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Host Identification for Strophitus undulatus (Bivalvia: Unionidae), the Creeper, in the Upper Susquehanna River Basin, Pennsylvania

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ABSTRACT.—Hosts for *Strophitus undulatus* (Bivalvia: Unionidae) were identified through laboratory infestations. *Strophitus undulatus* had a low degree of host specificity, transforming on 15 of 22 species examined, including three non-native species and one anadromous species. Suitable hosts included five cyprinid species, two salmonids, two centrarchids, two percids and *Acipenser oxyrhynchus* (Atlantic sturgeon), *Ameiurus natalis* (yellow bullhead), *Cottus cognatus* (slimy sculpin) and *Notophthalmus viridescens viridescens* (red-spotted newt). Ten hosts were previously unknown. No metamorphosis was observed in a control treatment without a potential host. Recovery of juveniles occurred 12–41 d after infestation at 13–18 C. Duration of glocidial attachment to the hosts declined with increasing water temperature.

INTRODUCTION

Freshwater mussels of the families Margaratiferidae and Unionidae are the most imperiled North American aquatic group, with only 24% of 297 species considered stable (Bogan, 1993; Williams *et al.*, 1993). Conservation efforts for this group continue to be hampered by lack of specific life history information, particularly knowledge of host relationships. Freshwater mussels have a highly specialized life history in which larvae (glochidia), brooded by females in modified gill chambers (marsupia) and released when mature, undergo a brief period as obligate ectoparasites on fish or amphibians. This life cycle is followed with rare exceptions (Kondo, 1990; Lellis and King, 1998). Host specificity varies widely across species however, with some unionids parasitizing a wide variety of unrelated host species (Trdan and Hoeh, 1982; Hove *et al.*, 1997), and others using only a few host species, often closely related (Yeager and Neves, 1986; Michaelson and Neves, 1995). Inappropriate hosts shed attached glochidia, usually within a few days, whereas appropriate hosts carry glochidia until transformation into the juvenile form, which excysts and becomes free-living. Hosts for only one quarter of the North American mussel species have been reported (Hoggarth, 1992; Watters, 1994). We identified hosts of *Strophitus undulatus*, the creeper, in the upper Susquehanna River basin, Pennsylvania, through laboratory studies. Despite early reports that *S. undulatus* transforms without the use of a host (Lefevre and Curtis, 1911; Howard, 1914a), subsequent studies have shown *S. undulatus* uses fish hosts (Baker, 1928; Hove *et al.*, 1997; Watters *et al.*, 1998; Wicklow and Beisheim, 1998).

METHODS

Laboratory experiments were conducted to identify suitable hosts for *Strophitus undulatus*. When possible, potential hosts were collected from areas devoid of mussels to avoid

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using fish with acquired immunity to glochidia (Arey, 1923). Most fishes were collected from Pine Creek, Tioga County, Pennsylvania, a tributary to the West Branch of the Susquehanna River. *Cottus cognatus* (slimy sculpin) were collected from Straight Run, and *Etheostoma zonale* (banded darter) from Little Pine Creek, both tributaries to Pine Creek. *Bufo americanus* tadpoles (American toad) and adult *Notophthalmus viridescens viridescens* (red-spotted newt) were collected from local ponds. *Acipenser oxyrhynchus* (Atlantic sturgeon), *Salmo salar* (Atlantic salmon) and *Salvelinus fontinalis* (brook charr), were taken from captive bred populations at the USGS Northern Appalachian Research Laboratory in Wellsboro, Pennsylvania. *Ameiurus natalis* (yellow bullhead), *Micropterus salmoides* (largemouth bass) and *Perca flavescens* (yellow perch) were collected from Tamarack Lake, Crawford County, Pennsylvania. We attempted to expose *S. undulatus* glochidia to a variety of aquatic species, including those likely to be present during glochidial release by *S. undulatus* as well as several non-native species (*Oncorhynchus mykiss* (rainbow trout), *Ambloplites rupestris* (rock bass), *M. salmoides*, *E. zonale*) and anadromous species (*A. oxyrhynchus*, *S. salar*) that may have been present historically (Cooper, 1983; Lee *et al.*, 1980).

A total of 86 *Strophitus undulatus* ranging in size from 41–80 mm and 8–50 g (mean 62 ± 8 mm, 27 ± 9 g) were collected from Pine Creek, Tioga County, Pennsylvania (41°44.099′N, 077°25.857′W) between 15 April and 13 May 1999 and transported in coolers without water to the USGS Northern Appalachian Research Laboratory in Wellsboro, Pennsylvania for experimentation. Unionid nomenclature follows Turgeon *et al.* (1988) and voucher specimens were deposited in the American Museum of Natural History, New York. At the laboratory, mussels were cleaned and measured, then divided equally into two glass aquaria (122 × 46 × 51 cm, L × W × D) containing 10 cm of sand substrate. Aquaria were supplied with 1 liter/min well water (9.8 C ambient) heated or chilled with a submerged stainless steel heat-exchanger connected to an external refrigerated circulator (Model 675, Fisher Scientific, Pittsburgh, Pennsylvania). Water was circulated within each aquarium by aeration from a 31 cm airstone set opposite the drain end of the tank. Each aquarium was illuminated with two 40W flourescent lamps (Cool White Deluxe, Osram Sylvania, Inc., Versailles, Kentucky) set 50 cm above the water surface and controlled by a programmable digital timer (Model 810030, Sper Scientific, Ltd., Scottsdale, Arizona). Photoperiod and temperature were systematically adjusted in one aquarium to match 26 y average conditions for Pine Creek at Cedar Run, Pennsylvania (1944–1970 period of record; Flippo, 1975). In the second aquarium, photoperiod and temperature were held constant at average 20 April conditions (8 C, 13.5 h light) for 4 wk before resuming normal seasonal patterns to delay glochidial release. Mussels were fed twice daily a mixture of cultured microalgaes that included *Nanochloropsis* sp. (Florida Aqua Farms, Inc., Dade City, Florida) and *Neochloris oleoabundans*, *Bracteacoccus grandis* and *Bracteacoccus giganteus* (University of Texas, Austin, Texas).

Naturally released glochidia and conglutinates were removed with a pipette from the *Strophitus undulatus* aquaria for use in laboratory infections. Glochidia were considered viable if they snapped shut upon exposure to salt (Zale and Neves, 1982). Potential hosts were examined for existing glochidial infections prior to experimentation. Small fishes, tadpoles and *Notophthalmus viridescens* (1–24 individuals/species) were exposed to *S. undulatus* glochidia in a 600 ml beaker aerated with an airstone at 12–19 C. Larger fishes (2–5 individuals/species; *Acipenser oxyrhynchus*, *Ameiurus natalis*, *Salmo salar*, *Salvelinus fontinalis*, *Micropterus salmoides*, *Perca flavescens*) were exposed to glochidia in buckets aerated by an airstone at 13–15 C. Glochidia were maintained in suspension by frequent agitation. Duration of exposure varied from 15–75 min, depending on the size of the container and the susceptibility of the host to glochidial attachment. Potential hosts were placed in aerated, flow-through, 38–76 liters aquaria by species at 13–18 C and fed chopped squid, fish or frozen brine shrimp daily. Uneaten food was removed promptly. No substrate was placed in the tanks, however potential hosts were provided with PVC pipe halves (10 cm long × 5 cm wide × 2.5 cm high) for cover and newts were provided with a small board held just below the water surface. We conducted only one replicate for each species due to spatial limitations. A control treatment was included in which glochidia were added to a 76-liters aquarium in the absence of a potential host in order to determine if transformation could occur without the use of a host. In addition, 50–100 conglutinates were placed in each of 27 sterile plastic petri dishes (100 × 15 mm, Plasta-Medic, Carson, California) containing either distilled water (n = 13) or boiled well water (n = 14). Dishes were cultured in an incubator (Model 5430, Precision Scientific, Chicago, Illinois) at 10 ± 1 C for 8–49 d and checked periodically for viability and development.

Glochidial attachment was verified for each species 2 d after exposure to glochidia. After a species carried glochidia for 4 d, we inspected material on the bottom of the tank three times a week for glochidia and transformed juveniles. The tank bottom was siphoned into a 100 μm mesh sieve, washed into a gridded petri dish and examined under a microscope. Juveniles were distinguished from glochidia by the presence of a foot, and were usually crawling on the bottom of the petri dish or in debris. Number of glochidia and juveniles were tabulated and a subsample preserved. Siphoning continued for at least 10 d after the last juveniles were found. A species was considered a host if encystment and metamorphosis to the juvenile stage occurred.

RESULTS

Strophitus undulatus released glochidia 26 April to 2 June (8.5–16.9 C) when held at a photoperiod and temperature regime that mimicked average natural conditions for Pine Creek (Fig. 1). The majority of conglutinates were released between 12 May and 27 May (13.6–15.6 C). Mussels subjected to a 4 wk seasonal delay released glochidia from 4 May to 18 June (8.0–15.6 C) with the majority released from 26 May to 18 June (13.3–15.6 C). There were two large release events within the delayed season tank on 9 June (15.5 C) and 18 June (15.6 C). We could not determine how many mussels contributed to any single release. Laboratory infestations were begun on 26 April 1999 and were completed by 26 July 1999.

Strophitus undulatus successfully metamorphosed on 15 of 22 potential hosts, including five cyprinid species, two salmonids, two centrarchids and two percids, as well as *Acipenser oxyrhynchus*, *Ameiurus natalis*, *Cottus cognatus* and *Notophthalmus viridescens* (Table 1). Three host species are non-native to the Susquehanna River drainage: *Oncorhynchus mykiss*, *Ambloplites rupestris* and *Micropterus salmoides*, while one anadromous species, *A. oxyrhynchus*, also acted as a host (Table 1). Hosts produced 1–36 juveniles with transformation rates varying from 2–51% (Table 1). The weighted average number of days until metamorphosis and mean temperature were related. Duration of glochidial attachment to the hosts declined with increasing temperature (Fig. 2). Seven species did not act as hosts, including two cyprinid species, one sucker, one ictalurid, one salmonid and one percid (Table 1). No transformation of glochidia was observed in the control treatment. Glochidia incubated in petri dishes remained viable for as long as 9 d postrelease, but no development was observed among individuals that were either free, attached to, or contained within conglutinates. Conglutinate stability varied, but some held in distilled water remained intact in excess of 14 d.

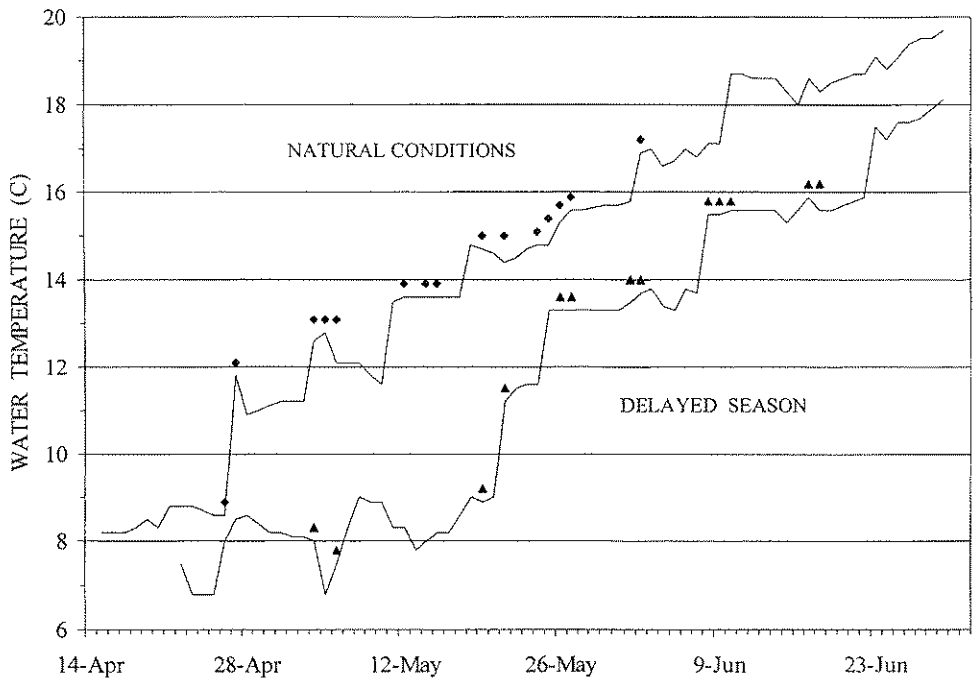

FIG. 1.—Release of glochidia by *Strophitus undulatus* held in tanks under a natural photoperiod and temperature regime ('natural conditions') or a 'delayed season,' in which temperature and photoperiod were held constant for 4 wk at 8 C, 13.5 h light before resuming normal seasonal patterns. Release events are indicated by diamonds for natural conditions and by triangles for delayed seasonal conditions

DISCUSSION

We identified 15 hosts for *Strophitus undulatus*, ten of which were previously unknown, bringing the total number of reported hosts to 29 for this species (Baker, 1928; Hove *et al.*, 1997; Watters *et al.*, 1998; Wicklow and Beisheim, 1998; Wicklow, pers. comm.—yellow perch). *Acipenser oxyrhynchus, Campostoma anomalum, Luxilus cornutus, Nocomis micropogon, Rhinichthys atratulus, Oncorhynchus mykiss, Salvelinus fontinalis, Ambloplites rupestris, Etheostoma olmstedi* and *Notophthalmus viridescens* are all reported as hosts for *S. undulatus* for the first time. Two species that have been previously identified as hosts for *S. undulatus*, *Etheostoma zonale* and *Pimephales notatus*, did not metamorphose glochidia in this study. *Pimephales notatus* shed all attached glochidia in the first 8 d. *Etheostoma zonale* shed most glochidia in the first 10 d, however after a period of inactivity, shed two more glochidia after 20 d and one more on day 29. As reported by Watters and O'Dee (1996), this may represent acquired immunity, although further studies are needed to test this hypothesis. Early reports that *S. undulatus* did not require a host (Lefevre and Curtis, 1911; Howard, 1914a) were not corroborated by this study. Duration of metamorphosis and temperature were significantly related in this study and others, with fewer days until metamorphosis occurring at higher temperatures (Howard and Anson, 1922; Zale and Neves, 1982; Weaver *et al.*, 1991). In addition, there was a trend towards a shorter interval of metamorphosis at higher temperatures.

Hoggarth (1992) summarized known host relationships for unionids and his data reveal

TABLE 1.—Results of laboratory trials to determine hosts of *Strophitus undulatus*. Non-native species are designated with an asterisk

Potential host species	Number of individuals exposed	Mean length (mm)	Mean temp. (C)	Number of glochidia shed	Period of metamorphosis (days)	Number of juveniles recovered	Percent metamorphosed
Control	n/a	n/a	18.1	102	n/a	0	0%
Acipenser oxyrhynchus, Atlantic Sturgeon	2	210	14.9	3	17	1	25%
Campostoma anomalum, Central stoneroller	1	81	15.5	7	20	2	22%
Exoglossum maxillingua, Cutlips minnow	7	65	16.9	8	n/a	0	0%
Luxilus cornutus, Common shiner	7	93	16.8	35	13–22	36	51%
Nocomis micropogon, River chub	3	77	16.9	57	12–16	5	8%
Pimephales notatus, Bluntnose minnow	6	51	15.7	7	n/a	0	0%
Rhinichthys atratulus, Blacknose dace	1	54	13.4	3	29	1	25%
Rhinichthys cataractae, Longnose dace	2	82	15.6	7	17–22	7	50%
Catostomus commersoni, White sucker	8	97	15.5	7	n/a	0	0%
Ameiurus natalis, Yellow bullhead	4	177	16.3	14	17–18	2	13%
Noturus insignis, Margined madtom	7	108	13.5	100	n/a	0	0%
*Oncorhynchus mykiss**, Rainbow trout	1	92	13.8	84	14–19	2	2%
Salmo salar, Atlantic salmon	4	97	13.4	5	n/a	0	0%
Salvelinus fontinalis, Brook charr	5	85	15.5	11	16–21	3	21%
Cottus cognatus, Slimy sculpin	7	54	13.4	33	34	1	3%
*Ambloplites rupestris**, Rock bass	4	70	13.8	69	18–29	9	12%
*Micropterus salmoides**, Largemouth bass	3	151	13.3	76	26	4	5%
Etheostoma olmstedi, Tessellated darter	6	60	13.2	94	32–37	20	18%
*Etheostoma zonale**, Banded darter	4	50	13.2	16	n/a	0	0%
Perca flavescens, Yellow perch	3	133	13.3	149	20–41	27	15%
Bufo americanus, American toad	24	20	18.4	14	n/a	0	0%
Notophthalmus viridescens, red-spotted newt	6	68	14.9	4	21	1	20%

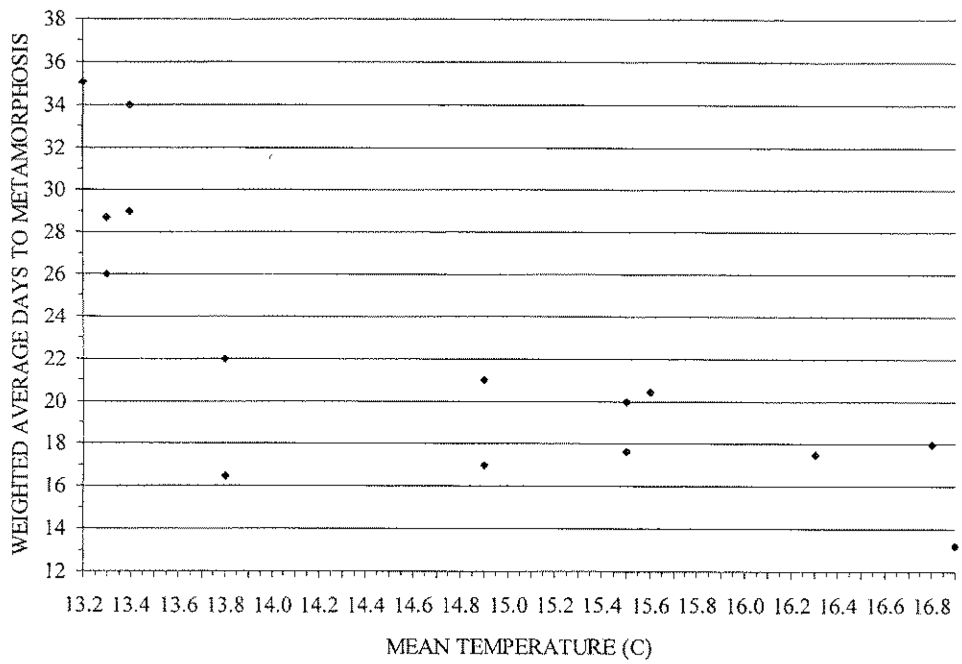

FIG. 2.—Relationship between weighted average number of days until metamorphosis and temperature for *Strophitus undulatus*. Each point represents an identified host for *S. undulatus*

a mean number of 4.4 host/species. *Strophitus undulatus* is therefore a host generalist, using more than the average number of taxonomically diverse host species. Only *Pyganodon grandis*, the giant floater, has more reported hosts (32) (Hoggarth, 1992). In addition to *S. undulatus* and *P. grandis*, many other species in the subfamily Anodontinae are also host generalists (Trdan and Hoeh, 1982; Barnhart and Roberts, 1997; Haag and Warren, 1997; Watters and O'Dee, 1998). Use of such a large number of host species should protect these unionid species against population decline as well as facilitate dispersal and recolonization (Trdan and Hoeh, 1982; Kat, 1984).

Host species differed significantly in attachment and metamorphosis rates, with 4 to 176 glochidia attaching to the hosts, and 2 to 51% of attached glochidia becoming juveniles. Many factors may affect variation in attachment, including immune response, swimming behavior and orientation of the host, although the role of these factors in susceptibility to attachment is unknown. Studies of other mussel species have also found a range of suitability among identified hosts (Waller and Holland-Bartels, 1988; Haag and Warren, 1997; Watters and O'Dee, 1998). Attachment rates in the field are typically significantly less than those obtained in the laboratory (Zale and Neves, 1982; Weaver *et al.*, 1991; Bruenderman and Neves, 1993), therefore percent metamorphosed is an important variable in the reproductive success of unionid species. We hypothesized that species with metamorphosis rates below 10% may be marginally suitable hosts for *Strophitus undulatus*, including *Nocomis micropogon*, *Oncorhynchus mykiss*, *Cottus cognatus* and *Micropterus salmoides*. Future studies should examine the importance of these hosts in the field. Nevertheless, loss of these hosts is presumed to have vastly different effects upon *S. undulatus* populations as compared to species such as *Luxilus cornutus*, *Rhinichthys cataractae*, *Etheostoma olmstedi* or *Perca flavescens*, which had metamorphosis rates of 15–51%.

Strophitus undulatus was also able to use both non-native and anadromous fishes as hosts including *Acipenser oxyrhynchus*, *Oncorhynchus mykiss*, *Ambloplites rupestris* and *Micropterus salmoides*. *Oncorhynchus mykiss*, *A. rupestris* and *M. salmoides* are present in Pine Creek and could act as hosts in the upper Susquehanna basin. In areas in which *M. salmoides* is native, it is also used as a host. Sturgeon are used as hosts for three other unionids: *Lampsilis teres*, the yellow sandshell, *Obovaria olivaria*, the hickorynut and *Quadrula pustulosa*, the pimpleback, all of which use the shovelnose sturgeon, *Scaphirhynchus platorhynchus*, although transformation was not observed for *L. teres* or *Q. pustulosa* (Surber, 1913; Howard, 1914b; Wilson, 1916; Coker *et al.*, 1921). Dams and other barriers to upstream movements can drastically affect the distribution of unionids with anadromous fish as primary hosts, for example in *Anodonta implicata*, the alewife floater, and its host, *Alosa pseudoharengus*, the alewife (Davenport and Warmuth, 1965; Smith, 1985).

Identification of mussel hosts has traditionally focused on fish species, however many studies have shown that amphibians act as hosts for unionids as well (Howard, 1951; Seshaiya, 1941; Walker, 1981; Watters, 1997; Watters and O'Dee, 1998; Wicklow and Beisheim, 1998). As recommended by Watters (1997), future studies need to expose a wider variety of aquatic organisms to mussel glochidia, rather than focus solely on fishes. This is the first case of a unionid capable of using newts as hosts. The red-spotted newt is unusual in that juveniles are completely terrestrial, whereas both the larval and adult stages are aquatic (Conant and Collins, 1991). Watters and O'Dee (1998) attempted infestations of *Lampsilis cardium* and *Utterbackia imbecillis* with decapod crustaceans but no juveniles were produced.

Strophitus undulatus is a habitat generalist, and uses two strategies for targeting potential hosts: first conglutinates are released into the water column that are attacked by fishes as a potential prey item, second, the conglutinates degrade, leaving glochidia on the stream bottom that can attach to fins and other soft tissues of benthic species (Wicklow and Beisheim, 1998). Thus, characteristics of *S. undulatus* glochidial release and habitat use complement its ability to parasitize a wide variety of aquatic species. Although host studies conducted in the laboratory do not unequivocally determine hosts used in the field, consideration of ecological characteristics of potential hosts such as feeding mode, habitat use, timing and habitats used in spawning can indicate which potential hosts are most likely to encounter mussel glochidia in situ. In Pine Creek *S. undulatus* generally releases glochidia in April to June in runs or pools. Using this information, we predict that species that prey on small drifting items in the water column or items on the substrate, use these habitats in spring months, and transform 10% or more *S. undulatus* glochidia would most likely be hosts of *S. undulatus* in Pine Creek. Using these criteria, we predict that *Campostoma anomalum*, *Luxilus cornutus*, *Rhinichthys atratulus*, *Rhinichthys cataractae*, and *Etheostoma olmstedi* are most likely hosts used by *S. undulatus* in Pine Creek and should be targeted for field studies.

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