F. burkei, P. decisum, P. strodeanum, T. intermedia*; Yeager & Saylor, 1995; Haag & Warren, 2003; White et al., 2008). *Pleurobema pyriforme* clearly is a member of the former group based on its ability to metamorphose robustly on an array of minnow species. Another feature shared by many minnow specialists, regardless of the breadth of host use, is robust metamorphosis on *Cyprinella* (Haag & Warren, 1997, 2003; White et al., 2008; Fritts et al. 2012b), and this feature is shared by *P. pyriforme*. Although other minnow species also facilitated robust metamorphosis, *Cyprinella venusta* or *Semotilus atromaculatus* are good candidates for use in captive propagation because they are abundant, widely distributed, and easily procured.

Percina nigrofasciata and another darter species, *Etheostoma edwini*, were previously identified as hosts for *M. penicillatus* (O'Brien & Williams, 2002), and together with our results this shows that this species is a specialist on a broad array of darter species similar to other *Medionidus* (Zale & Neves, 1982; Haag & Warren, 1997, 2003). *Percina nigrofasciata* is a good candidate for use in propagation because it is widely distributed and abundant throughout the Gulf Coastal Plain. Our finding of specialization on black basses by *H. subangulata* also is concordant with previous information about this species and other members of *Hamiota* (Haag & Warren, 1997; Haag et al., 1999; O'Brien & Brim Box, 1999). *Hamiota altilis* was also reported to use *Lepomis cyanellus* as a host, but this species was considered only marginally suitable because metamorphosis was low and variable among trials (Haag et al., 1999). We did not recover any juvenile *H. subangulata* from *L. cyanellus*, but that species and *L. gulosus* held glochidia for 12 days after inoculation, suggesting that metamorphosis may be possible on this species. *Micropterus salmoides* is a good candidate for use in propagation of *H. subangulata* because this species is readily available from hatcheries, and we found no difference in metamorphosis success on hatchery raised *M. salmoides* and wild individuals of other *Micropterus* species.

We confirmed that *Amblema neislerii* is a host generalist. A previous study reported metamorphosis of this species on five fish species in three families (O'Brien & Williams, 2002), but our results provide a clearer picture of the wide host breadth of this species. In addition, we observed metamorphosis on one species (*Gambusia holbrooki*) not considered a host by O'Brien and Williams (2002), but that study observed metamorphosis on *Notropis texanus*, which did not produce juveniles in our study. These results show that *A. neislerii* is capable of metamorphosing on many fishes, but considerable variation in host suitability exists among fish species. Metamorphosis success was consistently high only on darters, and these fishes are good candidates for use in propagation of *A. neislerii*. Because *A. neislerii* releases glochidia in mucus threads that apparently entangle fishes by chance, the benthic habits of darters may expose them to glochidia more frequently, which in turn may have resulted in the close relationship between these species. However, another group of benthic fishes, catfishes, were consistently poor hosts for *A. neislerii*.

Apart from the tribe Anodontini, generalist host use is poorly documented and appears to be rare in North American mussel species (Haag, 2012), and confirmation of this host strategy has several important implications. Because it can metamorphose on many fish species, *A. neislerii* may be limited by host abundance to a lesser extent than specialists. On the other hand, its broad host use means that it could compete for hosts with many other mussel species. Finally, the ability of *A. neislerii* to metamorphose robustly on the migratory *Morone saxatilis* suggests that population structure may be influenced by long distance dispersal to a greater extent than mussel species that are specialists on more sedentary fish species. Studies of the suitability of other migratory species such as sturgeons, Skipjack Herring (*Alosa chrysochloris*), and Alabama Shad (*Alosa alabamae*) also would be desirable. *Amblema plicata* also has been reported to parasitize fishes from 10 different families (Howard & Anson, 1922; Coker et al., 1921; Weiss & Layzer, 1995), but most of these potential hosts are unconfirmed, and remarkably, a comprehensive, quantitative host suitability study has never been conducted for this species. *Amblema plicata* is one of the most abundant and widespread species in North America, and better information is needed to more fully evaluate the evolutionary and conservation significance of host use in this genus.

The unique life cycle of freshwater mussels complicates the protection of these species because managers must consider the status not only of mussels but of host fish populations (McCargo & Peterson, 2010). All four species in this study use common fishes as hosts and therefore may have been affected by changes in fish populations to a lesser extent than mussel species that are specialists on imperiled fishes (e.g., Fritts et al., 2012a). Nevertheless, comprehensive host information is necessary for development of holistic management strategies, and these studies remain an important research need for mussel conservation (Haag & Williams, 2014).

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