

Early Life-history and Conservation Status of *Venustaconcha ellipsiformis* (Bivalvia, Unionidae) in Minnesota

DANIEL C. ALLEN,¹ BERNARD E. SIETMAN AND DANIEL E. KELNER²

Minnesota Department of Natural Resources, Division of Ecological Services, 500 Lafayette Road, Saint Paul 55155

MARK C. HOVE³ AND JENNIFER E. KURTH⁴

University of Minnesota, Department of Fisheries, Wildlife and Conservation Biology, 1980 Folwell Avenue, Saint Paul 55108

J. MIKE DAVIS

Minnesota Department of Natural Resources, Division of Ecological Services, 1801 South Oak Street, Lake City 55041

JEFFERY L. WEISS

Minnesota Department of Natural Resources, Lanesboro Area Fisheries, Route 2 Box 85, Lanesboro 55949

AND

DANIEL J. HORNBAACH

Macalester College, Department of Biology, 1600 Grand Avenue, Saint Paul, Minnesota 55105

ABSTRACT.—The ellipse, *Venustaconcha ellipsiformis* (Bivalvia: Unionidae), was first recorded in Minnesota from the Straight River in 1987, but we knew little of its distribution in the state, brooding behavior, glochidial host fish relationships or status. To examine these questions, we followed standard procedures to conduct an extensive, qualitative statewide mussel survey, described mantle flapping behavior from field and laboratory observations and identified suitable glochidia hosts in the laboratory and from naturally infested fishes. We found extant populations in five Mississippi River tributaries in southeastern Minnesota: the Cannon, Cedar, Root, Upper Iowa and Zumbro rivers. This appears to be the extent of its historic range in Minnesota as no valid records were found elsewhere. Among these, the largest population occurred in the headwaters of the Root River drainage, which was also the only drainage where we observed recent recruitment. Brooding *V. ellipsiformis* quickly flap a small mantle extension, often in response to passing shadows or jarring of the substrate, or their mantle extensions may be slowly undulated. We identified 11 fish species as suitable hosts for *V. ellipsiformis* glochidia in the laboratory: brook stickleback (*Culaea inconstans*), mottled sculpin (*Cottus bairdii*), slimy sculpin (*C. cognatus*), logperch (*Percina caprodes*), mud darter (*Etheostoma asprigene*), rainbow darter (*E. caeruleum*), Iowa darter (*E. exile*), fantail darter (*E. flabellare*), Johnny darter (*E. nigrum*), banded darter (*E. zonale*) and blackside darter (*P. maculata*). Rainbow darter, fantail darter and blackside darter were also found naturally infested with *V. ellipsiformis* glochidia. *Venustaconcha ellipsiformis* should remain classified as a “Threatened” species in Minnesota and management should include conserving populations within drainages due to its restricted range and likely low dispersal ability.

¹ Corresponding author present address: Oklahoma Biological Survey and Department of Zoology, University of Oklahoma, Norman 73019; e-mail: dallen@ou.edu

² Present address: United States Army Corps of Engineers, 190 5th Street East, Saint Paul, Minnesota 55101

³ Secondary author

⁴ Present address: University of Maine, Department of Wildlife Ecology, 5755 Nutting, Orono 04469

INTRODUCTION

Rare mussel management is improved with knowledge of species distribution and life history. *Venustaconcha ellipsiformis* (Conrad, 1836), the ellipse, is a small stout-shelled mussel that generally lives in small to medium sized streams with stable gravel or mixed sand and gravel bottoms (Cummings and Mayer, 1992). This species has a broad extralimital distribution in the central United States; including Arkansas, Illinois, Indiana, Iowa, Kansas, Michigan, Minnesota, Missouri, Ohio and Wisconsin. (Baker, 1928; Van der Schalie and Van der Schalie, 1963; Cummings and Mayer, 1992; Oesch, 1995; Obermeyer *et al.*, 1997; J.L. Harris, pers. comm.). *Venustaconcha ellipsiformis* was not included in earlier accounts of Minnesota unionids (Dawley, 1947). (Davis, 1988) was the first to report the species in Minnesota from the Cannon River drainage, and (Graf, 1997) later reported *V. ellipsiformis* from the Zumbro River and St. Croix River drainages. *Venustaconcha ellipsiformis* is currently listed as Extirpated from Ohio, Endangered in Kansas, Threatened in Iowa, Minnesota and Wisconsin; and a Species of Special Concern in Illinois, Indiana and Michigan. As part of this study, we wanted to determine the range of *V. ellipsiformis* in Minnesota.

Like most North American freshwater mussels, *Venustaconcha ellipsiformis* larvae (glochidia) are obligate parasites on fishes. Freshwater mussels benefit from this parasitic larvae life stage in several ways, including improved dispersal ability (Smith, 1985). Specialized extensions of the mantle, "mantle flaps," have evolved in other North American mussel species, and it is common for these species to flap mantles in a rhythmic motion. This behavior is thought to draw host fishes to females brooding glochidia (Haag and Warren, 2003), and it may serve to suspend glochidia in the water column and increase the likelihood of their encountering fish (Kraemer, 1970). *Villosa nebulosa* and *V. vibex* have been shown to release larger numbers of larvae when fishes are present, and *V. vibex* release large numbers of glochidia when host fish are able to make physical contact with the mussel (Haag and Warren, 2000). Piscivorous fish have been observed to strike at mantle flaps and were subsequently infested with glochidia (Haag and Warren, 1999). *Venustaconcha ellipsiformis* display mantle flaps while brooding, but mantle flapping behaviors have not been previously published.

Though few host suitability studies have been conducted using *Venustaconcha ellipsiformis* glochidia, its larvae have been shown to metamorphose on rainbow darters (*Etheostoma caeruleum*) under laboratory conditions, and three darter species (*E. blenniodes*, *E. spectabile* and *E. whipplei*) in the Spring River, Missouri, were naturally infested with *V. ellipsiformis* glochidia (Riusech and Barnhart, 2000). We wanted to confirm the glochidial host suitability of rainbow darter for Minnesota populations, expand the number of fish species tested for host suitability and determine natural infestations of fish with *V. ellipsiformis* glochidia in select Minnesota streams. To aid in the identification of juvenile *V. ellipsiformis* recovered from naturally infested darter species, we also conducted additional host suitability trials with *Lampsilis cardium* and *L. siliquoidea* glochidia on the darter species collected for natural infestation analysis.

In this paper we expand the known range of *Venustaconcha ellipsiformis* in Minnesota, describe mantle-flapping behaviors of brooding individuals, identify fishes that serve as hosts for *V. ellipsiformis* glochidia under natural and laboratory conditions and discuss how these factors are important for the species conservation.

METHODS

DISTRIBUTION

We gathered information from several sources to describe *Venustaconcha ellipsiformis* distribution in Minnesota. Most data were gathered during a statewide survey of unionids

from 1999 to 2004, totaling 1673 sample sites. These data are held and maintained in the Minnesota Department of Natural Resources (MN DNR) Natural Heritage Database. Rivers and streams were the primary focus of our study, although some lakes were sampled. At each site, we conducted a timed search of all microhabitats to collect live and dead mussels while wading, snorkeling or using SCUBA gear. At turbid sites we searched for mussels by sweeping our hands back and forth across the substrate and probing the substrate to find buried mussels and shells. Live mussels were identified, separated into three broad age groups based on the number of external annuli on their valves (1 to 5, 6 to 10 and >10), and the largest and smallest individual within each age group were measured for length along the longest anterior-posterior axis. Although external growth rings may not accurately represent the age of a mussel (Neves and Moyer, 1988; Downing *et al.*, 1992), we think it is a reasonable method to age younger mussels and the data help describe the general age composition of a population. Voucher specimens were deposited at the University of Minnesota's James Ford Bell Museum of Natural History (JFBM). We also included data from two additional mussel surveys. (Davis, 1988) surveyed 38 sites in the Cannon River drainage, and (Bright *et al.*, 1989) surveyed 83 sites in the Zumbro River drainage. These two surveys used a variety of qualitative and quantitative methods to characterize mussel assemblages. Species nomenclature follows (Turgeon *et al.*, 1998).

BROODING BEHAVIOR

We recorded mantle-flapping behaviors of brooding *Venustaconcha ellipsiformis* in the field and laboratory. We made field observations on 44 brooding *V. ellipsiformis* at sites in the North Fork Zumbro River (Oct. 1995), South Branch Middle Fork Zumbro River (Sep. 1996 and Nov. 1998), South Fork Zumbro River (Nov. 1997) and Deer Creek (Apr.–May 2004), a tributary of the Root River. For laboratory observations, we collected 2–10 brooding *V. ellipsiformis* each year and held them individually in 100–400 ml beakers in 40 L aquaria. We placed two of the brooding ellipse in gravel (3 cm deep) in a 40 L aquarium in 1996. Animals were held at 11 ± 2 C in 1998, 19 ± 2 C in 1995, 1996 and 2004; and 21 ± 2 C in 1997. Mantle morphology and flapping behavior follows nomenclature in (Kraemer, 1970).

HOST SUITABILITY

We followed standard methods to conduct glochidia host suitability trials for *Venustaconcha ellipsiformis* (Zale and Neves, 1982; Hove *et al.*, 2000). Fish were collected from central and southeastern Minnesota and held in aquaria (40 L or 400 L) at the University of Minnesota Wet Laboratory (UMN) for at least 20 d prior to glochidia infestation. We collected brooding *V. ellipsiformis* from the Middle Fork Zumbro River, Minnesota. Glochidia were tested for viability and fish were infested using one of two techniques. Most fish were exposed to glochidia by placing them in a 1 to 40 L bath with vigorous aeration. Other fish had glochidia pipetted directly onto gills. Fish were examined to confirm glochidia had attached, and moved to aquaria held at three temperature ranges: 11 ± 2 C, 19 ± 3 C and 21 ± 2 C. Fish were fed regularly and aquaria were siphoned regularly to check for presence of glochidia and juvenile mussels. An experiment was terminated when glochidia were no longer attached to fishes. Fish nomenclature follows (Nelson *et al.*, 2004).

NATURAL INFESTATIONS

We collected fishes naturally infested with glochidia from sites in the South Branch Middle Fork Zumbro River and Deer Creek where *Venustaconcha ellipsiformis* were abundant. On 5 Nov. 1998 we collected fishes from the South Branch Middle Fork Zumbro River. Trial I was conducted at UMN and Trial II was conducted at MN DNR Lanesboro Area Fisheries

Headquarters. We collected fishes from Deer Creek on 16 Apr. and 6 May 2004 and conducted trials at UMN. Otherwise, procedures follow those described for host-suitability trials.

We identified juvenile mussels recovered from naturally infested fishes using mussel species distributions in the Zumbro River and Root River drainages, brooding periods, glochidial valve characters, and results from our host-suitability trials. We generated a list of mussel species known to occur in the Zumbro and Root river systems from our data, (Bright *et al.*, 1989), and records at JFBM. We also reviewed (Coker *et al.*, 1921; Van der Schalie, 1936; Van der Schalie and Van der Schalie, 1963; Gordon and Layzer, 1989) to estimate mussel brooding periods in these streams. The result was a list of possible mussel species for our recovered juveniles. We generated scanning electron micrographs of glochidia from mussel species on this list using the following procedures. Glochidia were preserved in 95% ethanol and later placed in 100% ethanol. They were then mounted on scanning electron microscope (SEM) specimen stubs using double-faced adhesive tape. We coated specimens with gold using a Fullam Sputter Coater, and viewed them with a Hitachi S3500N variable pressure SEM with Windows NT operating system and Quartz PCI digital imaging software. Valve dimensions were measured to the nearest millimeter, and were converted to microns using the scale bar generated with each image. We measured the following glochidia characters described by (Hoggarth, 1999): valve length, valve height and hinge length. We identified juvenile mussels recovered from naturally infested darters based on characters of glochidia from species collected in Minnesota and descriptions in (Surber, 1912; Surber, 1915; Waller, 1987; Jirka and Neves, 1992; Hoggarth, 1999). However, we were unable to differentiate our recovered juveniles among *Venustaconcha ellipsiformis*, *Lampsilis cardium* or *L. siliquoidea* with absolute certainty. Therefore, we used one-way ANOVA to compare character measurements and ratios of paired valve character measurements among these species. Ratios were transformed using Arcsine (square root(ratio)) prior to analysis (Zar, 1996). If a test indicated a significant difference we ran a Tukey-Kramer HSD multiple means comparison (Zar, 1996). All statistical analyses were performed using JMP v. 3.2.2 (SAS Institute, Cary, NC). Significance level for all analyses was set at $\alpha = 0.05$.

To provide additional evidence for our juvenile identifications, we exposed *Lampsilis cardium* and *L. siliquoidea* glochidia from the Rum River, Minnesota, to fantail and rainbow darters, using methods previously described, to determine if they facilitated glochidial metamorphosis. If results were negative, it would confirm that the questionable juveniles from these darter species were *Venustaconcha ellipsiformis*.

RESULTS

DISTRIBUTION

We compiled data from 1794 sampling sites to describe the distribution of *Venustaconcha ellipsiformis* in Minnesota. Of these sites, 496 were from the St. Croix River drainage and drainages in southeastern Minnesota. A total of 446 live *V. ellipsiformis* were found in five primary tributaries to the Mississippi River: the Cannon, Cedar, Root, Upper Iowa and Zumbro river systems (Fig. 1, Table 1). We did not find any relic specimens in any other rivers across the state, and therefore we believe this represents the historical range of *V. ellipsiformis* in Minnesota. *Venustaconcha ellipsiformis* is the most abundant mussel species in the Root River drainage (relative abundance = 20.9% among 12 live species). Records of live individuals were found at 37.3% of the sites in the Root River drainage. This was the only drainage in which we found juveniles, and individuals 0 to 5 y old were found at 22.4% of the sites and composed 22.9% of all individuals found. *Venustaconcha ellipsiformis* is ranked 6th, 6th, 6th and 11th in relative abundance in the Zumbro (17 spp.), Cannon (13 spp.),

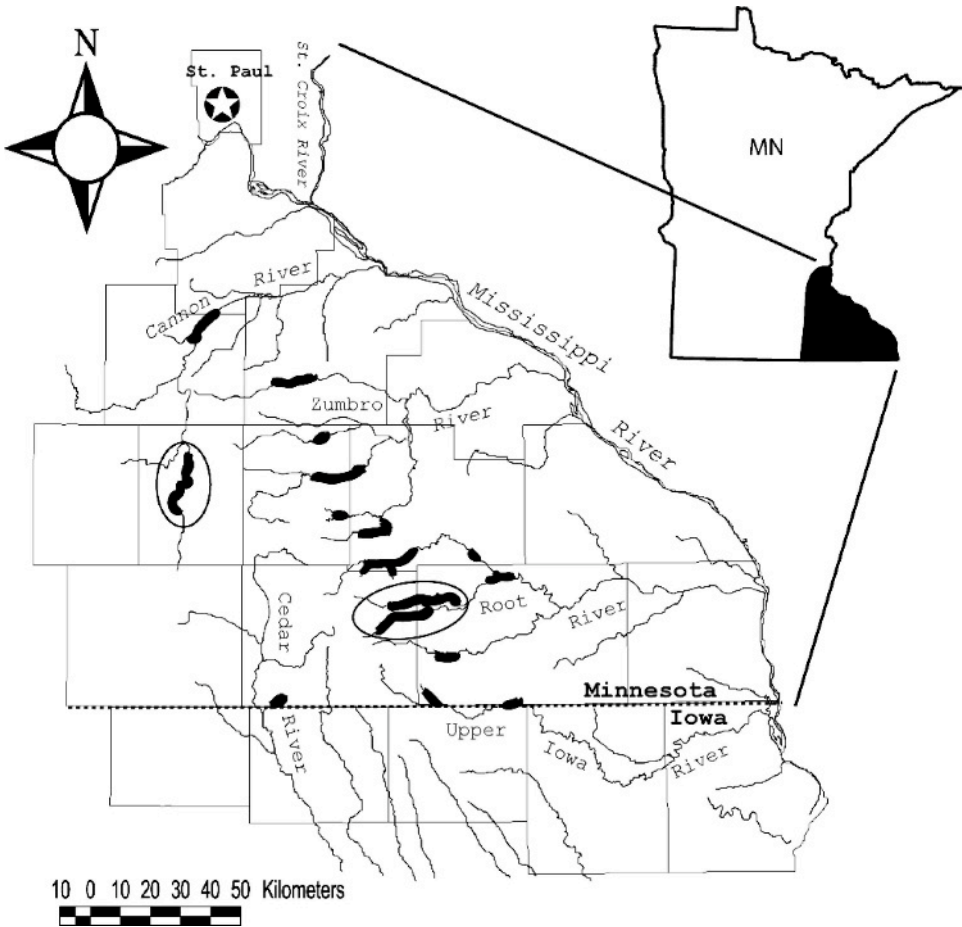


FIG. 1.—*Venustaconcha ellipsiformis* distribution in Minnesota. Thick black lines transposed on rivers represent areas where live *V. ellipsiformis* were recorded in this study. Black ovals represent the areas where *V. ellipsiformis* were most abundant

TABLE 1.—Population characteristics for *Venustaconcha ellipsiformis* in Minnesota

River drainage	Year sampled	No. sites sampled	Relative abundance (%)	No. live	Frequency of live individual(s) at sites (%)	Frequency of live or dead individual(s) at sites (%)	Min/max length (mm)
Cannon River	1987	29	2.1	41	8.2	22.9	58/88
Cedar River	1999	25	0.8	19	12.0	16	—
Root River	2002–03	67	20.9	328	37.3	55.2	16/101
Upper Iowa River	1999	15	1.9	24	33.3	33.3	—
Zumbro River	1988	83	2.9	34	10.8	19.3	44/83
Total	1987–2003	219	—	446	20.1	31.5	16/101

Upper Iowa (10 spp.) and Cedar River (13 spp.) drainages, respectively. The Straight River held 39 of the 41 live individuals found within the Cannon River drainage.

We found five specimens at JFBM cataloged as *Venustaconcha ellipsiformis* from drainages outside the range of the extant populations we located that we believe are misidentified. We examined two specimens from the St. Croix River (JFBM 5736) (see Graf, 1997) that are, in our opinion, juvenile *Actinonaias ligamentina*, a relatively common species in that drainage (Hornbach, 2001; Sietman, 2003). Given that this system has been well surveyed, 263 sites by us alone, and no other specimens have been found, we doubt it occurs there. *Venustaconcha ellipsiformis* has also been reported from some Minnesota River tributaries (Sietman, 2003), but after re-examining these sub-fossil specimens, we believe they are *A. ligamentina* (JFBM 9336, 12478, 13219) and *Lampsilis siliquoidea* (JFBM 11904), which are historically widespread in that drainage (Sietman, 2003).

BROODING BEHAVIOR

We observed brooding *Venustaconcha ellipsiformis* display two small mantle flaps during the spring and fall. Mantle flaps consisted of mantle extensions 5–10 mm long by 2–4 mm wide arranged along both sides of the posterior quarter, or less, of the ventral shell margin. Displaying mussels presented the internal portion of the mantle outwardly, creating an opening that exposed distended marsupia (Figs. 2A, 2B), which occasionally distended beyond the mantle margin. Mantle flaps were held in this position for extended periods. The internal surface of the mantle was relatively light in color, ranging from mottled cream, gray, tan, to brown, and occasionally had a small dark spot at the posterior margin (Fig. 2C). When the mantle was flapped, the external side of the mantle was presented briefly (Fig. 2D). Mantle flaps often had 4–10 thin, flexible tentacles (3–6 mm long), oriented perpendicular to the anterior-posterior axis of the mantle, arranged along the posterior quarter of the mantle margin. Brooding mussels were varied in their orientation. Most mussels were partially buried with ventral margins facing, and sometimes nearly touching the substrate. Other mussels oriented their mantle flaps laterally, to the point where some individuals were out of the substrate, lying on their side. Ten gravid *V. ellipsiformis* oriented in these ways were collected from Deer Creek on 16 Apr. 2004 (12 C) and exhibited mantle displays the following day in the laboratory. Additional mantle displays were observed in Deer Creek during May 2004, and in the North Fork Zumbro River during Oct. 1995. On 10 Nov. 2004 we observed a rainbow darter strike at the display of a brooding *V. ellipsiformis* (M. Hove, *pers. obs.*).

We observed brooding *Venustaconcha ellipsiformis* exhibit two different mantle-flapping behaviors: a brief simultaneous flap of both mantles, and a longer staggered undulation. Videos of both behaviors are posted on the internet at the website http://files.dnr.state.mn.us/natural_resources/animals/mussels/vellipsiform_display.mpg. The brief simultaneous flap was the most common mantle movement we observed. Here, both mantles flapped in unison for less than a second, where the mantle interior normally displayed was briefly turned inward to expose the mantle exterior. The exterior mantle surface was the same color as the surrounding mantle, a mottled brownish-gray background with tan blotches (Fig. 2D). Brooding *V. ellipsiformis* often went several minutes or longer between flapping events. We observed brooding individuals nearly always flap their mantles in response to vibrations (a finger tapping on the aquarium or aquarium shelf or rapidly moving fingers across water surface), and frequently in response to sudden changes in light intensity (*e.g.*, a shadow cast by a hand or twice in response to the passing shadow of a fathead minnow [*Pimephales promelas*] in the laboratory). We also observed this behavior in Deer Creek on 6 May 2004 where brooding individuals flapped mantles in response to the shadow of a hand passing over them.

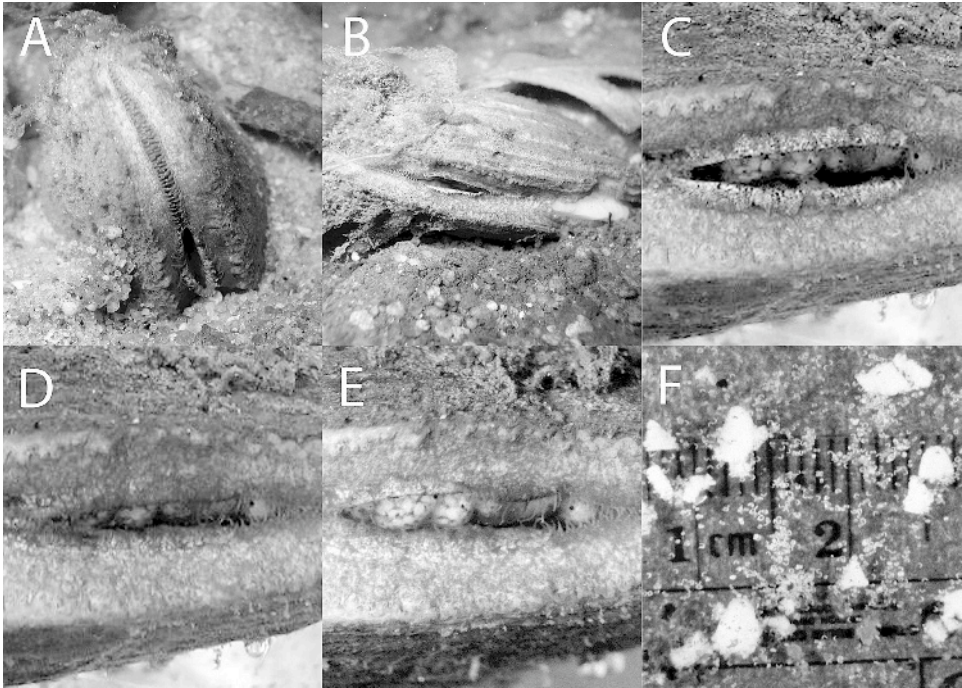


FIG. 2.—Orientations of brooding *Venustaconcha ellipsiformis* in natural conditions (A), (B). Resting position of mantle presenting mantle flaps (C), position of mantle when briefly closed (D), mantle undulation (E) and conglutinates (F)

The second mantle flapping behavior was characterized by a slow asymmetric undulation or ripple. We observed this in the laboratory during late Apr. 2004 when water temperature was raised to 16 C, and in Deer Creek during the evening of 10 Nov. 2004. An undulation usually began with a single mantle flap slowly undulating from the anterior to the posterior end (Fig. 2E). This movement continued down the mantle producing a slow ripple that traveled the length of the mantle over a period 5–10 s. Often this would be followed by the undulation of the opposite mantle flap, though we did observe individuals undulate only a single mantle flap.

Brooding *Venustaconcha ellipsiformis* released what appeared to be broken conglutinates and individual glochidia in the laboratory. Conglucinate sections were approximately 3–7 mm long, 3–5 mm wide and 1 mm thick, white to cream colored, with a lanceolate outline (Fig. 2F). In the laboratory we observed brooding *V. ellipsiformis* release individual glochidia and 1–10 broken conglutinates. On two occasions we observed *V. ellipsiformis* release conglutinates from their external aperture. During the winter of 1995–6 brooding females released conglutinates in the laboratory between Oct. and May, which were used in host suitability trials.

HOST-SUITABILITY

We identified suitable host species for *Venustaconcha ellipsiformis* in the laboratory. Of the 46 species (11 taxonomic families) we exposed to *V. ellipsiformis* glochidia, 11 species (3

TABLE 2.—Laboratory host-fish suitability analysis for *Venustaconcha ellipsiformis* glochidia

Species	Trial	Mean water temperature (C)	No. fish infested	No. fish survivors	Recovery period ¹ (d)	No. juveniles recovered	Mean no. juveniles/fish ²
METAMORPHOSIS OBSERVED							
Cottidae							
<i>Cottus bairdii</i>	I	21	4	0	19–36	64*	32.0
	II	21	6	0	18	3*	1.0
	III	21	4	0	16–28	32*	16.0
	IV	11	8	4	113–183	17	4.2
<i>Cottus cognatus</i>	I	19	5	1	30–59	143	47.7
	II	11	11	7	135–197	27	3.0
Gastrosteidae							
<i>Culaea inconstans</i>		21	8	3	18–35	74	13.4
Percidae							
<i>Etheostoma asprigene</i>		11	17	17	141–149	1	0.6
<i>Etheostoma caeruleum</i>		11	21	17	106–151	15	0.8
<i>Etheostoma exile</i>	I	21	8	8	18–30	41	5.1
	II	11	16	13	170–192	4	0.3
<i>Etheostoma flabellare</i>		21	8	6	18–35	56	8.0
<i>Etheostoma nigrum</i>	I	19	6	6	55–125	33	5.5
	II	19	4	2	35–95	47	23.5
	III	11	65	0	129–137	1*	0.0
<i>Etheostoma zonale</i>		11	9	0	149–176	2*	0.4
<i>Percina caprodes</i>	I	21	6	0	25–32	3*	1.0
	II	11	38	0	129–137	1*	0.1
<i>Percina maculata</i>	I	21	4	4	30–34	7	1.8
	II	21	7	7	18–21	3	0.4
	III	19	5	3	52–54	1	0.2
	IV	11	39	30	137–186	3	0.1
METAMORPHOSIS NOT OBSERVED							
Acipenseridae							
<i>Acipenser fulvescens</i>		11	4	4	1–7		
<i>Scaphirhynchus platyrhynchus</i>		11	2	2	1–7		
Catostomidae							
<i>Catostomus commersonii</i>	I	19	6	3	26–29		
	II	11	16	16	1–5		
<i>Hypentelium nigricans</i>		11	1	1	1–5		
<i>Moxostoma macrolepidotum</i>		21	1	1	2–6		
Centrarchidae							
<i>Lepomis cyanellus</i>	I	19	7	5	13–16		
	II	19	8	8	8–10		
	III	11	2	2	26–40		
<i>Lepomis gibbosus</i>	I	19	8	6	8–10		
	II	11	2	2	26–40		
<i>Lepomis humilis</i>		11	2	2	9–21		
<i>Lepomis macrochirus</i>	I	19	6	6	29–31		
	II	11	1	1	54–75		
<i>Micropterus salmoides</i>		19	2	2	25–27		
<i>Pomoxis nigromaculatus</i>		11	1	1	15–21		
Cyprinidae							
<i>Carassius auratus</i>	I	21	7	7	1–4		
	II	11	1	1	1–5		

TABLE 2.—Continued

Species	Trial	Mean water temperature (C)	No. fish infested	No. fish survivors	Recovery period ¹ (d)	No. juveniles recovered	Mean no. juveniles/fish ²
<i>Cyprinella spiloptera</i>	I	19	4	4	2-7		
	II	11	15	15	1-5		
<i>Luxilus cornutus</i>	I	19	1	1	2-7		
	II	11	4	4	1-5		
<i>Nocomis biguttatus</i>	I	11	6	6	1-3		
	II	11	1	1	1-5		
<i>Notemigonus crysoleucas</i>		19	5	5	26-29		
<i>Notropis atherinoides</i>	I	21	5	5	1-4		
	II	11	12	12	1-5		
<i>Notropis blennioides</i>		11	2	2	1-5		
<i>Notropis dorsalis</i>		11	23	23	1-5		
<i>Notropis stramineus</i>		11	2	2	1-5		
<i>Phoxinus eos</i>		11	2	2	1-5		
<i>Pimephales notatus</i>	I	21	8	8	2-5		
	II	21	8	8	1-4		
	III	11	6	6	1-5		
<i>Pimephales promelas</i>		11	16	16	1-5		
<i>Rhinichthys cataractae</i>	I	19	3	3	17-20		
	II	11	44	44	1-5		
Esocidae							
<i>Esox lucius</i>		19	4	4	31-33		
Gadidae							
<i>Lota lota</i>		19	4	4	37-39		
Gastrosteidae							
<i>Culaea inconstans</i>		19	3	3	26-31		
Ictaluridae							
<i>Ameiurus melas</i>		19	6	6	19-23		
<i>Noturus gyrinus</i>	I	11	5	5	1-5		
	II	11	6	6	1-5		
<i>Pylodictis olivaris</i>		11	15	15	3-10		
Percidae							
<i>Crystallaria asprella</i>		11	1	1	1-8		
<i>Perca flavescens</i>	I	19	6	6	22-25		
	II	19	4	1	24-26		
	III	19	8	8	25-28		
	IV	11	13	13	40-75		
<i>Percina caprodes</i>	I	21	8	8	9-18		
	II	21	3	2	8-11		
	III	19	4	1	57-60		
<i>Percina evides</i>		11	27	27	8-16		
<i>Percina phoxocephala</i>		11	19	17	142-182		
<i>Percina shumardi</i>	I	21	1	1	21-23		
	II	11	27	27	1-5		
<i>Sander vitreus</i>	I	19	4	4	20-23		
	II	19	4	2	21-24		
	III	19	5	3	27-29		
Umbridae							
<i>Umbra limi</i>		11	1	1	21-26		

TABLE 3.—Glochidia host-fish suitability analysis for *Lampsilis cardium* and *L. siliquioidea*

Species	Mean water temperature (C)	No. fish Infested	No. survivors	Recovery period ¹ (d)	No. juveniles recovered	Mean no. juveniles/fish ²
<i>Lampsilis cardium</i> Metamorphosis Observed						
Centrarchidae						
<i>Micropterus salmoides</i>	20	4	4	29–61	130	32
<i>Lampsilis cardium</i> Metamorphosis Not Observed						
Percidae						
<i>Etheostoma caeruleum</i>	20	17	17	5–8		
<i>Etheostoma flabellare</i>	20	9	9	5–8		
<i>Lampsilis siliquioidea</i> Metamorphosis Observed						
Centrarchidae						
<i>Micropterus salmoides</i>	20	4	4	22–47	35	9
<i>Lampsilis siliquioidea</i> Metamorphosis Not Observed						
Percidae						
<i>Etheostoma caeruleum</i>	20	14	14	8–13		
<i>Etheostoma flabellare</i>	20	9	9	1–5		

¹ Recovery period has two meanings depending on the species host suitability: (1) for species where metamorphosis was observed, it is the period of time when juvenile mussels were observed, and (2) for species where metamorphosis was not observed, it is the period when sloughed glochidia were observed

² Number of fish equals the average between the number of fish infested and survivors

taxonomic families) facilitated metamorphosis (Table 2). All *Etheostoma* and *Cottus* species tested facilitated metamorphosis, and transformation rates were generally higher at warmer water temperatures. Most percids retained *V. ellipsiformis* for at least 3 wk except for crystal and gilt darters (*Ammocrypta asprella* and *Percina evides*), and certain logperch (*P. caprodes*) trials. Most non-host fish families sloughed glochidia in 1–2 wk, although glochidia remained attached longer on Centrarchidae, Esocidae, Gadidae and Umbridae species; golden shiners (*Notemigonus crysoleucas*) and white suckers (*Catostomus commersoni*). We determined that rainbow darters (*E. caeruleum*) and fantail darters (*E. flabellare*) do not serve as hosts for *L. cardium* and *L. siliquioidea* glochidia (which allowed us to positively identify our recovered juveniles from these natural infestations), and confirmed host suitability of largemouth bass (*Micropterus salmoides*) (Table 3).

NATURAL INFESTATIONS

We recovered juvenile *Venustaconcha ellipsiformis* from three darter species naturally infested with glochidia from the Zumbro River and Root River drainages (Table 4). We generated SEM images of recovered juvenile mussels and glochidia from nine co-occurring mussel species, and used these images for identification (Fig. 3). *Lampsilis cardium*, *L. siliquioidea* and *V. ellipsiformis* glochidia valve characters appeared superficially similar to glochidial valves of the recovered juvenile mussels. Analysis of these characters however,

←

¹ Recovery period has two meanings depending on the species host suitability: (1) for species where metamorphosis was observed, it is the period of time when juvenile mussels were observed and (2) for species where metamorphosis was not observed, it is the period when sloughed glochidia were observed

² Number of fish equals the average between the number of fish infested and survivors

* Trial incomplete, test fish died before the study ended

TABLE 4.—Juvenile *Venustaconcha ellipsiformis* recovered from naturally infested darters from the Middle Fork Zumbro River and Deer Creek, Minnesota

Species	Trial	Mean water temperature (C)	No. fish	Juvenile recovery period (d)	No. juveniles recovered	Mean no. juveniles/fish
Middle Fork Zumbro River						
<i>Percina maculata</i>	I	11	1	20–140	22	22
	II	21	3	15–26	8	2.7
Total			4		30	7.5
<i>Etheostoma flabellare</i>	I	11	8	65–147	16	2
	II	21	11	6–26	20	1.8
Total			19		36	1.9
<i>Etheostoma nigrum</i>		21	1	0	0	0.0
Deer Creek (Root River Drainage)						
<i>Etheostoma flabellare</i>		16	16	37–85	66	4.1
<i>Etheostoma caeruleum</i>		16	40	1–85 ¹	220	5.5

¹ Juvenile *V. ellipsiformis* were recovered from fish as soon as they were brought into the laboratory in late Apr.

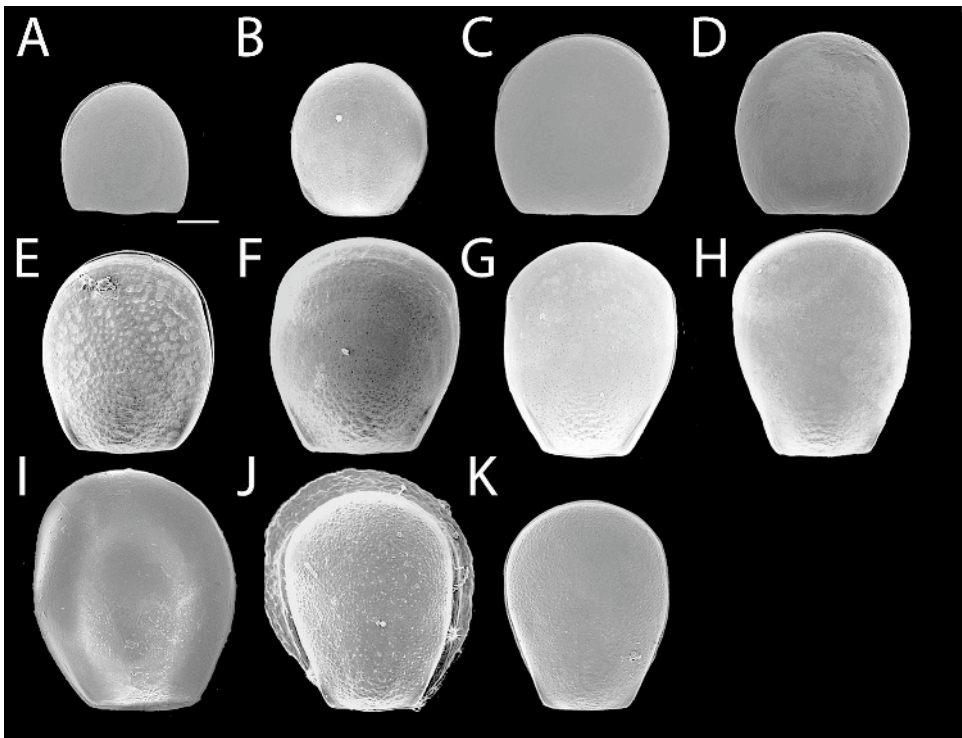


FIG. 3.—Selected unionid species glochidia and our recovered juveniles from naturally infested fish (see methods for locality information), scale bar is 50 μ m. *Fusconaia flava* (A), *Toxolasma parvus* (B), *Elliptio dilatata* (C), *Amblema plicata* (D), *Actinonaias ligamentina* (E), *Lampsilis siliquioidea* (F), *Lampsilis cardium* (G), *Venustaconcha ellipsiformis* (H), *Obovaria olivaria* (I), juvenile *V. ellipsiformis* from Zumbro River drainage (J) and juvenile *V. ellipsiformis* from Root River drainage (K)

TABLE 5.—Glochidial valve dimensions ($\bar{x} \pm 1$ SD (μm)) of *Lampsilis cardium*, *L. siliquoidea*, *Venustaconcha ellipsiformis* and juvenile mussels recovered from naturally infested darters. Means that share a letter are not statistically different according to a Tukey's HSD test ($\alpha = 0.05$), sample sizes are in parentheses

Valve character	Species			
	<i>L. cardium</i>	<i>L. siliquoidea</i>	<i>V. ellipsiformis</i>	Recovered juveniles
Height	260 \pm 13 ^a (6)	280 \pm 8 ^b (7)	260 \pm 7 ^a (6)	265 \pm 12 ^a (12)
Length	213 \pm 11 ^a (6)	240 \pm 5 ^b (7)	200 \pm 11 ^a (6)	206 \pm 9 ^a (12)
Hinge length	106 \pm 9 ^a (6)	128 \pm 4 ^b (7)	99 \pm 8 ^a (6)	106 \pm 6 ^a (12)
Length/height	0.82 \pm 0.02 ^a (6)	0.86 \pm 0.02 ^a (7)	0.77 \pm 0.04 ^b (6)	0.78 \pm 0.03 ^b (12)

showed that height ($P < 0.01$), length ($P < 0.0001$), and hinge length ($P < 0.0001$) of *L. siliquoidea* glochidial valves were significantly different than *L. cardium*, *V. ellipsiformis* and recovered juvenile mussels (Table 5). Results were similar when only juveniles from blackside darters (*Percina maculata*) were analyzed. Length-height ratio of *V. ellipsiformis* glochidia and recovered juveniles (both for all juveniles pooled, and from blackside darters only) was significantly smaller than the *Lampsilis* species ($P < 0.0001$), but were not significantly different from one another (Table 5).

Infestation rates varied among fish species and between drainages. Darters collected during the fall from the South Branch Middle Fork Zumbro River were held at two temperatures. We recovered 16 juvenile *Venustaconcha ellipsiformis* from 8 fantail darters held at 11 C and 20 juveniles from 11 fantail darters held at 21 C. A single blackside darter (*Percina maculata*) facilitated metamorphosis of 22 juveniles at 11 C and three blackside darters facilitated metamorphosis of eight juveniles at 21 C. Juveniles excysted for an extended period of time (3–21 wk) at 11 C and a reduced period (1–3 wk) at 21 C (Table 4). At 11 C, we recovered 54% and 81% of juvenile *V. ellipsiformis* from fantail and blackside darters during the last third of the excystment period, respectively. Juvenile *V. ellipsiformis* were recovered from aquaria fairly evenly throughout the excystment period for darters held at 21 C.

DISCUSSION

DISTRIBUTION

We found extant populations of *Venustaconcha ellipsiformis* in the Root, Cannon, Zumbro, Cedar and Upper Iowa River drainages. All but one live record was found in medium-sized tributaries and smaller streams. (Eckblad *et al.*, 2002) also found that populations of *V. ellipsiformis* were mainly restricted to smaller streams within the Iowa portion of the Upper Iowa River watershed as well as the Turkey River watershed, which confirms our findings that this species occurs mainly in headwater reaches in the upper Midwest. In Minnesota, it appears that headwater tributaries of the Root River, and to a lesser extent the Straight River of the Cannon River system, hold the most abundant populations of *V. ellipsiformis*. Although *V. ellipsiformis* was apparently less abundant in other drainages, it is encouraging that it still persists in all the systems it occurred historically given the apparent decline and loss of species in other southern Minnesota drainages (Sietman, 2003). While we only found juvenile specimens at sites in the Root River drainage, juveniles have been found in the Zumbro River drainage as recently as 2003 (M. E. Havlik, pers. comm.).

The distribution of *Venustaconcha ellipsiformis* is unique relative to other unionids in Minnesota in that it is the only species restricted to southeastern Mississippi River tributaries

and does not occur in either the Minnesota or St. Croix River systems. Aside from the Mississippi River main-stem, the Minnesota and St. Croix River systems have the most species rich unionid faunas in the state (Graf, 1997; Sietman, 2003), and the absence of *V. ellipsiformis* from both of these systems is curious. One explanation for this distributional pattern might be glacial history. The southeastern corner of Minnesota escaped the Wisconsin glaciations that ended 10,000 y ago, the most recent glacial advances in Minnesota (Fremling, 2005). Therefore, it is possible that *V. ellipsiformis* took refuge in this area and has been slow to expand its range.

The distribution of unionid species are strictly linked to the distribution of their host fish(es) (Watters, 1992; Graf, 2002). The host species identified in this study (darters, sculpins and brook stickleback) are fishes with low vagility, which may limit the ability of *Venustaconcha ellipsiformis* to disperse large distances relative to mussel species that use larger, more mobile fishes as hosts. Most upper Midwest stream darters are rarely found in large channelized rivers (Page, 1983; Jenkins and Burkhead, 1994), with the exception of logperch and slenderhead darters (Becker, 1983). Mottled sculpins live in streams with cold to cool temperatures and generally do not occupy waters larger than streams (Jenkins and Burkhead, 1994). Some *Etheostoma* and *Percina* species are believed to move downstream during the winter and return to smaller streams to spawn (Page, 1983), but the extent of these migrations is unclear. (May, 1969) observed four variegated darters (*Etheostoma variatum*) move almost 3 miles downstream from the riffle they inhabited in Dec. Other than seasonal migrations, however, mark and recapture studies have shown that many darters show only marginal local movements (*i.e.*, from riffles to adjacent pools) (Reed, 1968; Freeman, 1995). Thus, behaviors reported for most suitable host species of *V. ellipsiformis* suggest these fishes may not enter large channelized rivers and move into other watersheds during the period of glochidial encystment. This suggests *V. ellipsiformis* has a relatively low dispersal rate and may explain in part why it is not more widely distributed in Minnesota.

BROODING BEHAVIOR

The mantle display of *Venustaconcha ellipsiformis* is relatively small, less than one-quarter the length of the ventral margin, whereas several other lampsiline mussels display large highly developed mantle flaps while brooding glochidia. Three *Lampsilis* species and two *Villosa* species produce relatively large, ornate mantle flaps that are over one-third the length of the ventral shell margin (Kraemer, 1969, 1970; Kraemer and Swanson, 1985; Haag and Warren, 1997, 1999; Haag *et al.*, 1999). We have also observed mantle flaps over one-third the length of the ventral valve margin of *Lampsilis cardium*, *L. higginsii*, *L. siliquoidea* and *Ligumia recta* (Allen, Davis, Hove, Sietman, pers. obs.). Recent phylogenetic analysis of the Subfamily Ambleminae confirms *V. ellipsiformis* is a member of the Tribe Lampsilini, but it did not group closely with the afore mentioned species (Campbell *et al.*, 2005). Rather *V. ellipsiformis* appears to be closely related to *Pytochobrancus fasciolaris*, a species that uses conglutinates to attract fish hosts (Watters, 1999), although this relationship was not highly supported (Campbell *et al.*, 2005). In addition to having relatively small mantle flaps, *V. ellipsiformis* flap their mantles in ways not reported for other species. *Lampsilis cardium* flap their mantles in regular symmetric pulses for long periods throughout the summer where flapping frequency varied with light intensity (Kraemer, 1970). Brooding *L. siliquoidea*, *L. fasciola* and *L. reeviana* also flap their mantles fairly rapidly and regularly (Kraemer, 1970). *Lampsilis siliquoidea* and *L. reeviana* have been observed flapping their mantles in response to jarring of the substrate or water waves near the flaps, which is similar to what we observed in *V. ellipsiformis*. The display morphology of *V. pleasii* is very similar to that of *V. ellipsiformis*, and has been reported to have a quick mantle flap that is particularly sensitive to shadows

and vibrations (M. C. Barnhart, pers. comm.). We did not observe regular, rhythmic mantle flapping in *V. ellipsiformis* in the laboratory or under natural conditions as described for *Lampsilis* species (Kraemer, 1970). The quick mantle flap was observed only in response to a passing shadow or jarring of the substrate, and the asymmetric undulation was relatively slow compared to mantle flapping behaviors exhibited by other lampsiline species.

Venustaconcha ellipsiformis orient their ventral margin and mantle display toward or angled slightly away from the substrate, and the display is usually very close in proximity to the substrate. The display was often difficult to observe in a natural setting due to this orientation. This is unlike the displays of some *Lampsilis* species that are oriented parallel to the substrate and toward the water column (Kramer, 1970) and have been shown to evoke a feeding response from their large piscivorous hosts (Haag and Warren, 1999). Brooding ellipse also release glochidia individually or in broken conglomerates (Fig. 2F), and given that darters often use their pectoral fins to locomote, this may suspend glochidia resting near the mussel and facilitate incidental infestation. Above all, the brooding behavior of *V. ellipsiformis* seems well suited to attract their small benthic fish hosts that search for aquatic insects beneath small rocks.

HOST SUITABILITY AND NATURAL INFESTATIONS

A variety of small stream fishes facilitate *Venustaconcha ellipsiformis* glochidia metamorphosis. We showed that several darter species, two sculpin species and brook stickleback support *V. ellipsiformis* glochidia metamorphosis in the laboratory. We also observed black-side darters, fantail darters and rainbow darters facilitate metamorphosis of naturally infested *V. ellipsiformis* glochidia. We found that fantail darters were infested with *V. ellipsiformis* glochidia at higher rates in the Root River drainage than in the Zumbro River drainage, which concurs with other findings of increased glochidia infestation rates at sites with higher abundance of the mussel species (McClain and Ross, 2005). Interestingly, the infestation rates of our naturally infested fish varied from our transformation rates from laboratory trials. For example, rainbow darters in our host suitability trials produced very few juveniles, which may lead us to believe it is a marginal host. However, our naturally infested rainbow darters produced significantly more juveniles, suggesting that it is an important host for *V. ellipsiformis* populations in Deer Creek. We did not collect sculpins or stickleback while searching for fishes at *V. ellipsiformis* beds. It seems likely additional darter and sculpin species could be hosts for *V. ellipsiformis*, and that host use could vary among sites and drainages. Banded sculpin and orangethroat darters, redbfin darters, and greenside darters collected from the Spring River, Missouri were found to be naturally infested with *V. ellipsiformis* glochidia (Riusech and Barnhart, 2000), although morphological characters used to distinguish *V. ellipsiformis* glochidia from other Spring River lampsilines (Obermeyer *et al.*, 1997) were not described.

We positively identified juvenile mussels recovered from naturally infested darters as *Venustaconcha ellipsiformis*, which can be distinguished from co-occurring mussel species at our study sites. *Venustaconcha ellipsiformis* glochidia have a sub-elliptical outline, which distinguishes them from anodontine glochidia that are hooked and have either a triangular or 'ax-head' outline (Hoggarth, 1999). Several features separate *V. ellipsiformis* glochidia from glochidia released by co-occurring amblemine mussels in the Zumbro River and Root River drainages. Six amblemine, lampsiline and pleurobemine species release glochidia close to or during the fall in the Zumbro River upstream of Zumbro Lake and seven amblemine and lampsiline species release glochidia in the spring in the Root River drainage. *Amblesma plicata*, *Elliptio dilatata*, *Fusconaia flava* and *Toxolasma parvus* glochidia are smaller in height and have a more circular outline than *V. ellipsiformis*. *Actinonaias*

ligamentina glochidia are smaller and their malleated surface clearly distinguishes them from *V. ellipsiformis* glochidia. *Obovaria olivaria* glochidia are similar in outline but larger than *V. ellipsiformis* glochidia. *Lampsilis cardium* and *L. siliquoidea* glochidia are similar in size to *V. ellipsiformis* glochidia, but they have subspatulate asymmetric valves with a rough surface compared to the subelliptical symmetric valves with smooth, loose looped surfaces of *V. ellipsiformis*. While glochidia of *L. siliquoidea*, *L. cardium* and *V. ellipsiformis* are similar, valve length-height ratio distinguished *V. ellipsiformis* and the recovered juveniles from both *Lampsilis* species. Furthermore, rainbow and fantail darters did not facilitate metamorphosis of *L. cardium* or *L. siliquoidea* glochidia, providing additional evidence that the recovered juveniles were *V. ellipsiformis*. Although blackside darters were not tested for host suitability with either *Lampsilis* species, the valve dimensions of juveniles recovered from blackside darters were not significantly different from the other juveniles, suggesting they were all *V. ellipsiformis*.

CONSERVATION IMPLICATIONS

Management of rare mussel species is improved with greater understanding of their life-histories, and results from this study have implications on the conservation of *Venustaconcha ellipsiformis*. The humble display of *V. ellipsiformis* suggests the efficacy of luring its host species might be negatively affected by increasing turbidity of its habitat. Increased turbidity has been shown to reduce prey consumption among select Midwest shiners (Bonner and Wilde, 2002). Furthermore, the water quality and quantity of these drainages must be maintained at levels that do not negatively impact populations of *V. ellipsiformis* and its host species. Because it uses benthic, less vagile fishes such as darters as hosts, *V. ellipsiformis* may take a relatively long time to recolonize streams if a population were to become extirpated. (McLain and Ross, 2005) observed low dispersal rates for tessalated darters (*Etheostoma olmstedi*) during the glochidial release period of *Alasmidonta heterodon*, and speculated that this may cause patchy distribution and hinder colonization or recovery of *A. heterodon* populations. This differs from mussel species that commonly inhabit large rivers where recovery can occur more rapidly if habitat conditions improve and source populations are reasonably close by (Sietman *et al.*, 2001). This is likely due in part to the general greater mobility of their large river host fish. The presence of small dams throughout these drainages, as well as larger dams in the Mississippi River between these drainages, are likely to further decrease the dispersal rates of *V. ellipsiformis*, and other mussel species (Watters, 1995). The improbability that an extirpated population of *V. ellipsiformis* could recolonize makes habitat protection and improvement measures at the watershed level essential conservation goals.

There is likely to be restricted gene flow in species with low dispersal rates and patchy distributions, as populations between drainages and basins may be genetically isolated from each other. (Berg *et al.*, 1998) found *Quadrula quadrula* exhibited a relatively high level of gene flow among populations. They speculated this was related to its mobile large-river fish host, the flathead catfish (*Pylodictis olivaris*) (see Schwebach *et al.* (2002) who list channel catfish (*Ictalurus punctatus*) as a suitable host), as gene flow over larger spatial scales is a function of host fish movements (Berg *et al.*, 1998). Therefore, a mussel species with low dispersal rates may also have a low level of gene flow between populations, and this may have implications for its long-term conservation.

The Minnesota Department of Natural Resources classified *Venustaconcha ellipsiformis* as "Threatened" in 1996, mainly because of its restricted range, and we believe this species should remain listed as "Threatened." However, if this species is to be managed effectively,

more must be considered than its range. We contend that *V. ellipsiformis* sub-populations are more isolated than mussel species whose hosts can disperse juvenile mussels more rapidly and broadly. Our laboratory and field observations lead us to recommend that *V. ellipsiformis* management attention should be focused at the local and regional scale.

Acknowledgments.—Many organizations and people supported this project. We thank M.C. Barnhart for information on *Venustaconcha* displays, M.E. Havlik and J. L. Harris for information on *V. ellipsiformis* distributions in Minnesota and Arkansas. We thank MN DNR staff for assistance with the Statewide Mussel Survey. A variety of organizations supported field and laboratory work at the UMN. We thank Tom Anderson, Jason Berkner, Tessa Diedrich, Robin Engelking, Erin Haverly, Katie Hillegass, Marissa McGill, Carrie Nelson, Margaret Peteler and Whitney Taylor for assisting with recovery of juveniles from naturally infested darters, and identification of juvenile mussels recovered from darters. Dr. Anne Kapuscinski graciously offered space and resources in the UMN Wet Laboratory that were essential in completing this research. We thank Konrad Schmidt, Taylor Polomis, Rod Ramsell and Shane McBride of the MN DNR, and Jerry Grant of the UMN for assistance with fish collection. Dave Heath, Don Hardy, Glen Miller, Tony Deneka, Robert Bright, Dan Graf and Marian Havlik provided suggestions on mussel collection sites and potential host fishes. We thank Dale Newton of the MN DNR for video editing. We thank Dr. Caryn C. Vaughn and two anonymous reviewers for thoughtful review of our manuscript. Funding for the Statewide Mussel Survey was approved and supported in part by the Minnesota Legislature, 1999 Minnesota Laws, Chapter 231, Section 16, Subdivision 15 (a), as recommended by the Legislative Commission on Minnesota Resources from the Minnesota Environment and Natural Resources Trust Fund, the Federal Wildlife Conservation and Restoration Program Authorized by the Commerce, Justice and State Appropriations Act of 2001, Title IX, Public Law 106–553 and the U. S. Fish and Wildlife Service who provided funds through Minnesota's State Wildlife Grants Program. Partial support for host relationship research was received from the Minnesota Nongame Wildlife Tax Checkoff and the Reinvest in Minnesota Program through the Minnesota Department of Natural Resources' Natural Heritage and Nongame Research Program, and University of Minnesota's Undergraduate Research Opportunities Program and James Ford Bell Museum of Natural History. Additional funding was provided by the Minnesota Legislature, ML 1997 Chapter 216, Section 15, Subdivision 15b as recommended by the Legislative Commission on Minnesota Resources from the Minnesota Environmental and Natural Resources Trust Fund.

LITERATURE CITED

- BAKER, F. C. 1928. The fresh water Mollusca of Wisconsin. Part II. Pelecypoda. *Bull. Wisc. Geol. Nat. Hist. Surv.*, **70**:1–495.
- BECKER, G. C. 1983. Fishes of Wisconsin. The University of Wisconsin Press, Madison, Wisconsin. 1052 p.
- BERG, D. J., E. G. CANTONWINE, W. R. HOEH AND S. I. GUTTMAN. 1998. Genetic structure of *Quadrula quadrula* (Bivalvia: Unionidae): little variation across large distances. *J. Shellfish Res.*, **17**:1365–1373.
- BONNER, T. H. AND G. R. WILDE. 2002. The effect of turbidity on prey consumption by prairie stream fishes. *Trans. of the Am. Fish. Soc.*, **131**:1203–1208.
- BRIGHT, R. C., E. PLUMMER AND D. OLSON. 1989. A survey of the mussels of the Zumbro River drainage, southeastern Minnesota. University of Minnesota Bell Museum of Natural History, 181 p.
- CAMPBELL, D. C., J. M. SERB, J. E. BUHAY, K. J. ROE, R. L. MINTON AND C. LYDEARD. 2005. Phylogeny of North American amblomines (Bivalvia, Unionidae): prodigious polyphyly proves pervasive across genera. *Invert. Biol.*, **124**:131–164.
- COKER, R. E., A. F. SHIRA, H. W. CLARK AND A. D. HOWARD. 1921. Natural history and propagation of freshwater mussels. *Bull. Bur. Fish.*, **37**:77–181.
- CUMMINGS, K. S. AND C. A. MAYER. 1992. Field guide to freshwater mussels of the Midwest. Illinois Natural History Survey Manual 5, Champaign. 194 p.
- DAVIS, M. 1988. Freshwater mussels (Mollusca: Bivalvia: Unionidae) of the Cannon River drainage in southeastern Minnesota. Minnesota Department of Natural Resources Nongame Wildlife Program Report, 70 p.

- DAWLEY, C. W. 1947. Distribution of aquatic mollusks in Minnesota. *Am. Midl. Nat.*, **38**:671–697.
- DOWNING, W. L., J. SHOSTELL AND J. A. DOWNING. 1992. Non-annual external annuli in the freshwater mussels *Anodonta grandis grandis* and *Lampsilis radiata siliquoidea*. *Freshwater Biol.*, **28**:309–317.
- ECKBLAD, J., B. OTSBY AND K. TENNESON. 2002. The unionid mussels of the Upper Iowa and Turkey River watersheds. *J. Iowa Acad. Sci.*, **109**:43–49.
- FREEMAN, M. C. 1995. Movements by two small fishes in a large stream. *Copeia*, **1995**:361–367.
- FREMLING, C. R. 2005. Immortal river: the Upper Mississippi in ancient and modern times. Univ. of Wisc., Madison, Wisconsin. 429 p.
- GORDON, M. E. AND J. B. LAYZER. 1989. Mussels (Bivalvia: Unionidea) of the Cumberland River: review of the life histories and ecological relationships. United States Fish and Wildlife Service Biological Report 89, 99 p.
- GRAF, D. L. 1997. Distribution of unionid (Bivalvia) faunas in Minnesota, USA. *Nautilus*, **110**:45–54.
- . 2002. Historical biogeography and late glacial origin of the freshwater pearly mussel (Bivalvia: Unionidae) faunas of Lake Erie, North America. *Occas. Pap. Mollusks*, **6**:175–211.
- HAAG, W. R. AND M. L. WARREN, JR. 1997. Host fishes and reproductive biology of 6 freshwater mussel species from the Mobile Basin, USA. *J. N. Am. Benthol. Soc.*, **16**:576–585.
- AND ———. 1999. Mantle displays of freshwater mussels elicit attacks from fish. *Freshwater Biol.*, **42**:35–40.
- AND ———. 2000. Effects of light and presence of fish on lure display and larval release behaviours in two species of freshwater mussels. *Anim. Behav.*, **60**:879–886.
- AND ———. 2003. Host fishes and infection strategies of freshwater mussels in large Mobile Basin streams, USA. *J. N. Am. Benthol. Soc.*, **22**:78–91.
- , ——— AND M. SHILLINGSFORD. 1999. Host fishes and host-attracting behavior of *Lampsilis altilis* and *Villosa vibex* (Bivalvia: Unionidae). *Am. Midl. Nat.*, **141**:149–157.
- HOGGARTH, M. A. 1999. Descriptions of some of the glochidia of the Unionidae (Mollusca: Bivalvia). *Malacologia*, **41**:1–118.
- HORNBAACH, D. J. 2001. Macrohabitat factors influencing the distribution of naiads in the St. Croix River, Minnesota and Wisconsin, USA, p. 213–230. *In*: G. Bauer and K. Wächtler (eds.). Ecology and evolution of the freshwater mussels Unionoida. Ecological Studies Vol. 145., Springer-Verlag, Berlin.
- HOVE, M. C., K. R. HILLEGASS, J. E. KURTH, V. E. PEPI, C. J. LEE, P. A. MAHONEY, A. R. KAPUSCINSKI AND M. BOMIER. 2000. Considerations for conducting host suitability studies, p. 27–34. *In*: R. A. Tankersley, D. I. Warmoltz, G. T. Watters, B. J. Armitage, P. D. Johnson and R. S. Butler (eds.). Freshwater Mollusk Symposia Proceedings. Ohio Biological Survey, Columbus.
- JENKINS, R. E. AND N. M. BURKHEAD. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland. 1079 p.
- JIRKA, K. J. AND R. J. NEVES. 1992. Reproductive biology of four species of freshwater mussels (Mollusca: Unionidae) in the New River, Virginia and West Virginia. *J. Freshwater Ecol.*, **7**:35–44.
- KRAEMER, L. R. 1969. Flapping behavior in the Lampsilinae (Pelecypoda: Unionidae): some aspects of its neurobiology. *Malacologia*, **9**:272.
- . 1970. The mantle flap in three species of *Lampsilis* (Pelecypoda: Unionidae). *Malacologia*, **10**:225–282.
- AND C. M. SWANSON. 1985. Functional morphology of “eyespot” of mantle flaps of *Lampsilis* (Bivalvia: Unionacea): evidence for their role as effectors, and basis for hypothesis regarding pigment distribution in bivalve mantle tissues. *Malacologia*, **26**:241–251.
- MAY, B. 1969. Observations on the biology of the variegated darter, *Etheostoma variatum* (Kirtland). *Ohio J. Sci.*, **69**:85–92.
- MCLAIN, D. C. AND M. R. ROSS. 2005. Reproduction based on local patch size of *Alasmidonta heterodon* and dispersal by its darter host in the Mill River, Massachusetts. *J. N. Am. Benthol. Soc.*, **24**:139–147.
- NELSON, J. S., E. J. CROSSMAN, H. ESPINOSA-PEREZ, L. T. FINDLEY, C. R. GILBERT, R. N. LEA AND J. D. WILLIAMS. 2004. Common and scientific names of fishes from the United States, Canada, and Mexico. American Fisheries Society Special Publication 29, Bethesda, Maryland. 386 p.

- NEVES, R. J. AND S. N. MOYER. 1988. Evaluation of techniques for age determination of freshwater mussels (Unionidae). *Am. Malacol. Bull.*, **6**:179–188.
- OBERMEYER, B. K., D. R. EDDS, C. W. PROPHET AND E. J. MILLER. 1997. Freshwater mussels (Bivalvia: Unionidae) in the Verdigris, Neosho, and Spring River basins of Kansas and Missouri, with emphasis on species of concern. *Am. Malacol. Bull.*, **14**:41–55.
- OESCH, R. D. 1995. Missouri naiades: a guide to the mussels of Missouri. Missouri Department of Conservation, Jefferson City. 271 p.
- PAGE, L. M. 1983. Handbook of darters. TFH Publications, Inc., Neptune City, New Jersey. 271 p.
- REED, R. J. 1968. Mark and recapture studies of eight species of darters (Pisces: Percidae) in three streams of northwestern Pennsylvania. *Copeia*, **1968**:172–175.
- RIUSECH, F. A. AND M. C. BARNHART. 2000. Host suitability and utilization in *Venustaconcha ellipsiformis* and *Venustaconcha pleasii* (Bivalvia: Unionidae) from the Ozark Plateaus, p. 83–91. In: R. A. Tankersley, D. I. Warmoltz, G. T. Watters, B. J. Armitage, P. D. Johnson and R. S. Butler (eds.). Freshwater Mollusk Symposia Proceedings. Ohio Biological Survey, Columbus.
- SCHWEBACH, M., D. SHRIEVER, N. DILLON, M. HOVE, M. MCGILL, C. NELSON, F. THOMAS AND A. KAPUSCINSKI. 2002. Channel catfish is a suitable host species for mapleleaf glochidia. *Ellipsaria*, **4**:12–13.
- SIETMAN, B. E. 2003. Field guide to the freshwater mussels of Minnesota. Minnesota Department of Natural Resources, St. Paul. 144 p.
- , S. D. WHITNEY, D. E. KELNER, K. D. BLODGETT AND H. L. DUNN. 2001. Post-extirpation recovery of the freshwater mussel (Bivalvia: Unionidae) fauna in the upper Illinois River. *J. Freshwater Ecol.*, **16**:273–281.
- SMITH, D. G. 1985. Recent range expansion of the freshwater mussel *Anodonta implicata* and its relationship to clupeid fish restoration in the Connecticut River system. *Freshwater Invert. Bio.*, **4**:105–108.
- SURBER, T. 1912. Identification of the glochidia of freshwater mussels. Report of the U.S. Commission of Fisheries for 1912 and Special Papers., 10 p.
- . 1915. Identification of the glochidia of fresh-water mussels. Bureau of Fisheries Document, No. 813., 10 p.
- TURGEON, D. D., J. F. QUINN, JR., A. E. BOGAN, E. V. COAN, F. G. HOCHBERG, W. G. LYONS, P. M. MIKKELSEN, R. J. NEVES, C. F. E. ROPER, G. ROSENBERG, B. ROTH, A. SCHELTEMA, F. G. THOMPSON, M. VECCHIONE AND J. D. WILLIAMS. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks, 2nd edition. American Fisheries Society Special Publication 26, Bethesda, Maryland. 526 p.
- VAN DER SCHALIE, H. 1936. The relationship of the gravid periods of certain mussels in Michigan to the pearl button industry. *Trans. Am. Fish. Soc.*, **66**:406–410.
- AND A. VAN DER SCHALIE. 1963. The distribution, ecology, and life history of the mussel, *Actinonaias ellipsiformis* (Conrad), in Michigan. *Occ. Pap. Mus. Zool.*, No. 633. 17 p.
- WALLER, D. R. 1987. Studies on *Lampsilis* mussels of the upper Mississippi River. Ph. D. Dissertation. Iowa State University, Ames, Iowa. 203 p.
- WATTERS, G. T. 1992. Unionids, fishes, and the species-area curve. *J. Biogeogr.*, **19**:481–490.
- . 1995. Small dams as barriers to freshwater mussels (Bivalvia: Unionidae) and their hosts. *Biol. Conserv.*, **75**:79–85.
- . 1999. Morphology of the conglutinate of the kidneyshell freshwater mussel, *Ptychobranchus fasciolaris*. *Invert. Bio.*, **118**:289–295.
- ZALE, A. V. AND R. J. NEVES. 1982. Fish hosts of four species of lampsiline mussels (Mollusca: Unionidae) in Big Moccasin Creek, Virginia. *Can. J. Zool.*, **60**:2535–2542.
- ZAR, J. H. 1996. Biostatistical analysis, 3rd edition. Prentice Hall, Upper Saddle River, New Jersey. 662 p.