Zale
Neves
1982

Reproductive Biology of Four Freshwater Mussel Species (Mollusca: Unionidae) in Virginia[1]

ALEXANDER V. ZALE AND RICHARD J. NEVES

Newins-Ziegler Hall, University of Florida, Gainesville, Florida 32611 and
Virginia Cooperative Fishery Research Unit, Department of Fisheries and Wildlife Sciences,
Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061

Abstract. The reproductive biology of four mussel species (subfamily Lampsilinae), *Villosa nebulosa, V. vanuxemi, Medionidus conradicus,* and *Lampsilis fasciola,* was investigated during a 14-month study of the mussel community in Big Moccasin Creek, southwestern Virginia. Examination of histological sections of gonadal tissue from males and females of each species collected from April 1979 to May 1980 revealed that active gametogenesis proceeded throughout the year. Distinct and separate spawning periods for the four species in 1979 were as follows: *M. conradicus,* July 8-16; *V. vanuxemi,* July 25-30; *V. nebulosa,* August 13-20; and *L. fasciola,* late August. Periodic inspection of developing embryos in female marsupia indicated that glochidia of each species required 7 to 8 weeks to develop after fertilization. Mature glochidia were readily identified to genus but differentiation of *V. nebulosa* from *V. vanuxemi* was difficult. Drift nets (130-μm mesh) set downstream from the mussel community captured glochidia of *M. conradicus* throughout the year except July and August; glochidia of *V. vanuxemi* from October to May; and glochidia of *V. nebulosa* from April to early August. Females of *L. fasciola* discharged glochidia from May to mid-August.

Within the Unionidae, species of the subfamily Lampsilinae and many Anodontinae are bradytichtic (long-term) breeders. Ova are released by females into their suprabranchial cavity in late summer or early fall and are then fertilized by sperm received through the incurrent siphon. Embryos are passed into water tubes of the gills, where they develop into mature larvae (glochidia). Glochidia remain in the gills until their release during the following spring or summer. They are obligate parasites on the fins or gills of fishes until they metamorphose to the free-living juvenile stage.

General differences in reproductive biology among unionid subfamilies were fairly well documented in early studies (Coker, Shira, Clark & Howard 1921), although the periods of gametogenesis, spawning, fertilization, larval development, and release of glochidia have been described for relatively few species. Early investigators reported periods of female gravidity (Ortmann 1909; Surber 1912; Utterback 1916) but did not discuss the gametogenic cycle. Matteson (1948) conducted a detailed life history of *Elliptio complanatus* that included gametogenesis, fertilization, and glochidial development. Subsequent studies on the gametogenic cycles of *Actinonaias ellipsiformis* (van der Schalie and van der Schalie 1963), *Amblema plicata* (Stein 1969), *Pleurobema cordatum* (Yokley 1972), and *Anodonta* spp. (Heard 1975) confirmed that reproductive strategies differ among subfamilies. However, the reproductive cycle of species constituting the unique mussel fauna of the Cumberland Plateau Region, southeastern U.S., has not been previously described.

Our study of mussel reproduction was conducted on four lampsiline species of the Upper Tennessee River drainage and included three Cumberlandian species, *Villosa (=Micromya) nebulosa, Villosa vanuxemi, Medionidus conradicus,* and the more ubiquitous *Lampsilis*

---

[1]Contribution of the Virginia Cooperative Fishery Research Unit jointly sponsored by the U.S. Fish and Wildlife Service, the Virginia Commission of Game and Inland Fisheries, and Virginia Polytechnic Institute and State University.

fasciola. Our objectives were to follow the stages of gametogenesis in males and females through an annual cycle, describe mature glochidia of the four species, and determine the period of glochidial release by females of each species.

STUDY AREA

Big Moccasin Creek, a third-order tributary of the North Fork of the Holston River, flows through Russell and Scott counties in southwestern Virginia. The study area (36°47'30"N, 82°11'50"W; 616 m elevation) encompassed a 400-m stream section above river mile 51.3 (km 82) at the intersection of state route 676 and 677. The creek at this location runs through open pasture and averages 7 m in width and 0.2 m in depth. Substrate composition is primarily cobble and gravel; bedrock and silt occur in localized areas. Water chemistry characteristics during low flow conditions in October were as follows: temperature 14°C, pH 8.2, dissolved oxygen 9.0 mg/l, conductivity 250 μmhos, hardness 175 mg/l, and total alkalinity 180 mg/l. Weekly ranges in water temperature, determined with a 30-day recording thermograph, are summarized in Figure 1.

The mussel community at the study site, based on 30 random 0.5m^2 quadrat samples, consisted of seven species; mean density was 18.7 mussels/m^2 (Table 1). No additional mussel species occurred upstream from the site.

MATERIALS AND METHODS

Specimens of *Villosa nebulosa, V. vanuxemi,* and *Medionidus conradicus* were collected weekly at the study site from April to October 1979 and semi-monthly from November 1979 to May 1980. We attempted to obtain equal numbers of males and females, but females were often underrepresented because sex ratios in the populations were unequal (Zale 1980). The population of *Lampsilis fasciola* was sampled less intensively because of its low density (Table 1). Mussels were collected by hand and transported to the laboratory in cloth bags packed in crushed ice. Specimens were relaxed in propylene phenoxitol, fixed in 10% buffered formalin, and preserved in 70% ethyl alcohol. The reproductive cycle of each species was studied by histological sectioning of the gonads. Serial sections (7μm thick) of the gonadal mass were cut with a microtome, affixed to glass slides, and stained by using standard hematoxylin-eosin techniques (Humason 1972). Slide preparations were examined under a compound microscope at several magnifications. The reproductive stage of each mussel was described and recorded. Absence of gametes immediately after a period of reproductive maturity was assumed to indicate that spawning had occurred.

Mussels were aged by counting external growth rings on the shells. The validity of growth checks as annuli was verified by marking and measuring specimens at the study site during November 1979 and reexamining them one year later.

We monitored embryogenesis by inspecting the contents of female marsupia weekly. Developing larvae were obtained by rupturing the marsupia with a sharp probe, and the stage of development was described for the young of each female.

Mature glochidia of each species were photographed, measured, and examined for morphometric characters useful in species identification. Lengths, breadths, and hinge lengths of 50 glochidia from each of five gravid females per species were measured. Length is defined as the maximum antero-posterior dimension parallel to the hinge, and breadth as the maximum dorso-ventral dimension perpendicular to the hinge.

Three drift nets (930 cm^2 in mouth area and with 130-μm mesh) were set below the mussel community on each sampling date to collect glochidia in the stream drift. The collection period could not be standardized because periodic turbid conditions clogged drift nets within

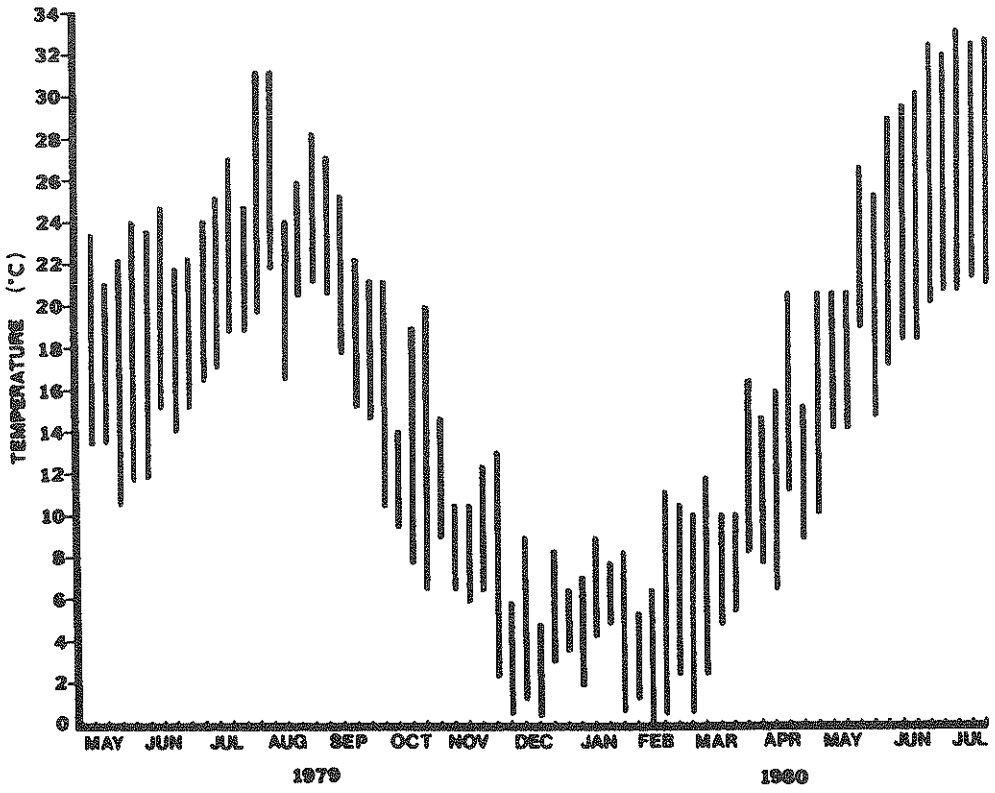

Fig. 1. Weekly water temperature range (°C) in Big Moccasin Creek, May 1979 to July 1980.

about 2 hours. Drift samples were washed from the nets and preserved in 10% buffered formalin. In the laboratory, rose bengal was added to the samples to facilitate sorting. Subsamples of drift placed in a gridded petri dish were examined with a dissecting microscope. Glochidia of Lampsilinae were easily distinguished from those of the other two subfamilies at the site by their size and distinctive shape (Surber 1912). Lampsiline glochidia were removed and identified to genus. *Villosa nebulosa* and *V. vanuxemi* were combined because they could not be reliably distinguished from each other.

RESULTS

Gametogenesis

Gonadal sections of 314 *Villosa nebulosa*, 126 *V. vanuxemi*, 158 *Medionidus conradicus*, and 37 *Lampsilis fasciola* made from specimens collected between April 1979 and May 1980. Both sexes of the four species first reached sexual maturity at age 3 (in the fourth summer of life). Gametogenesis was evident in both sexes of mature *V. nebulosa* throughout the year. Acini of males in March were widely spaced and consisted primarily of nutritive granules, with some spermatogonia, spermatocytes, and spermatids (Fig. 2). The number of spermatogonia increased in April but the acini remained compact and widely separated. By June the acini had expanded to occupy most of the gonadal mass, and many spermatids were present. Spermatozoa were first detected in early July and were abundant by early August.

TABLE I

Species composition, density, and relative abundance of mussels at the study site, Big Moccasin Creek, Virginia

Species	Density (No./m²)	Relative Abundance (%)
Lampsilinae		
Medionidus conradicus (Lea, 1834)	12.7	68.0
Villosa nebulosa (Conrad, 1834)	4.5	23.8
Villosa vanuxemi (Lea, 1838)	1.1	6.1
Lampsilis fasciola (Rafinesque, 1820)	0.1	0.7
Unioninae		
Pleurobema oviforme (Conrad, 1834)	0.3	1.4
Fusconaia barnesiana (Lea, 1838)	+	+
Anodontinae		
Alasmidonta minor (Lea, 1845)	+	+

+ = less than 0.1

On August 13, the acini were packed with mature sperm (Fig. 2), and the gonado-visceral mass of males appeared thick and swollen. One week later (August 20), few sperm remained and acini were again widely spaced. By August 27 no mature sperm remained in the testes. The appearance of granules and spermatogonia in September indicated the initiation of a new spermatogenic cycle. By mid-October the acini appeared to be in a condition similar to that described for March collections. No obvious changes in testicular condition were noted during winter (December-February).

Ovarian tissue of *V. nebulosa* in March was characterized by thin-walled and widely spaced alveoli with oogonia (Fig. 3). In May, alveoli had thicker walls and were packed closer together; developing oocytes were surrounded by nutritive material. By late June many oocytes were developing within the alveolar walls, and some ovocytes had moved into the lumina. These walls deteriorated in July and nutritive granules were less abundant; most eggs were large and appeared to be nearly mature. By August 13, ovocytes had developed fully and alveolar walls were attenuated, and by August 20, no eggs remained in the ovaries (Fig. 3). By mid-October, walled alveoli had re-formed and oogenesis was again evident. Sections of ovaries collected in November appeared similar to sections of those collected in spring. As judged by histological sections of male and female gonads, most of the population of *V. nebulosa* in Big Moccasin Creek spawned between August 13 and 20. All females examined, spawned during this period, but the release of sperm continued into the following week.

The gametogenic cycles for *M. conradicus* and *V. vanuxemi* were similar to those of *V. nebulosa*, differing only in the dates of spawning (Table 2). In *M. conradicus*, males and females released gametes primarily during July 8-16, and in *V. vanuxemi*, during July 23-30 (though sperm were also shed during the following week).

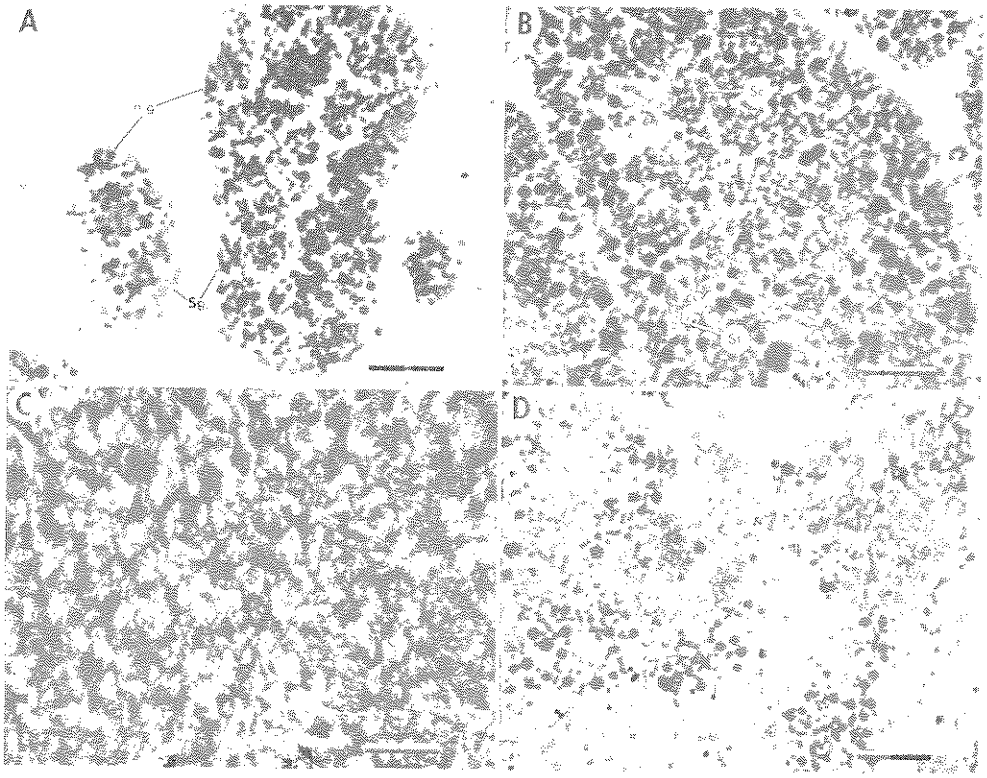

Fig. 2. Histological sections of testes of *Villosa nebulosa* collected March 11 (A), June 19 (B), August 13 (C), and August 20 (D). Abbreviations: n.g., nutritive granules; Sg., spermatogonia; Sc., spermatocytes; St., spermatids. Bar = 50 μm.

Too few specimens of *L. fasciola* were collected to describe the gametogenic cycle of this species as completely as that of the other three species. In early September, males appeared to have partly spent testes, and a female contained early embryos in her marsupia. Spawning probably occurred in late August. Release of gametes by *L. fasciola* did not appear to be as complete as in the other lampsilines in Big Moccasin Creek. Many residual gametes remained in the gonads during the winter, and active gametogenesis continued throughout the year.

Hermaphroditism was not observed in any sectioned specimens of *V. nebulosa, V. vanuxemi,* or *L. fasciola*; however, a single hermaphroditic *M. conradicus* was collected. This specimen had embryos in the marsupia and typical female shell morphology, but testicular tissue comprised about 5% of the gonad (Fig. 4).

Parasitic trematodes were frequently observed in gonadal tissue sections of *V. nebulosa, V. vanuxemi,* and *M. conradicus;* none were found in *L. fasciola.* Trematode infestations were most frequent in the two species of *Villosa* (Table 3). Degree of infestation varied from a few trematodes in an otherwise healthy gonad to numerous trematodes that resulted in the total disintegration of reproductive tissue. Older mussels were more frequently and more heavily infested, and many of the older (>10 years) *Villosa* were so heavily parasitized that virtually no recognizable gonadal tissue remained.

Development of Glochidia

Early embryos found in the marsupia of *Villosa nebulosa* on August 20, shortly after

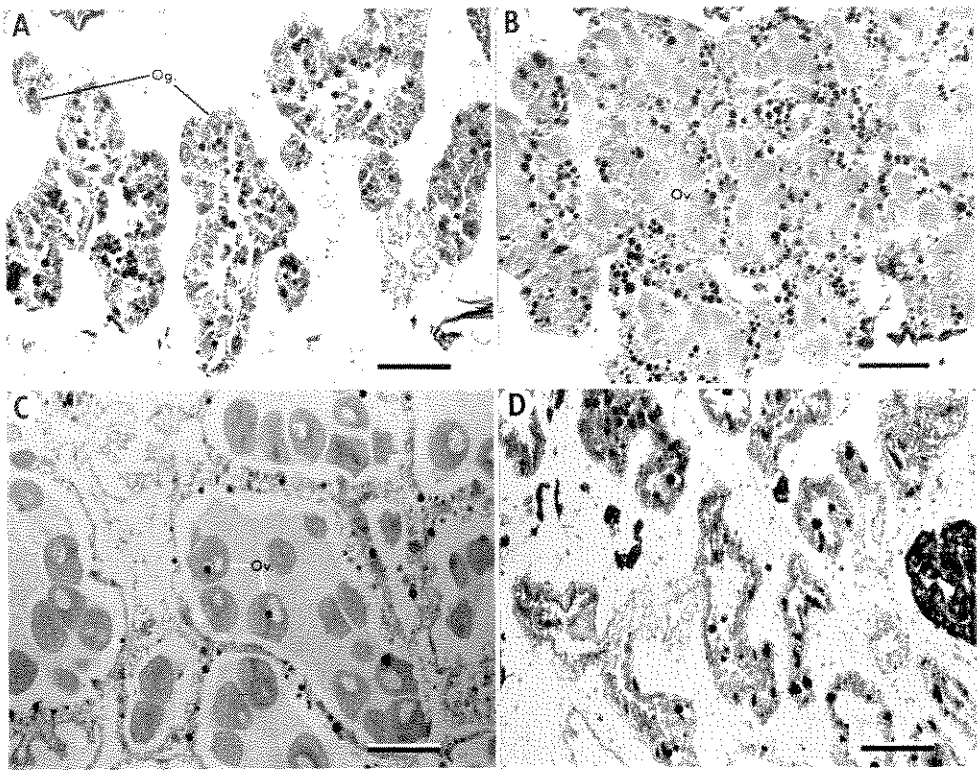

Fig. 3. Histological sections of ovaries of *Villosa nebulosa* collected March 11 (A), June 25 (B), August 13 (C), and August 20 (D). Abbreviations: Og., oogonia; Ov., ovocytes. Bar = 200 μm.

TABLE II

Primary spawning periods of lampsiline mussels in Big Moccasin Creek.

Species	Spawning Period	Water Temperatures (°C)
Medionidus conradicus	July 8-16	17.0 - 25.2
Villosa vanuxemi	July 23-30	18.7 - 24.6
Villosa nebulosa	August 13-20	16.4 - 24. 0
Lampsilis fasciola	Late August	16.4 - 25.8

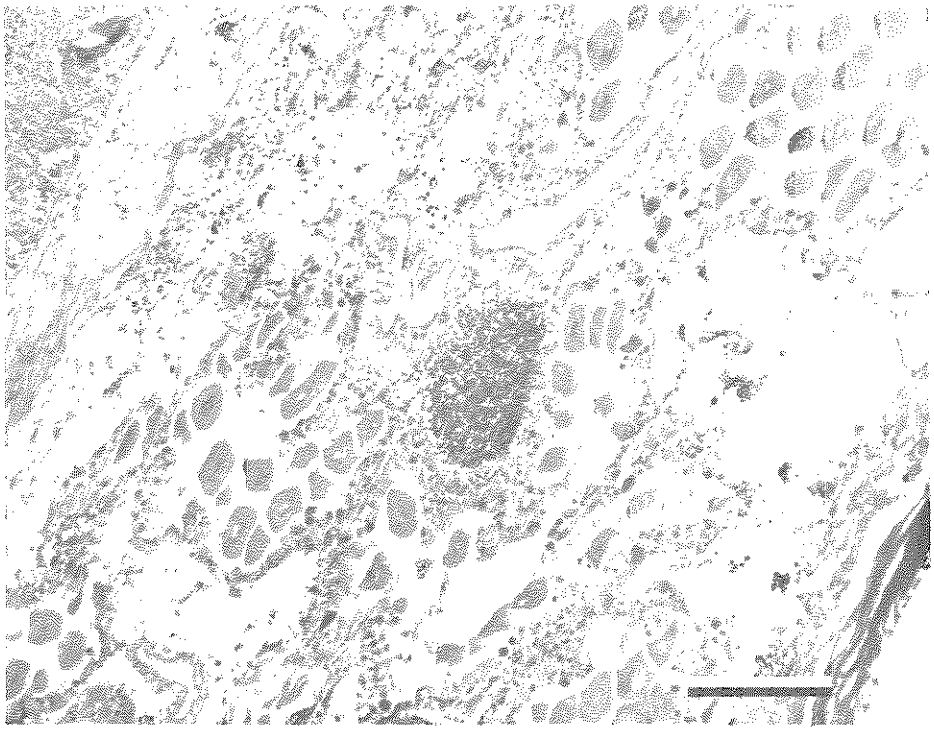

Fig. 4. Histological section of hermaphroditic gonad of *Medionidus conradicus* collected June 11. Bar = 200 μm.

TABLE III

Frequency of trematode infestation in gonads of lampsiline mussels from Big Moccasin Creek, Virginia.

	No. Examined	Percent Parasitized
Villosa vanuxemi	126	31.7
Villosa nebulosa	314	22.9
Medionidus conradicus	158	19.0
Lampsilis fasciola	37	0.0

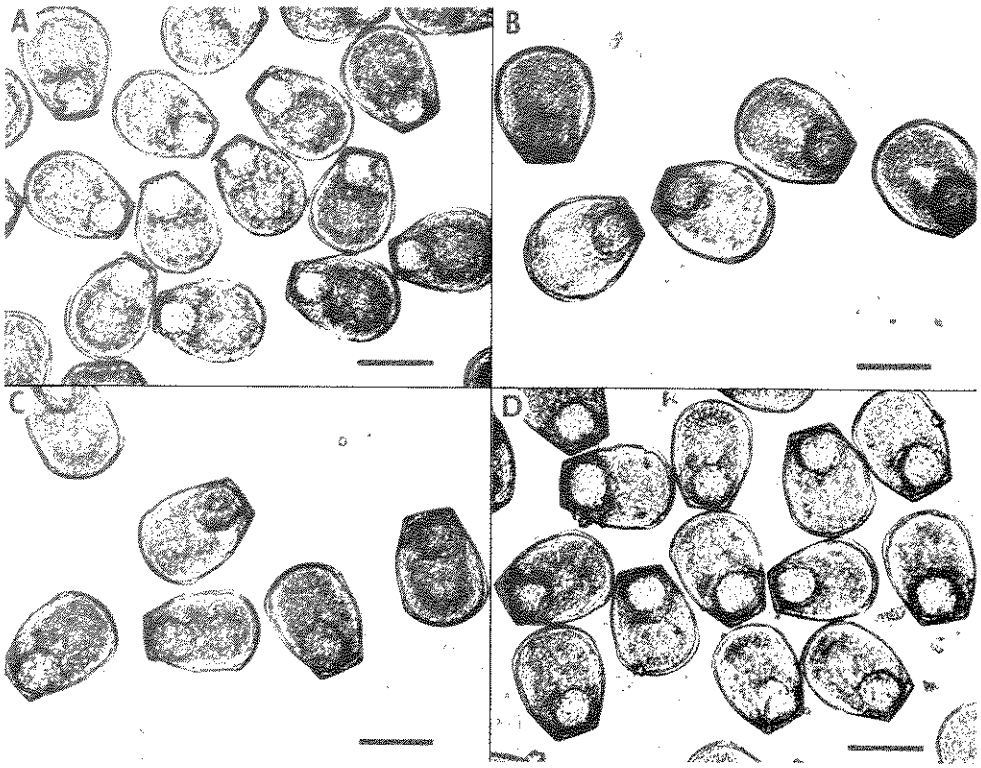

Fig. 5. Mature glochidia of *Medionidus conradicus* (A), *Lampsilis fasciola* (B), *Villosa vanuxemi* (C), and *Villosa nebulosa* (D). Bar = 200 μm.

TABLE IV

Dimensions (μm) of the glochidia of lampsiline mussels, Big Moccasin Creek, Virginia.

Species	Breadth Mean±SD	Breadth Range	Length Mean±SD	Length Range	Hinge Length Mean±SD	Hinge Length Range
Villosa nebulosa	287.1±13.6	259.0-333.0	220.4±12.8	196.1-262.7	115.4± 9.9	96.2-140.6
Villosa vanuxemi	303.3± 8.0	277.5-325.6	221.5± 7.3	207.2-240.5	116.8± 5.1	103.6-129.5
Medionidus conradicus	273.8±10.5	236.8-299.7	217.8± 7.5	199.8-236.8	92.7± 4.7	77.7-103.6
Lampsilis fasciola	293.2± 9.2	266.4-318.2	238.2± 8.8	218.3-266.4	111.2± 6.9	96.2-136.9

spawning, consisted of a spheroid mass of cells enclosed within a vitelline membrane. Rudimentary valve development was evident in embryos collected 1 week later (August 27). By September 10, larvae had the typical shape of *Villosa* glochidia (Fig. 5). The valves were thin and fragile, and most of the mantle cells remained in a central oval mass. Cells of the adductor muscle were beginning to differentiate. Valves of larvae examined one week later were noticeably thicker, and the adductor muscle was readily visable. Mantle cells lined the interior of the valves. Glochidia from females collected on October 2 appeared structurally mature, but remained inactive when stimulated with a fine probe or saline solution. Mature, active glochidia were obtained on October 11.

Developmental stages of the glochidia of *M. conradicus* and *V. vanuxemi* paralleled those of *V. nebulosa*. Early embryos of *M. conradicus* were collected soon after oviposition on July 16, and had completed development by September 4. Embryos of *V. vanuxemi* were first obtained from marsupia on July 30, and had completed development by September 10. Embryogenesis for these three lampsiline species thus required 7 to 8 weeks. Early embryos of *L. fasciola* were collected on September 3; however, insufficient numbers of females were collected in subsequent weeks to enable us to adequately describe glochidial development.

Identification of Glochidia

Mature glochidia of M. conradicus, L. fasciola, V. nebulosa and *V. vanuxemi* differed slightly in mean size and morphology (Fig. 5). Glochidia of *M. conradicus* had the smallest mean breadth, length, and hinge length (Table 4). In addition to their smaller size, glochidia of this species were characterized by small-diameter adductor muscles, delicately structured valves, and smoothly rounded valve edges with angular corners only at the hinge. Glochidia of *L. fasciola* were longest and appeared rather robust and rotund. The *Villosa* spp. were distinguished by their greater mean breadth-to-length ratios and roughly parallel valve edges. Average valve breadth of *V. vanuxemi* exceeded that of *V. nebulosa;* however, the considerable overlap in the ranges for this and other dimensions precluded their use as distinguishing characters (Table 4).

Drift of Glochidia

Stream drift was sampled on 45 dates between May 1979 and May 1980. Glochidia were abundant (several hundred) in most samples and readily visible after exposure to rose bengal stain. Lampsiline glochidia were present in the water column during most of the year (Table 5).

Glochidia of *M. conradicus* occurred in the drift during May and June 1979 but were rare or absent in samples collected in July and August. They were again collected in samples from September through early November, declined in abundance in late November, were absent by December, and then reappeared, often in great abundance, from January through May.

Only 31 glochidia of *L. fasciola* were collected in drift samples, from May to August 1979 and in May 1980. They were not collected from mid-August 1979 through April 1980.

Glochidia of *Villosa* spp. were present in nearly all samples from May to mid-August 1979. They were then absent for 6 weeks, reappeared in early October, and occurred regularly throughout most of the winter and spring (Table 5). From the occurrence of glochidial infections on the respective host fishes of *V. nebulosa* and *V. vanuxemi* in Big Moccasin Creek (Zale 1980), it appears that drifting glochidia were probably *V. vanuxemi* in fall and winter, and primarily *V. nebulosa* in spring and summer.

DISCUSSION

Gametogenesis in all four species occurred throughout the year, with no evidence of inactive periods, as have been reported for some species (Heard 1969; Smith 1978). The

TABLE V

Occurrence of lampsiline glochidia in drift samples at the study site, Big Moccasin Creek from May 1979 to May 1980. (P = present).

Sampling Date	Species *Medionidus conradicus*	*Lampsilis fasciola*	*Villosa nebulosa and vanuxemi*
1979			
May 5	P	P	P
May 12	P		P
May 20	P		P
May 27	P		P
Jun 1	P		P
Jun 11	P	P	P
Jun 19	P	P	P
Jun 25	P		
Jul 2	P	P	P
Jul 8			
Jul 16	P	P	P
Jul 23			P
Jul 30		P	P
Aug 6			P
Aug 13			P
Aug 20	P		
Aug 27			
Sep 4	P		
Sep 10	P		
Sep 17	P		
Sep 25	P		
Oct 2	P		P
Oct 11	P		
Oct 18	P		P
Oct 25	P		P
Nov 1	P		P
Nov 8			P
Nov 15			P
Nov 27	P		P
Dec 4			P
Dec 17			P
Dec 31			
1980			
Jan 17	P		
Jan 29	P		P
Feb 12			
Feb 27	P		P
Mar 11	P		P
Mar 27	P		P
Apr 11	P		P
Apr 17	P		P
Apr 24	P		P
May 1	P		P
May 8	P	P	P
May 15	P		P
May 21	P	P	P

reproductive cycle was reinitiated soon after release of gametes and continued until the next spawning period. The stage of gametogenesis among conspecifics during all sampling dates was highly synchronized, and time of spawning was well-defined. All eggs and most sperm were apparently released within 1 week by members of a species; this spawning synchrony would tend to maximize fertilization success. Release of sperm by males during low-flow conditions in summer and fall would further increase the likelihood of fertilization. No unfertilized eggs were found in the marsupia of females during the spawning period. Environmental cues that initiate spawning in freshwater mussels are unknown, although water temperature and photoperiod are probably involved.

Both sexes of the four species first became sexually mature at age 3. *Actinonaias ellipsiformis* first reached sexual maturity at age 3 (van der Schalie and van der Schalie 1963), whereas *Amblema plicata* first reproduced at age 4 (Stein 1969). Sexual maturity appeared to be sex-dependent in *Margaritifera margaritifera* from Massachusetts; males matured at age 7 and females at age 9 (Smith 1979). In general, headwater populations appear to have shorter life-spans than riverine populations and may therefore reach sexual maturity at an earlier age.

Parasitism by digenetic trematodes affected the reproductive potential of mussels in Big Moccasin Creek. Nearly one-third of the *V. vanuxemi* specimens harbored at least some trematodes, and many of the older mussels were rendered functionally sterile. Similar trematode infestations have been found in the gonads of *A. ellipsiformis* from Michigan (van der Schalie and van der Schalie 1963) and several unionid species from Pennsylvania (Dennis 1970). Light infestations of unionicolid water mites were often observed in and around the gills of lampsiline mussels from Big Moccasin Creek but no tissue damage was apparent.

Freshwater mussels can be considered ovoviviparous, since fertilization and embryogenesis occur within the female, but the stages of larval development have not been adequately described. Lillie (1895) investigated glochidial development in the Anodontinae, and Wood (1974) corroborated these early observations. No comparable studies on the Lampsilinae have been conducted, and our coverage of embryogenesis was cursory. The early embryos of *M. conradicus, V. nebulosa,* and *V. vanuxemi* required about 7 to 8 weeks to develop into glochidia under natural conditions. Matteson (1948) reported that embryos of *Elliptio complanatus* matured in 2 weeks, and Yokley (1972) estimated 4 to 6 weeks between fertilization and glochidial release in *Pleurobema cordatum*. Glochidia of *Margaritifera margaritifera* developed in 30 days (Smith 1976), whereas those of *Anodonta cygnea* required 2 months (Wood 1974). These time periods for glochidial development are not directly comparable however, because of differences in water temperature and other environmental variables.

The release of glochidia by *M. conradicus* occurred almost throughout the year, beginning in September and continuing into the following summer until it abated during the period of embryogenesis in July and August. In winter samples, glochidia were rare or absent during periods of extreme cold (<5°C) but common in drift samples collected on warm days. As a consequence of extended glochidia release by *M. conradicus,* infections of host fish and juvenile recruitment occurred throughout the year under a variety of environmental conditions (Zale 1980).

In *V. vanuxemi,* glochidial release began in October. Most glochidia were discharged by mid-spring but an occasional female remained partly gravid through July. A similar periodicity of glochidial release was reported for *Anodonta cygnea* (Dartnall and Walkey 1979). The period of glochidial discharge by *V. vanuxemi* at the study site occurred concurrently with the presence of its fish host, the banded sculpin, *Cottus carolinae* (Zale 1980). Sculpins were abundant from fall 1979 to spring 1980 but were collected infrequently during summer.

Release of glochidia by *V. nebulosa* and *L. fasciola* occurred from April to mid-August. In Big Moccasin Creek, the hosts of *V. nebulosa* are the rock bass *(Ambloplites rupestris)* and

smallmouth bass *(Micropterus dolomieui); L. fasciola* completed metamorphosis only on smallmouth bass (Zale 1980). During fall and winter centrarchids remained in deep pools and were rarely collected over mussel beds. In late spring however, they constructed nests in riffle areas and were in the immediate area where glochidia were being discharged. The synchrony between glochidial release by all four mussel species and physical presence of host fishes may partly account for the reproductive success of these lampsiline mussels in Big Moccasin Creek.

LITERATURE CITED

COKER, R. E., SHIRA, A. F., CLARK, H. W., & HOWARD, A. D. 1921. Natural history and propagation of fresh-water mussels. *Bull. U.S. Bur. Fish.*, 37: 76-181.

DARTNALL, H. J. G., & WALKEY, M. 1979. The distribution of glochidia of the swan mussel, *Anodonta cygnea* (Mollusca) on the three-spined stickleback, *Gasterosteus aculeatus* (Pisces). *J. Zool.*, 189: 31-37.

DENNIS, S. D. 1970. Pennsylvania mussel studies (June 1, 1968 - October 1, 1969). Center Aquat. Biol., East. Mich., Ypsilanti, Mich. 138 pp.

HEARD, W. H. 1969. Seasonal variation in gonad activity in freshwater mussels and its systematic significance. *Bull. Am. Malacol. Union*, 1969: 53 (Abstract).

HEARD, W. H. 1975. Sexuality and other aspects of reproduction in *Anodonta* (Pelecypoda: Unionidae). *Malacologia*, 15: 81-103.

HUMASON, G. L. 1972. Animal tissue techniques. W. H. Freeman and Co., San Francisco. 641 pp.

LILLIE, F. R. 1895. The embryology of the Unionidae. *J. Morphol.*, 10: 1-100.

MATTESON, M. P. 1948. Life history of *Elliptio complanatus* (Dillwyn, 1817). *Am. Midl. Nat.*, 40: 690-723.

ORTMANN, A. E. 1909. The breeding season of Unionidae in Pennsylvania. *Nautilus*, 22: 91-95, 99-103.

SMITH, D. G. 1976. Notes on the biology of Margaritifera margaritifera margaritifera in central Massachusetts. *Am. Midl. Nat.*, 96: 252-256.

SMITH, D. G. 1978. Biannual gametogenesis in *Margaritifera margaritifera* (L.) in northeastern North America. *Bull. Am. Malacol. Union*, 1978: 49-53.

SMITH, D. G. 1979. Sexual characteristics of *Margaritifera margaritifera* (Linnaeus) populations in central New England. *Veliger*, 21: 381-383.

STEIN, C. B. 1969. Gonad development in the three-ridge naiad, *Amblema plicata* (Say, 1817). *Annu. Rep Am. Malacol. Union*, 1969: 30 (Abstract).

SURBER, T. 1912. Identification of the glochidia of freshwater mussels. *U.S. Bur. Fish. Doc. No.* 771. pp. 1-10.

UTTERBACK, W. I. 1916. Breeding records of Missouri mussels. *Nautilus*, 30: 13-21.

VAN DER SCHALIE, H., & VAN DER SCHALIE, A. 1963. The distribution, ecology, and life history of the mussel *Actinonaias ellpsiformis* (Conrad) in Michigan. *Occas Pap. Mus. Zool. Univ. Mich.*, 633: 1-17.

WOOD, E. 1974. Development and morphology of the glochidium larva of *Anodonta cygnea*. *J. Zool.*, 173: 1-13.

YOKLEY, P., JR. 1972. Life history of *Pleurobema cordatum* (Rafinesque 1820) (Bivalvia:Unionacea). *Malacologia*, 11: 351-364.

ZALE, A. V. 1980. The life histories of four freshwater lampsiline mussels (Mollusca:Unionidae) in Big Moccasin Creek, Russell County, Virginia. MS Thesis, VPI & SU, Blacksburg, VA 256 pp.