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EARLY LIFE HISTORY AND CONSERVATION STATUS OF THE MONKEYFACE, *THELIDERMA METANEVRA* (MOLLUSCA: BIVALVIA) IN MINNESOTA AND WISCONSIN

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ABSTRACT

Conservation and restoration of freshwater mussel species requires an understanding of current and historical distributions as well as key aspects of life history. Most freshwater mussels (Unionoida) depend on particular species of host fish for the development and dispersal of the parasitic glochidia larvae. The degree of host specificity varies and is not well known for many mussel species. We tested 90 fish species in 18 families as potential hosts for the Monkeyface mussel (*Theliderma metanevra*), determined its brooding period, and assessed its distribution and current status in Minnesota and Wisconsin. *Theliderma metanevra* brood embryos and glochidia from late April-early August in the St. Croix River. In laboratory experiments, glochidia metamorphosed on 21 cyprinid species (11 genera) but not on other taxa, confirming the host association between *Theliderma* spp. and minnows. The historical and recent distribution of *T. metanevra* in the upper Midwest reflects geological dispersal barriers as well as its apparent sensitivity to a range of human disturbances. These results contribute to an understanding of the evolutionary diversification of the tribe Quadrulini and inform efforts to conserve this regionally threatened species.

KEY WORDS *Quadrula metanevra*, freshwater mussels, host fish, minnows, distribution, brooding

INTRODUCTION

In recent decades there has been a surge in the study of freshwater mussels (Unionoida) spurred by the recognition that many taxa have become extinct and many more are at risk (Bogan, 1993; Ricciardi & Rasmussen, 1999; Lydeard et al., 2004). Particular interest has focused on the brief period during which the larvae (glochidia) are obligate parasites on fish (Zale & Neves, 1982; Kat, 1984; Parmalee & Bogan, 1998) and on adaptations that facilitate this process (Haag & Warren, 2003; Barnhart et al., 2008). Glochidia must be encysted on the gills, fins, or skin of their host in order to complete metamorphosis into juveniles (Rogers-Lowery & Dimock, 2006). For many mussel species, fish hosts are unknown or reported hosts are based on potentially erroneous identifications (Haag & Warren, 2003).

Conservation and restoration of any freshwater mussel species requires an understanding of its current and historical distribution as well as key aspects of its life history, such as glochidia brooding period and

host use (National Native Mussel Conservation Committee, 1998). The Monkeyface mussel (*Theliderma metanevra*) (Rafinesque, 1820) (formerly *Quadrula*) is a thick-shelled, commercially valuable species that is broadly distributed in medium-sized and large rivers of the Mississippi and Mobile river basins, but it has declined in recent decades in many areas (Cummings & Mayer, 1992; Oesch, 1995; Parmalee & Bogan, 1998; Williams et al., 2008). In Minnesota and Wisconsin, *T. metanevra* is classified as threatened species (Natural Heritage & Nongame Research Program, 1996; Wisconsin Department of Natural Resources, 2004).

Host fish associations vary among genera in the tribe Quadrulini (sensu Graf & Cummings, 2007). Catfishes (Ictaluridae) are the primary hosts for *Amphinaias* (formerly within the *Quadrula pustulosa* species group), *Quadrula* (including *Q. fragosa* and *Q. quadrula*), *Cyclonaias tuberculata*, and *Tritogonia verrucosa* (Coker et al., 1921; Howells et al., 1996; Hove et al., 1997; Howells, 1997; Haag & Warren, 2003; Steingraeber et al., 2007; Hove et al., 2011; Hove et al., 2012), whereas *Theliderma intermedia* and *T. cylindrica* (formerly within the *Quadrula metanevra* species group) transform most robustly or only on minnows (Cyprinidae) (Yeager & Neves, 1986; Yeager & Saylor, 1995; Fobian, 2007). Earlier studies suggested that hosts for *T. metanevra* were Bluegill (*Lepomis macrochirus*), Green Sunfish (*L. cyanellus*) and Sauger (*Sander canadensis*) (Surber, 1912a; Howard, 1914; Wilson, 1916). These host determinations were based on the occurrence of natural glochidial infestations on fishes, but encysted glochidia can be difficult to identify, and transformation to the juvenile stage was not observed. Given results from laboratory host studies on other species of *Theliderma*, transformation of *T. metanevra* glochidia on minnows seems more likely than on either sunfishes or perches. In addition to host information, accurate knowledge of the glochidia brooding period is necessary for future host work and potential propagation efforts.

Our objectives for this study were to 1) describe the glochidia brooding period in the northern range of *T. metanevra*, 2) identify host fish suitability in laboratory trials, and 3) determine the historical distribution and current status of *T. metanevra* in Minnesota and Wisconsin, and discuss how its current status may be influenced by host use.

METHODS

Brooding and host suitability

We studied *Theliderma metanevra* at two sites in the St. Croix River: Interstate State Park (45°23’36”N, 92°39’47”W) and Franconia access (45°22’03”N, 92°41’21”W), Minnesota and Wisconsin. This is the approximate northern limit for *T. metanevra* and the sites support diverse mussel assemblages (Hornbach et al., 1996), including several regionally and globally imperiled species. To document the brooding season we collected at least 20 *T. metanevra* from the Interstate site biweekly from May to November 1997 and April to October 1998, but we were not able to sample in June 1998. We examined the gills of each individual by opening the shells slightly with modified O-ring pliers or a flathead screwdriver. Brooding females were identified as those with swollen gills. We were not able to distinguish males from non-brooding females by this method.

Host suitability was examined using standard methods of artificially inoculating fishes with glochidia and monitoring the success of these infections (e.g., Neves et al., 1985). Host trials were conducted from May to August, 2006-2009, at the University of Minnesota Wet Laboratory or Minnesota Pollution Control Agency Biomonitoring Laboratory. During this period, 15 separate trials were conducted with glochidia from a total of 30 female mussels and using a total of 90 fish species, with special emphasis on minnows (Cyprinidae). Most fishes used in host trials were collected with a seine from rivers and lakes in Minnesota. When possible, we collected fishes from water bodies without *T. metanevra* populations to minimize use of fishes with acquired immunity caused by previous glochidial exposure (Reuling, 1919). For those few fishes that were collected near *T. metanevra* populations, we assumed those fishes had at most only partial immunity and would still produce some juveniles even if overall metamorphosis success was reduced (Dodd et al., 2005, 2006). Some fishes were collected from the Saline or Black rivers in Arkansas, or the Black, Little, St. Francis, or Whitewater rivers in southeastern Missouri, and others were obtained from hatcheries. Fish were held in the laboratory for at least two weeks or were inspected for pre-existing glochidia infections prior to being inoculated with glochidia.

Gravid mussels often spontaneously released glochidia during transport or soon after returning to the laboratory. For host trials, we used glochidia that were recently released by females, or we removed glochidia by puncturing the gravid gill and flushing the contents with a syringe. Prior to inoculating fishes, a sample of glochidia from each female mussel was tested for viability by salt exposure (Coker et al., 1921). If >30% of glochidia were unresponsive or showed only a weak shell closure response, glochidia from that female were not used for inoculation. After glochidia were obtained, adult mussels were returned to their collection site.

We inoculated fish in a vigorously aerated wa-

ter bath (1-7 L) containing several hundred to several thousand glochidia. Multiple fish were inoculated in the same bath, and each bath contained glochidia from multiple female mussels. After exposure, the number of attached glochidia was assessed by examining fish under a dissecting microscope while another person applied a gentle stream of water over the gills to keep them wet and separate the gill filaments. After approximately 10-20 glochidia had attached to fishes 2-10 cm in length, or 50-100 glochidia to fishes >10 cm (Hove et al., 2000), they were removed from the glochidial suspension and placed in community holding tanks. Water temperature of the holding tanks was 19-25°C.

Three to four days after inoculation, each fish was re-examined for encysted glochidia. If glochidia were no longer present on any individuals, the trial for that fish species was ended. If encysted glochidia remained on the gills after 3-4 days, all individuals of that fish species were placed together in a separate aquarium for additional monitoring. Subsequently, water from the aquarium floor was siphoned every 3-4 days and washed across two sieves with 1 mm and 125 µm mesh openings, respectively. Particulates from the 125 µm filter were placed in gridded Petri dishes and examined under a dissecting microscope. Transformed juveniles were distinguished from glochidia by the presence of a foot and movement of the valves. A sample of transformed juveniles from each trial was preserved in 95% ethanol. A trial was terminated after three consecutive periods of siphoning without finding a juvenile.

Distribution and status

We compared the recent and historical distribution of *T. metanevra* in Minnesota and Wisconsin to evaluate its status. Most data used to determine recent distribution of live individuals were from Minnesota and Wisconsin departments of natural resources (DNR) surveys completed from 1999 to 2010 and 1985 to 2008, respectively. Surveys in Minnesota were based on qualitative methods (i.e., timed searches; Allen et al., 2007). Methods for Wisconsin surveys were similar, except some sites were also quantitatively sampled using quadrats (Piette, 2005). Border waters (Mississippi and St. Croix rivers) were sampled both by MN DNR and WI DNR. We also included information from post-1985 surveys on the Cannon (Davis, 1987), Zumbro (Bright et al., 1988) and Minnesota (Bright et al., 1990) rivers (Minnesota), Chippewa River (Wisconsin) (Balding, 1992; Balding & Balding, 1996) and Mississippi (Hornbach et al., 1992) and St. Croix (Hornbach, 2001) rivers. In total, these studies represent a comprehensive survey of our study area. We treated live individuals collected within the last 25 years as recent records, which is likely within the lifespan of *T. metanevra* based on longevity estimates for other quadruline species (Haag & Rypel, 2011).

To determine *T. metanevra*'s historical distribution, we gathered data from several sources, including 1) relic shells found during recent surveys listed above, 2) museum specimens housed at the University of Minnesota's James Ford Bell Museum of Natural History, Milwaukee Public Museum, Ohio State University Museum of Biological Diversity, and Illinois Natural History Survey Mollusk Collection, and 3) literature pertaining to the region (Grier, 1922; Baker, 1928; Dawley, 1944; van der Schalie & van der Schalie, 1950; Finke, 1966; Havlik & Stansbery, 1978; Mathiak, 1979; Fuller, 1980; Thiel, 1981; Havlik, 1983; Theler, 1993; Theler, 2000). Recent surveys included most areas sampled in these earlier studies, except that Mississippi River navigation pools 9 and 11 were not sampled as thoroughly as other pools in recent surveys.

RESULTS

Brooding and host suitability

Females brooded glochidia in all four demibranchs, and the brooding period was similar in both years. Gravid female *T. metanevra* were found from 7 May to 29 July in 1997, and from 28 April to 3 August in 1998 (Fig. 1). Brooding females were absent before and after this period. The proportion of gravid mussels varied among sample dates, with 37% being the highest recorded.

Of the 90 fish species in 18 families tested, glochidia metamorphosed on 21 of 40 minnow species but not on any other fishes (Table 1). *Cyprinella spiloptera* and *Macrhybopsis storeriana* produced the greatest number of juveniles per individual, but *Campostoma anomalum, Clinostomus elongatus, Cyprinella lutrensis, Luxilus chrysocephalus* , and *L. zonatus* each produced >25 juveniles per individual in some trials. However, juvenile mussel production was highly variable among trials for these species, and production also varied among congeneric species. For example, although *Cyprinella spiloptera* produced large numbers of glochidia in some trials, other trials produced none, and other species of *Cyprinella* produced few juveniles (*C. whipplei, C. venusta*). *Nocomis* and *Pimephales* produced moderate but variable numbers of juveniles, and *Hybognathus, Margariscus, Rhinichthys*, and *Semotilus* produced consistently low numbers. Within the Cyprinidae, ten *Notropis* species and 9 other species were tested and none proved to be acceptable hosts. None of the previously reported hosts (*Lepomis macrochirus, L. cyanellus, Sander canadensis*) or their congeners produced juveniles, and most sloughed glochidia in < 8 days. The duration of the parasitic period on suitable hosts varied with water temperature and ranged from 7-46 days, but

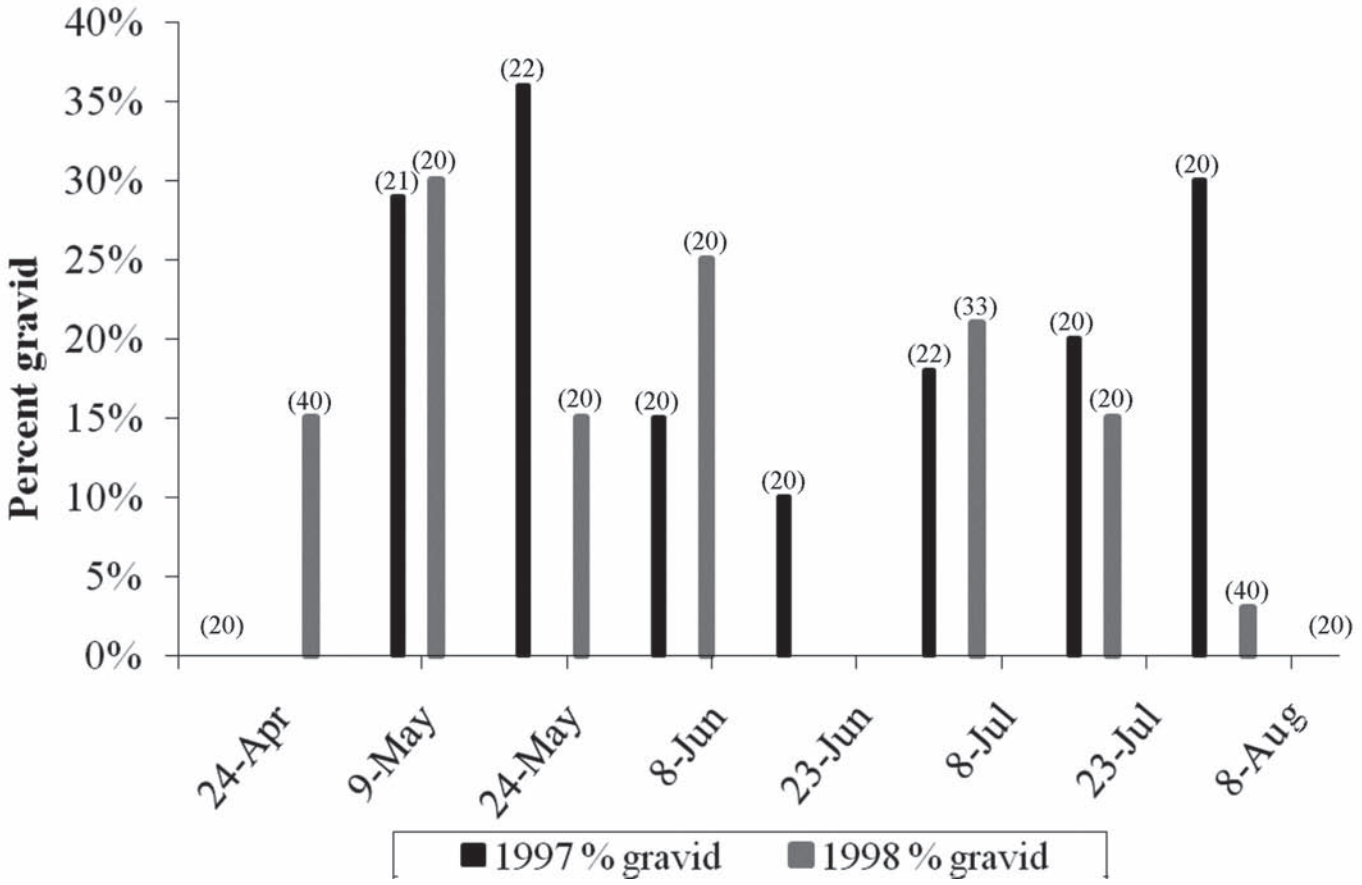

FIGURE 1

Theliderma metanevra brooding periods in the St. Croix River during 1997 and 1998. Number of animals observed is in parentheses.

most juvenile mussels metamorphosed between 13-25 days post inoculation.

Distribution and status

Historically, *T. metanevra* occurred throughout much of the main stems of the upper Mississippi, Minnesota, and Wisconsin rivers, and in the lower reaches of some larger Mississippi River tributaries (Fig. 2). In the last 25 years, a total of 2,182 live individuals were collected in the St. Croix (1,377), Wisconsin (569), Mississippi (225) and Chippewa (11) rivers. *Theliderma metanevra* is now apparently extirpated from interior Minnesota, including 391 km of the Minnesota River and from 376 km of the Wisconsin River above Prairie du Sac Dam. Empty, weathered valves were collected at single sites in the Des Moines and Cedar rivers (Minnesota), and the Black River and Mill Creek (Wisconsin). *Theliderma metanevra*'s range has apparently decreased in the lower Chippewa River, Wisconsin, and in portions of the Mississippi River, where populations are disjunct (Fig. 2). On the basis of the presence of juvenile individuals, reproducing populations are present in the Mississippi, St. Croix, and lower Wisconsin rivers; no evidence of recent reproduction has been documented in the Chippewa River.

DISCUSSION

Brooding and host suitability

Early studies describe *T. metanevra* as tachytictic (short-term brooder), bearing glochidia from May to July (Lefevre & Curtis, 1910; Ortmann, 1911; Utterback, 1915; Surber, 1912b; Baker, 1928), and our study confirms this. In a more southerly population in the Tennessee River, *T. metanevra* was gravid from late March to July (Garner et al., 1999). The brooding period in the St. Croix River (late April to early August), near the northern limit of the species' range, was about a month behind this southern population. The brooding period at our study site also corresponds to the time during which gravid females display their mantle lure (Sietman et al., 2012). Most other quadruline species are short-term spring-summer brooders (Howard, 1914; Coker

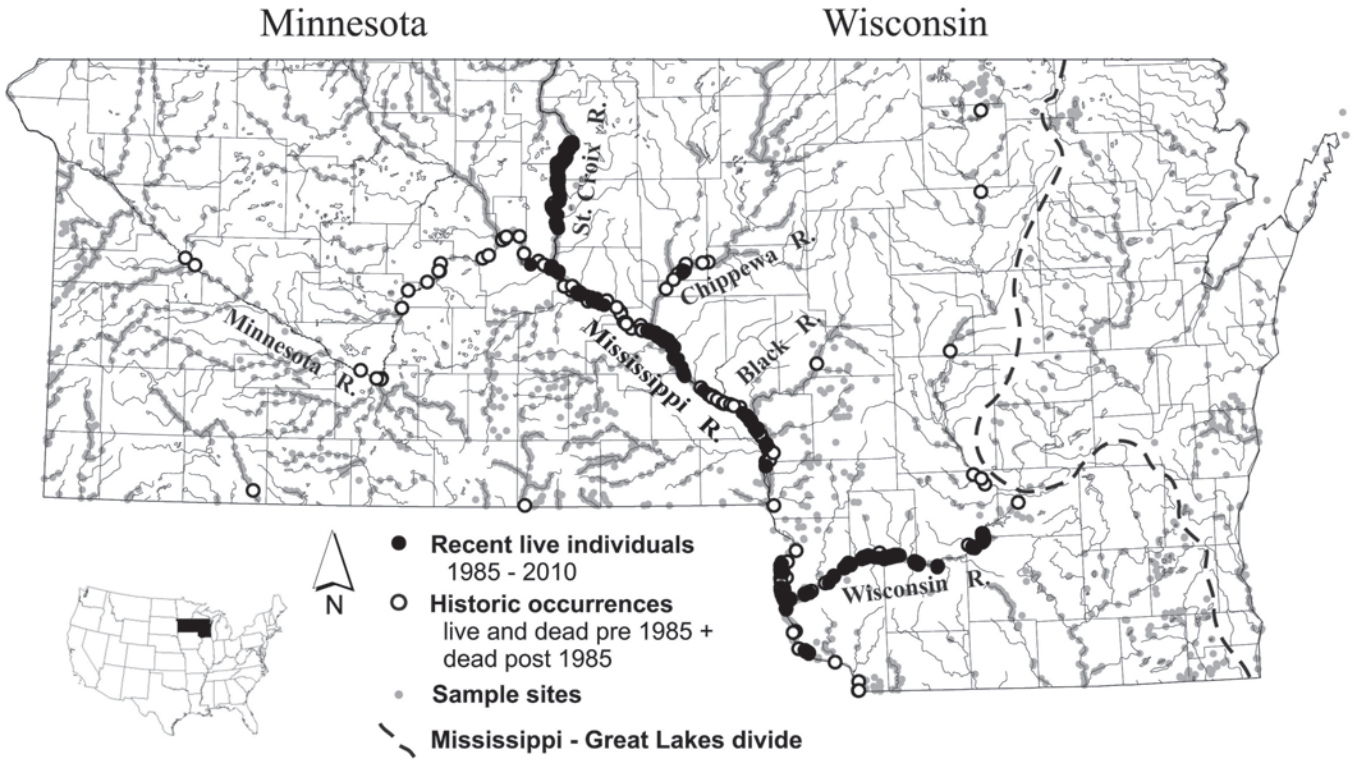

FIGURE 2
Recent and historical distribution of *Theliderma metanevra* in Minnesota and Wisconsin.

et al., 1921; van der Schalie, 1936; Yeager & Neves, 1986; Yeager & Saylor, 1995; Howells, 2000), except for winged mapleleaf (*Quadrula fragosa*) (Sietman et al., 2012; Hove et al., 2012) and washboard (*Megalonaias nervosa*) (Woody & Holland-Bartels, 1993), which brood glochidia for a brief time in the fall.

Gravid female *T. metanevra* display a diminutive mantle lure to attract hosts, and glochidia are ejected in a loose mass when the lure is attacked by fishes or otherwise disturbed (Sietman et al., 2012), a behavior Barnhart et al. (2008) defined as reflexive release (see display photos and video footage online at http://www.dnr.state.mn.us/mussels/quadrula). Many unionid species release conglutinates (aggregates of glochidia) to attract host fishes (Haag & Warren, 2003; Barnhart et al., 2008; White et al., 2008), but we did not find evidence for this in *T. metanevra*. Individuals in the laboratory occasionally released puerile conglutinates composed of immature glochidia or eggs, and this type of premature abortion of the brood is a common response to stress in quadruline mussels (Lefevre & Curtis, 1912); however, mature glochidia were never released in conglutinates. These findings indicate that *T. metanevra* does not use conglutinates as a host infection strategy.

A wide variety of minnow species in several genera were suitable hosts for *T. metanevra*, similar to host use of *T. cylindrica*, which metamorphosed robustly on 8 minnow species in 3 genera, and marginally on several non-cyprinid species (Yeager & Neves, 1986; Fobian, 2007). In contrast, *T. intermedia* metamorphosed only on 2 minnows, *Erimystax dissimilis* and *E. insignis* (Yeager & Saylor, 1995), showing the wide range in host specificity in this genus. The other species of *Theliderma* are either presumed extinct (*T. stapes*) or hosts have not been identified *(T. sparsa*). After multiple laboratory trials, our findings did not corroborate previous reports of *Lepomis cyanellus*, *L. macrochirus* and *Sander canadensis* as hosts for *T. metanevra* (Surber, 1912a; Howard, 1914; Wilson, 1916), results that have been repeated in the literature for nearly a century (e.g., Fuller, 1974; Parmalee & Bogan, 1998). Although controlled, replicated host trials can show the potential suitability of fishes as hosts, it is also necessary to examine patterns of naturally occurring infections and to consider other ecological factors that may determine which host species are most important in the wild.

Of the suitable minnow hosts we identified, *Cyprinella spiloptera* is likely an important natural host for *T. metanevra* in our study region because it produced

the strongest metamorphosis, and it is widespread and abundant in rivers where *T. metanevra* occurs (Becker, 1983; Dieterman, 2008). Other co-occurring minnows that are less abundant or more localized in our study area, but are potentially important hosts include *Luxilus cornutus, Macrhybopsis storeriana, Pimephales notatus*, and *Pimephales promelas*. It is likely that several fish species we identified as suitable hosts in the lab rarely, if ever, serve as natural hosts in our study region because their primary habitats do not overlap with those of *T. metanevra*. Fishes such as *Semotilus, Rhinichthys, Campostoma, Clinostomus*, and *Nocomis* are found primarily in smaller tributaries (Becker, 1983) and probably are rarely exposed to glochidia of *T. metanevra* in the wild.

The use of minnows as glochidial hosts by *Theliderma* contrasts with other quadruline genera, all of which use catfishes (Ictaluridae) (Coker et al., 1921; Howells et al., 1996; Howells, 1997; Haag & Warren, 2003; Steingraeber et al., 2007; Barnhart et al., 2008). *Amphinaias asperata* glochidia transformed only on *Ictalurus punctatus*, but not on 15 cyprinids or additional fish species from other families (Haag & Warren, 2003). Similarly, *Cyclonaias tuberculata, Tritogonia verrucosa*, and *Quadrula fragosa* transformed only on species in the Ictaluridae, and not on a wide variety of minnows or other fishes (Hove et al., 1997, 2011, 2012; Steingraeber et al., 2007). The use of cyprinids as hosts may be a primitive trait among the Quadrulini. Molecular phylogenies of the North American Ambleminae place Quadrulini as sister to the rest of the subfamily (including the tribes Amblemini, Lampsilini, and Pleurobemini; sensu Serb et al., 2003; Campbell et al., 2005). Specialization on catfishes is not reported for any other unionid clade, but use of Cyprinidae is shared with many species in the Pleurobemini (Bruenderman & Neves, 1993; Haag & Warren, 2003; White et al., 2008). However, it is equally likely that use of minnows arose independently in the Pleurobemini and *Theliderma*. Nevertheless, within the Quadrulini, *Theliderma* is sister to a larger clade including *Amphinaias, Cyclonaias, Quadrula*, and *Tritogonia* (Serb et al., 2003; Campbell et al., 2005); specialization on catfishes supports the inclusiveness of this latter group and the evolutionary distinctiveness of *Theliderma*.

Transformation of juveniles was inconsistent among trials for several fish species, with some trials producing large number of juveniles and others producing few or none (e.g., *Cyprinella, Luxilus*, and *Pimephales* spp.). We were unable to document the cause for these inconsistencies but they could have been related to water quality issues, unhealthy glochidia, or predation of newly transformed juveniles by the host fish. We recommend holding small fishes and catostomids in suspended nets or using a false bottom tank or a modified recirculating aquatic housing aquarium system when testing host suitability. Aquatic housing units (e.g., Aquatic Habitats, Aquatic Ecosystems, Inc.) are multiple tank flow-through systems that allow researchers to hold fish individually and collect sloughed glochidia and transformed juveniles with a filter cup placed under the outfall of each tank. These measures can help protect juveniles from possible predation by fishes within experimental chambers. The potential for inconsistent results among trials due to numerous, external factors underscores the value of replication in laboratory host trials. We further recommend that host trials include as a positive control species that are known hosts when such information exists. Inclusion of controls can aid in assessing when other factors may have influenced results of host trials (e.g., poor glochidial health, water quality issues, cross contamination of siphonate).

Distribution and status

Theliderma metanevra is a species of large and medium sized rivers (Cummings & Mayer, 1992), and in the upper Midwest it occurred historically only in portions of the Mississippi River and its larger tributaries. Barrier waterfalls on the Mississippi River at Minneapolis-St. Paul, and a 10 km reach of steep rapids on the St. Croix River at Taylors Falls, Minnesota, further limited the post-glacial upstream dispersal of *T. metanevra* and other aquatic organisms (Underhill, 1957; Graf, 1997; Hornbach, 2001). Because of its large number of suitable hosts that together occur across a range of stream sizes and habitats, unknown factors other than host fish limitation are probably responsible for the restriction of *T. metanevra* to large rivers.

The recent decline of *T. metanevra* suggests it is sensitive to human disturbance. Rivers where it has been extirpated from large areas are, or have been, heavily affected by dams, wetland drainage, or water quality degradation associated with agricultural and urban land development; these areas include the Minnesota River (Lundeen & Koschak, 2011), Wisconsin River (Wisconsin State Board of Health, 1927; Mathiak, 1979), and the Mississippi River below Minneapolis-St. Paul (Scarpino, 1985). The St. Croix River apparently supports the largest remaining population of *T. metanevra* in our study area, as well as several other rare mussel species (Hornbach, 2001), likely because it has largely escaped these impacts (Fago & Hatch, 1993; Wenger et al., 2000).

Prior to impoundment of the Mississippi River for navigation, *T. metanevra* was locally abundant even after intense exploitation by the button industry (Grier, 1922), but the species declined considerably after

impoundment (Finke, 1966; Fuller, 1980; Thiel, 1981). Even though populations persist in portions of the Mississippi River, they are sparse and disjunct. Minnow populations in the Mississippi River also appear to have declined after impoundment, or their distribution within the stream channel changed, with many species now being restricted to channel margins or backwaters (Winston et al., 1991; Dettmers et al., 2001). Consequently, the decline of *T. metanevra* may be due to loss of host fishes or habitat changes that limit their occurrence near main-channel mussel beds.

Because minnows are less vagile than larger fishes such as catfishes (Hill & Grossman, 1987; Pellett et al., 1998; Daugherty & Sutton, 2005), *T. metanevra* may not recolonize formerly inhabited areas as readily as other quadrulines. We see evidence of this in the Minneapolis-St. Paul region of the Mississippi River where populations of *Amphinaias pustulosa*, *A. nodulata*, and *Quadrula quadrula*, species which use catfishes as host, were extirpated (Fuller, 1980) but have since recolonized this reach; in contrast, *T. metanevra* remains absent in the area even though it occurred there historically. Consequently, reintroduction of captively propagated juveniles or translocated adults of *Theliderma* may be necessary to recover populations, whereas it may be less necessary for other quadruline species, at least in areas where host fish movement is not restricted.

Our study reveals key aspects of the life history and status of *T. metanevra* which will benefit efforts to conserve this regionally threatened species and contribute to an understanding of the evolutionary diversification of the Quadrulini. Identifying suitable hosts in the laboratory is an important step in understanding unionid life histories but it is also essential to identify hosts used in the wild. Further early life history research should be directed toward recovering juvenile *T. metanevra* from naturally infested fishes (Boyer et al. 2011). The current distribution of *T. metanevra* in the upper Midwest is reduced, and this species may not be able to readily recolonize areas where it has been extirpated. Invasive bivalves (i.e., *Dreissena* sp.) within most of its current range are also a constant threat (Schloesser et al., 1996). Therefore, we agree with the current threatened status of this species in Minnesota and Wisconsin. For reintroduction efforts that involve culturing juvenile mussels, we recommend the use of species within the genera *Cyprinella* and *Luxilus* due to their high juvenile production rates and co-occurrence with *T. metanevra*. *Pimephales* may also be a useful host due to the ease of obtaining large numbers of these species from hatcheries or bait dealers.

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TABLE 1

Fishes identified as suitable hosts for *Theliderma metanevra* glochidia in the laboratory[a]. Recovery period is the number of days post-infection during which juvenile mussels were observed or, for trials that produced no juveniles, the number of days until individuals ceased to carry glochidial infections. Location of fish collections if other than Minnesota are: MO = Missouri, AR = Arkansas, HR = hatchery raised. †Juveniles observed during first siphonate check. *Number of fish equals the average between the number of fish infested and survivors. Fish nomenclature follows Nelson et al. (2004), except for taxonomic revisions in Wood et al. (2002), Blum et al. (2008) and Strange & Mayden (2009).

Species	Trial	Water temp. range(C)	No. fish infested (survivors)	Recovery period (d)	No. juveniles recovered	Mean no. juveniles/fish*
Campostoma anomalum	May-07	19-20	3 (2)	15-30	158	63.2
	Jun-07	19-20	10 (2)	15-23	10	1.7
Campostoma oligolepis (MO)	May-07	19-20	3 (1)	15-25	8	2.0
	Jun-07	19-20	7 (0)	15-23	4	1.1
Clinostomus elongatus	Jun-08	22-24	14 (0)	8-16	80	12.3
	Jun-08	22-24	2 (0)	13-21	48	48.0
Cyprinella galactura (MO)	Jun-08	22-24	16 (16)	7-21	234	14.6
	May-09	22-24	3 (1)	13-21	24	12.0
Cyprinella lutrensis	Jul-06	21-22	1 (0)	21	0	0
	May-07	19-20	6 (2)	15-25	142	35.5
	Jun-07	19-20	10 (9)	16-25	143	15.1
Cyprinella spiloptera	Jun-06	21-22	18 (9)	13-21	8	0.6
	Jul-06	21-22	21 (8)	13-27	77	5.3
	Jun-07	19-20	11 (8)	7	0	0
	Jun-07	19-20	9 (6)	28	0	0
	Aug-07	23-25	9 (9)	10†	7	0.8
	Jun-08	22-24	5 (4)	9-28†	1275	283.3
	Jun-08	22-24	8 (7)	7-25	474	63.2
Cyprinella venusta (AR)	May-07	19-20	8 (8)	15-22	70	8.8
	Jun-07	19-20	10 (10)	3	0	0
	Jun-07	19-20	12 (6)	16-23	55	6.1
Cyprinella whipplei (MO)	Jun-07	19-20	11 (11)	3	0	0
	Jun-07	19-20	14 (14)	15-18	9	0.6
Hybognathus hankinsoni	May-06	19-20	1 (1)	11	0	0
	May-07	19-20	3 (3)	15-25	12	4.0

TABLE 1
(Continued)

	Jun-07	19-20	8 (2)	23-32	14	2.8
Hybognathus nuchalis (AR)	Jun-07	19-20	3 (2)	18-29	4	1.6
Hybognathus nuchalis (MO)	May-09	22-24	2 (0)	12-13	2	2.0
Luxilus chrysocephalus (MO)	May-07	19-20	4 (4)	15-25	379	94.8
	Aug-07	19-20	8 (8)	14-46	69	8.6
Luxilus cornutus	May-06	19-20	9 (2)	25	0	0
	Jul-06	22-23	12 (6)	10	0	0
	Jun-08	22-24	26 (26)	7-21	124	4.8
	Jul-09	22-24	4 (4)	13-21	61	15.3
Luxilus zonatus (MO)	May-07	19-20	4 (4)	15-30	104	26.0
	Aug-07	19-20	6 (5)	14-24	84	15.3
Macrhybopsis storeriana	May-07	19-20	1 (0)	16-26	159	159.0
	May-09	22-24	2 (2)	17-21	91	45.5
Margariscus margarita	May-07	19-20	1 (1)	9	0	0
	Jun-08	22-24	12 (3)	18-21	1	0.1
	May-09	22-24	4 (4)	9-24	32	8.0
Nocomis biguttatus	Jun-06	21-22	2 (1)	18	0	0
	Jun-07	19-20	9 (7)	4	0	0
	Aug-07	19-20	2 (2)	14-46	25	16.7
	Jun-08	22-24	21 (5)	11-14	1	0.1
Pimephales notatus	Jun-06	19-20	8 (1)	9	0	0
	Jul-06	21-22	3 (1)	13-22	2	1.0
	May-07	19-20	6 (5)	16-30	70	12.7
	Jun-07	19-20	9 (9)	3	0	0
	Jun-07	19-20	11 (10)	16-25	60	5.7
Pimephales promelas	May-07	19-20	6 (2)	16-22	20	5.0
	Jun-07	19-20	15 (4)	16-25	152	16.0
Rhinichthys cataractae	May-07	19-20	3 (2)	16-30	34	13.6
	Jun-07	19-20	10 (1)	23	0	0
	Jun-07	19-20	9 (8)	4	0	0
	Aug-07	19-20	9 (4)	20-34	14	2.2
Rhinichthys obtusus	Jun-06	21-22	6 (5)	16-24	3	0.5
	Jul-06	21-22	20 (20)	15-17	1	0.1
	May-07	19-20	2 (1)	23	0	0
	Jul-07	19-20	12 (2)	14	0	0
	Aug-07	19-20	24 (23)	18	0	0

TABLE 1
(Continued)

Semotilus atromaculatus	Jun-06	21-22	15 (11)	16-24	2	0.2
	Jul-06	22-23	20 (20)	10	0	0
	Jun-07	19-20	10 (10)	4	0	0
	Jun-07	19-20	29 (16)	10	0	0
	Jul-07	21-22	29 (12)	11	0	0

[a] Fish species that did not facilitate glochidia metamorphosis (number of trials, total number of fish tested, range of maximum number of days to glochidia rejection): *Acipenser fulvescens* (HR) (1, 2, 5), *Scaphirhynchus albus* (HR) (1, 2, 5), *Lepisosteus osseus* (1, 1, 4), *Lepisosteus platostomus* (1, 3, 4), *Chrosomus eos* (2, 29, 4-10), *Chrosomus erythrogaster* (2, 15, 10-12), *Cyprinus carpio* (1, 16, 4), *Hybopsis amblops* (MO) (2, 23, 8-11), *Lythrurus umbratilis* (1, 10, 11), *Macrhybopsis hyostoma* (1, 8, 3), *Notemigonus crysoleucas* (2, 9, 14-17), *Notropis atherinoides* (4, 31, 4-11), *Notropis blennius* (1, 6, 5), *Notropis buccatus* (MO) (1, 2, 5), *Notropis dorsalis* (2, 16, 5-8), *Notropis hudsonius* (2, 6, 5-14), *Notropis nubilus* (MO) (1, 3, 5), *Notropis percobromus* (2, 5, 5-9), *Notropis texanus* (1, 12, 8), *Notropis topeka* (HR) (2, 15, 4-8), *Notropis volucellus* (2, 29, 3-4), *Phenacobius mirabilis* (1, 14, 7), *Pimephales vigilax* (3, 28, 5-15), *Carpiodes cyprinus* (1, 2, 5), *Catostomus commersonii* (1, 10, 4), *Hypentelium nigricans* (1, 1, 5), *Ictiobus bubalus* (1, 1, 4), *Moxostoma duquesnei* (1, 5, 4), *Moxostoma macrolepidotum* (1, 2, 4), *Ameiurus melas* (4, 21, 4-7), *Ameiurus natalis* (1, 1, 4), *Ictalurus punctatus* (3, 12, 3-4), *Noturus exilis* (2, 7, 4-5), *Noturus flavus* (1, 4, 3), *Noturus gyrinus* (4, 11, 3-4), *Esox lucius* (1, 2, 4), *Umbra limi* (1, 1, 9), *Oncorhynchus mykiss* (HR) (1, 4, 4), *Percopsis omiscomaycus* (1, 1, 4), *Lota lota* (1, 2, 9), *Gambusia affinis* (MO) (2, 20, 1-17), *Fundulus catenatus* (MO) (1, 2, 11), *Fundulus diaphanus* (1, 3, 4), *Fundulus olivaceus* (MO) (1, 1, 11), *Culaea inconstans* (1, 9, 4), *Cottus bairdii* (1, 2, 18), *Morone chrysops* (1, 1, 5), *Ambloplites rupestris* (1, 3, 5), *Lepomis cyanellus* (4, 21, 3-10), *Lepomis gibbosus* (1, 3, 5), *Lepomis humilis* (1, 4, 4), *Lepomis macrochirus* (2, 12, 3-4), *Lepomis megalotis* (MO) (1, 3, 5), *Micropterus dolomieu* (2, 7, 3-4), *Micropterus salmoides* (1, 3, 4), *Pomoxis annularis* (1, 2, 5), *Pomoxis nigromaculatus* (2, 9, 3-4), *Etheostoma caeruleum* (1, 3, 5), *Etheostoma flabellare* (2, 7, 4-7), *Etheostoma nigrum* (1, 12, 4), *Etheostoma zonale* (1, 5, 7), *Perca flavescens* (1, 26, 8), *Percina caprodes* (1, 4, 4), *Percina maculata* (1, 11, 4), *Percina phoxocephala* (1, 3, 4), *Percina shumardi* (1, 4, 4), *Sander canadensis* (2, 22, 5-9), *Sander vitreus* (1, 1, 4), *Aplodinotus grunniens* (1, 1, 5).

WALKERANA The Journal of the Freshwater Mollusk Conservation Society

OUR PURPOSE

The Freshwater Mollusk Conservation Society (FMCS) is dedicated to the conservation of and advocacy of freshwater mollusks, North America's most imperiled animals. Membership in the society is open to anyone interested in freshwater mollusks who supports the stated purposes of the Society which are as follows:

1) Advocate conservation of freshwater molluscan resources;

2) Serve as a conduit for information about freshwater mollusks;

3) Promote science-based management of freshwater mollusks;

4) Promote and facilitate education and awareness about freshwater mollusks and their function in freshwater ecosystems;

5) Assist with the facilitation of the National Strategy for the Conservation of Native Freshwater Mussels (Journal of Shellfish Research, 1999, Volume 17, Number 5), and a similar strategy under development for freshwater gastropods.

OUR HISTORY

The FMCS traces it's origins to 1992 when a symposium sponsored by the Upper Mississippi River Conservation Committee, USFWS, Mussel Mitigation Trust, and Tennessee Shell Company brought concerned people to St. Louis, Missouri to discuss the status, conservation, and management of freshwater mussels. This meeting resulted in the formation of a working group to develop the National Strategy for the Conservation of Native Freshwater Mussels and set the ground work for another freshwater mussel symposium. In 1995, the next symposium was also held in St. Louis, and both the 1992 and 1995 symposia had published proceedings. Then in March 1996, the Mississippi Interstate Cooperative Research Association (MICRA) formed a mussel committee. It was this committee (National Native Mussel Conservation Committee) whose function it was to implement the National Strategy for the Conservation of Native Freshwater Mussels by organizing a group of state, federal, and academic biologists, along with individuals from the commercial mussel industry. In March 1998, the NNMCC and attendees of the Conservation, Captive Care and Propagation of Freshwater Mussels Symposium held in Columbus, OH, voted to form the Freshwater Mollusk Conservation Society. In November 1998, the executive board drafted a society constitution and voted to incorporate the FMCS as a not-for-profit society. In March 1999, the FMCS held it's first symposium "Musseling in on Biodiversity" in Chattanooga, Tennessee. The symposium attracted 280 attendees; proceedings from that meeting are available for purchase. The second symposium was held in March 2001 in Pittsburgh, Pennsylvania, the third in March 2003 in Raleigh, North Carolina, the fourth in St. Paul, Minnesota in May 2005, the fifth in Little Rock, Arkansas in March 2007, and the sixth in Baltimore, Maryland in April 2009. The society also holds workshops on alternating years, and produces a newsletter three times a year.

FMCS SOCIETY COMMITTEES

Participation in any of the standing committees is open to any FMCS member. Committees include:

Awards

Environmental Quality and Affairs

Gastropod Distribution and Status

Genetics

Guidelines and Techniques

Information Exchange - Walkerana and Ellipsaria

Mussel Distribution and Status

Outreach

Propagation and Restoration

TO JOIN FMCS OR SUBMIT A PAPER

Please visit our website for more information at http://www.molluskconservation.org

Or contact any of our board members or editors of WALKERANA to talk to someone of your needs. You'll find contact information on the back cover of this publication.

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