Life history of the endangered James spinymussel *Pleurobema collina* (Conrad, 1837) (Mollusca: Unionidae)

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Abstract. The reproductive period, host fish requirements, and population characteristics of the James spinymussel [*Pleurobema collina* (Conrad, 1837)] were studied from 1987 to 1989 in the James River drainage, West Virginia and Virginia. This summer brooder was gravid from late May through early August and released the majority of glochidia in early June through late July. The mean fecundity was roughly 13,000 brooded eggs/female. Observations in the field and laboratory implicated fishes of the Cyprinidae as hosts for glochidia of the James spinymussel. Induced infestations of glochidia on fishes in the laboratory confirmed seven host species: the bluehead chub [*Nocomis leptocephalus* (Girard)], rosyside dace (*Clinostomus funduloides* Girard), satinfin shiner [*Cyprinella analostana* (Girard)], rosefin shiner [*Lythrurus ardens* (Cope)], central stoneroller [*Campostoma anomalum* (Rafinesque)], blacknose dace [*Rhinichthys atratulus* (Hermann)], and mountain redbelly dace [Phoxinus oreas (Cope)]. The age class structure of two populations, obtained by thin-sectioning valves collected in muskrat middens, ranged from 3 to 19 yrs with evidence of strong and weak year classes. Incidence of spines differed significantly among populations. The mean annual mortality rate of adults was 15.6 ± 1.4%.

The James spinymussel [*Pleurobema collina* (Conrad, 1837)] is one of three spined species of freshwater mussels in the United States (Fig. 1). The historic range of this species, endemic to the James River watershed, is thought to have occurred upstream of Richmond, Virginia, throughout the larger tributaries of the river basin. However, a survey on the status of this species in 1984 revealed its occurrence in only two small tributaries to the James River, an approximately 90% reduction in range (Clarke and Neves, 1984). As a result of this reduction in range and its rarity, the James spinymussel was listed by the federal government as endangered in July 1988. Additional populations have been reported since its federal listing (Hove, 1990).

As with most endemic mussel species, little is known of the life history and ecology of the James spinymussel. Boss and Clench (1967) described various anatomical characteristics and sexual dimorphism of *Pleurobema collina*. They suggested that it was probably a short-term brooder, releasing glochidia in the summer. Habitat of *P. collina* included streams ranging in size from 3 to 23 m wide and 15 to 100 cm deep (Clarke and Neves, 1984).

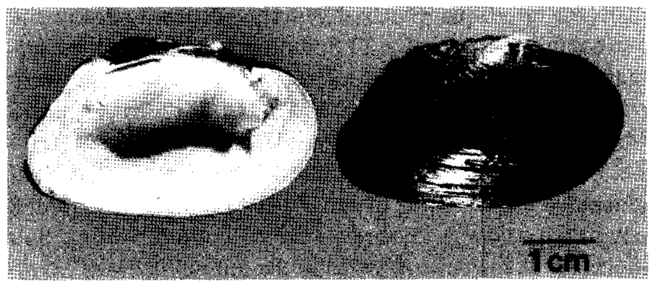

Fig. 1. *Pleurobema collina* from Craig Creek, Virginia.

The species occupied sediments of cobble and sand in reaches with slow to moderate currents. The spinymussel occurred historically in larger streams such as the James River opposite the city of Maidens where the river is about 150 m wide (museum records, Ohio State University). Other aspects of its biology were unknown. The purpose of this study, therefore, was to determine the reproductive period, required fish hosts, and population characteristics of the James spinymussel in the headwaters of the James River, West Virginia and Virginia.

MATERIALS AND METHODS

Three populations of *Pleurobema collina* were monitored weekly during spring 1988 and 1989 to determine the period of gravidity. These populations were in

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South Fork Potts Creek, Monroe County, West Virginia; Craig Creek, Craig County, Virginia; and Johns Creek, Craig County, Virginia. Gravidity was checked by separating the valves approximately 1 cm to observe whether the outer gills were swollen with conglutinates. Observations were made on gill coloration, degree of gill inflation, and conglutinates released by gravid females. In spring 1988, eight gravid females at the Craig Creek study site were marked by scoring the right valve. Seven of these females were collected again in spring 1989 and placed in a 0.5 x 0.5-m area to facilitate their relocation. These mussels were monitored weekly from 26 May through 8 August 1989, and the numbers of gravid and nongravid females were recorded weekly. During each sampling, five to seven of the marked females were relocated and checked for gravidity.

To determine the period of glochidial release, stream drift was sampled in 1988 at the study site in South Fork Potts Creek. Drifting glochidia were collected with square-framed drift nets (0.45 m^2) constructed of 130-micron nylon mesh fitted with removable cod-ends. Three drift nets were placed equidistantly, perpendicular to the current downstream of a 20 m long pool that held approximately 30 adult *Pleurobema collina.* Drift samples were collected for 2 hrs between 1300 and 1700 hrs from 26 May through 12 August 1988 and preserved in 10% formalin, buffered with sodium borate to prevent dissolution of glochidial valves. Drift material was examined in a gridded petri dish under a dissecting microscope (25-40x), and glochidia were counted. Because the mussel fauna of South Fork Potts Creek consisted only of the squawfoot [*Strophitus undulatus* (Say, 1817)] and *P. collina,* glochidia of *P. collina* were readily identified by their smaller size and lack of hooks. Cross-sectional area of the stream, and the velocity of surface water 5 m downstream of the sampling site were used to estimate discharge. Densities of glochidia were computed from measurements of water depth and velocity at the net opening and from counts of glochidia/sample. A 90-day Ryan thermograph (Model J) recorded temperature continuously from 30 May to 14 July 1988.

The determination of probable fish hosts was initiated by examination of fishes collected by electrofishing in South Fork Potts Creek in spring and summer 1988. Weekly collections of fishes began on 23 May 1988 when gravid *Pleurobema collina* were first observed. Fishes were collected from a 50-m reach of stream below the drift sampling site. The collection and examination of fishes continued through 4 August 1988. Captured fishes were anesthetized, identified, visually inspected on the gills for glochidial infestations, and returned to the stream. Incidence of glochidial attachment was recorded.

Laboratory experiments were conducted to confirm the identification of fish hosts of *Pleurobema collina.* Fishes were collected from streams outside of the James River drainage to eliminate the possibility of acquired immunity from prior exposure to glochidia (Neves *et al.*, 1985). Test species were collected with backpack electroshocker and by seining. Collected fishes were held at 16-23° C in test aquaria (40 l and 96 l capacity), at least 5 d prior to infestation.

Mature glochidia were obtained from collected gravid females that were subsequently returned to their natal stream. When gravid females were brought into the laboratory, they were held at room temperature (approximately 25° C) or in a recirculating circular stream (approximately 15° C). Mussels transported to the laboratory were held in beakers to ensure containment of glochidia. Females either released their conglutinates naturally within three to nine days or aborted them after handling. Glochidia were separated from aborted conglutinates by gently drawing the conglutinates in and out of a pipette. The procedures for infestation, subsequent examination of fishes, and recovery of juveniles were performed according to Zale and Neves (1982) with one exception. American eels [*Anguilla rostrata* (Lesueur)], because of difficulty in handling, were infested by placing them in 100 ml of water with 300 to 600 glochidia under vigorous aeration for seven to nine min. The effectiveness of this technique was confirmed on four swallowtail shiners [*Notropis procne* (Cope)] prior to testing the eels. Juvenile mussels were identified by their opaque, dimpled valves and by their foot movements. A fish was considered a host if encystment and metamorphosis to the juvenile stage occurred.

POPULATION CHARACTERISTICS

Twenty-three *Pleurobema collina* were marked on 20 June 1988 upstream of the study site on South Fork Potts Creek to verify that growth lines formed annually. The specimens were given a unique mark, and the edges of their valves were double-notched to identify the 1988 annulus. The number of annuli, total length, and mark for each mussel were recorded. In late summer and fall 1989, these mussels were retrieved and inspected for recent annual growth rings.

The ages of the specimens were determined by thin sectioning of valves with the technique described by Neves and Moyer (1988). Valves of *Pleurobema collina* were collected from muskrat middens at Johns Creek and its tributary Dicks Creek in Craig County, Virginia. One hundred paired valves were sectioned, then aged using a dissecting microscope. Each valve was aged at least three times to provide a precise estimate. A von Bertalanffy growth equation was computed from length-at-age data and was fit by nonlinear procedures to derive the parameters of the equation (SAS Institute, 1982). The annual mortality rate (M) for 97 of the adult mussels (ages 4-19) collected in muskrat middens was computed using the estimator of Robson and Chapman (1961):

$$M=1-T/\,(\sum N_x+T-1))$$

$$\text{Variance} = (T/\sum N_x+T-1)) \times ((T/\sum N_x+T-1))-((T-1)/\sum N_x+T-2)))$$

where N_x is the number in each successive age class (x) and $T = N_1 + 2N_2 + 3N_3 + \ldots XN_x$. This estimator assumes constant cohort recruitment and survival rate, and equal vulnerability of adults to muskrat predation.

Because the incidence of spines was seemingly variable among streams sampled in the upper James River watershed, we tested these differences using multiple comparisons for population proportions (Zar, 1984). Presence of spines on valves collected from Dicks, Johns, South Fork Potts, Craig, and Catawba creeks was compared.

Common and scientific names for mussels and fishes are according to Turgeon *et al.* (1988) and Robbins *et al.* (1991).

RESULTS

REPRODUCTIVE PERIOD

The period of gravidity of *Pleurobema collina* was nearly the same in 1988 and 1989 (Table 1). Gravid females of *P. collina* in South Fork Potts Creek were collected between 23 May and 9 August 1988, and between 23 May and 8 August 1989. Limited surveys in Johns and Craig Creeks in 1988 located gravid *P. collina* on 30 May in Craig Creek and between 27 June and 4 July in Johns Creek. In 1989, gravid females were observed in Craig Creek between 26 May and 11 July. The period of gravidity of the James spinymussel was longer in South Fork Potts Creek in 1989 than in either Johns Creek or Craig Creek.

Efforts to determine the peak of the gravidity period were hampered by two weeks of high flows in early June 1989. On 26 May 1989, five of the eight females marked in 1988 were examined at the Craig Creek study site, and one of them was gravid. On 3 June, two more marked females were found and placed with the others. On this day, five of the seven females were gravid. During the following two weeks (9-23 June), the water was so murky or the current so swift that the marked females could not be collected for examination. The females were checked again on 27 June, and only two of the six examined were gravid. The marked females were examined again on 4 and 11 July, but none was gravid. Gravidity apparently peaked in mid-June during the high flow period.

RELEASE OF GLOCHIDIA

Table 1. Gravidity of female *Pleurobema collina* at study sites in Craig, Johns and South Fork Potts Creeks in 1988 and 1989.

Collection date	Study site	Number examined	Number gravid	Percentage of females gravid[1]
1988				
12 May	Johns Creek	1	0	
23 May	S. Fk. Potts Creek	36	15	
30 May	Craig Creek	18	10	
27 June	Johns Creek	8	6	
04 July	Johns Creek	6	4	
11 July	S. Fk. Potts Creek	15	4	
14 July	S. Fk. Potts Creek	5	2	
25 July	S. Fk. Potts Creek	16	7	
09 August	S. Fk. Potts Creek	11	11	
12 August	S. Fk. Potts Creek	8	0	
1989				
23 May	S. Fk. Potts Creek	8	5	
26 May	Craig Creek	6	1	20%
		10	2	
03 June	Craig Creek	6	5	83%
	S. Fk. Potts Creek	12	1	
06 June	S. Fk. Potts Creek	7	2	
27 June	Craig Creek	6	2	33%
04 July	Craig Creek	7	1	14%
11 July	Craig Creek	7	0	0%
16 July	S. Fk. Potts Creek	8	5	
28 July	S. Fk. Potts Creek	17	5	
08 August	S. Fk. Potts Creek	2	1	

[1]Females marked in 1988.

Drift sampling in 1988 provided a record of the changes in glochidial density with stream discharge (Table 2). Only individual glochidia (no conglutinates) were collected in drift nets. Glochidial densities peaked twice, once in late June (9.6 glochidia/m^3) and again during mid-July (15.9 glochidia/m^3). The mean summer water temperature stabilized around 23^{o} C (Fig. 2). The densities of glochidia increased three days after the flow approached the mean summer level of 0.05 m^3/sec on 23 June.

Valves of the glochidia of *Pleurobema collina* are subovate and symmetrical. The exterior surface is smooth with very few pits. Glochidia are transparent and colorless, and the dorsal hinge is slightly convex. No significant difference was evident in length, height, and hinge length of glochidia from South Fork Potts and Craig Creeks (p-values: length = 0.39, height = 0.28, hinge length = 0.29). The length of valves ranged from 0.18 to 0.22 mm (mean ± 1 SD = 0.19 ± 0.01 mm), and the height of valves ranged from 0.14 to 0.20 mm (0.17 ± 0.01 mm). The hinge length of the valves ranged from 0.10 to 0.16 mm (0.13 ± 0.01 mm). The adductor muscle is attached to approximately 15% of the inside surface area of the valve and is just dorsal and anterior to the valve's center.

Early in the gravidity period, the outer gills of females became significantly enlarged. As the glochidia matured, conglutinates changed color, and the hue of the gills changed from creamy white to pale gray or tan. Released conglutinates were subcylindrical, thin, and compressed. A tan-colored row of pigmentation occurred down the center of the conglutinate, and the glochidia were arranged in two staggered rows around its perimeter. The tips of the conglutinates were usually rounded. One to three conglutinates from each of 25 females from South Fork Potts and Craig Creeks ranged from four to 14 mm long (8.7 ± 3.0 mm) and from one to 1.5 mm (1.0 ± 0.1 mm) wide. Some of the conglutinates were V-shaped, consisting of two conglutinates joined at one end. Pigmentation varied among conglutinates and within females, from nonpigmented to fully pigmented. Prematurely released conglutinates from two females were unusually pale and curled into circular or helical shapes.

An estimate of mean fecundity was obtained from a sample of 28 gravid females that released conglutinates in

Table 2. Water temperature, stream discharge, and density of *Pleurobema collina* glochidia in South Fork Potts Creek, 1988.

Sample date	Daily median temperature (^{o}C)	Discharge (m^3/sec)	Glochidial density (N/m^3)
26 May	18	–	0
30 May	14	–	0
03 June	19	0.446	<1
06 June	16	0.209	<1
10 June	21	0.148	0
13 June	15	0.106	0
20 June	21	0.031	0
23 June	23	0.050	6.7
27 June	24	0.013	9.6
30 June	*	0.025	5.6
05 July	*	0.010	0
08 July	25	0.010	1.6
11 July	25	0.012	15.9
14 July	24	0.024	0
18 July	*	0.020	0
21 July	*	0.038	0
25 July	*	0.025	<1
02 August	*	0.035	0
04 August	*	0.033	0
09 August	*	0.015	0
12 August	*	0.022	0

*Thermograph failure.

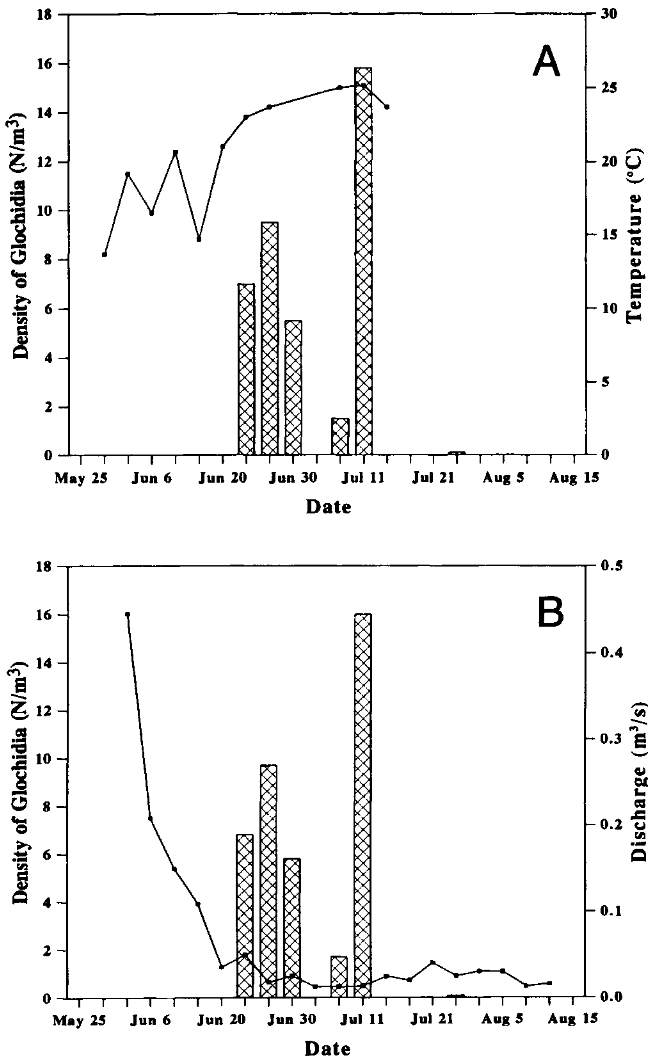

Fig. 2. Densities of *Pleurobema collina* glochidia in stream drift, with accompanying water temperature (A) and discharge data (B).

Table 3. Numbers of released conglutinates, glochidia, and unfertilized eggs per conglutinate from female *Pleurobema collina* collected in South Fork Potts and Craig Creeks.

Date released	Collection site	Number of conglutinates	Number of glochidia	Number of unfertilized eggs
1988				
08 June	S. Fk. Potts Creek		45	4
			66	3
09 June	S. Fk. Potts Creek	137	69	7
			96	12
09 June	Craig Creek	122	92	6
			112	12
23 June	S. Fk. Potts Creek	109	78	6
			85	5
23 June	S. Fk. Potts Creek	110		
02 July	Johns Creek	106		
05 July	Johns Creek	90		
13 July	S. Fk. Potts Creek	113	100	7
			100	11
1989				
05 June	Craig Creek	124	128	6
			134	6
05 June	Craig Creek		135	10
			114	7
13 June	S. Fk. Potts Creek	168		
16 June	S. Fk. Potts Creek	150		
11 July	S. Fk. Potts Creek		158	14
			102	11
	Means	123	101	8

captivity. During 1988 and 1989, ten females released between 90 and 168 conglutinates (123 ± 23.1) in the laboratory (Table 3). Preserved samples of conglutinates from eight of the 28 females were suitable for counting glochidia. The number of glochidia in two conglutinates from each of these females ranged from 45 to 158 (101 ± 29.2). Mean fecundity/female, to include glochidia (12,423) and unfertilized eggs (984), therefore was 13,407 ± 3,986.

FISH HOST DETERMINATIONS

Fourteen of the 21 fish species known to inhabit South Fork Potts Creek were examined for glochidial infestations during the drift sampling period in 1988 (Table 4). Glochidia were observed on common shiners, rosyside daces, bluehead chubs, pumpkinseeds, and fantail darters. No glochidia were observed on central stonerollers, redbreast sunfishes, longfin darters, rock basses, margined madtoms, smallmouth basses, creek chubs, northern hog suckers, or white suckers. The frequency of glochidial infestation was high on common shiners, rosyside daces, and bluehead chubs (Table 4).

Successful attachment of *Pleurobema collina* glochidia to fishes in laboratory infestations was low. Although 35 to 65 glochidia were placed directly on the gills, only three to 18 glochidia remained attached one hr later. However, once attached to a host, most glochidia

Table 4. Incidence of *Pleurobema collina* glochidial infestations on fishes collected in South Fork Potts Creek, 26 May through 4 August 1988.

Fish species	Number inspected	Percent infested
Cyprinidae		
Luxilus cornutus (Mitchell) (common shiner)	50	32
Clinostomus funduloides Girard (rosyside dace)	5	20
Nocomis leptocephalus (Girard) (bluehead chub)	183	19
Campostoma anomalum (Rafinesque) (central stoneroller)	81	0
Semotilus atromaculatus (Mitchill) (creek chub)	3	0
Centrarchidae		
Lepomis gibbosus (Linné) (pumpkinseed)	8	12
Lepomis auritus (Linné) (redbreast sunfish)	45	0
Ambloplites rupestris (Rafinesque) (rock bass)	9	0
Micropterus dolomieu Lacepède (smallmouth bass)	6	0
Percidae		
Etheostoma flabellare Rafinesque (fantail darter)	40	8
Etheostoma longimanum Jordan (longfin darter)	13	0
Ictaluridae		
Noturus insignis (Richardson) (margined madtom)	6	0
Catostomidae		
Hypentelium nigricans (Lesueur) (northern hog sucker)	2	0
Catostomus commersoni (Lacepède) (white sucker)	1	0
Total	452	

remained on the fish throughout the metamorphosis period. A fish species was considered a host of *P. collina* if attachment, encystment, and metamorphosis to the juvenile stage resulted. Several fish species experienced high mortality and subsequently were retested. Seven species of cyprinids were identified as suitable hosts of *P. collina* and included the bluehead chub, rosyside dace, satinfin shiner, rosefin shiner, central stoneroller, blacknose dace, and mountain redbelly dace (Table 5). The bluehead chub produced the greatest mean number of juveniles/individual (10.2), and the mountain redbelly dace produced the fewest (0.62). Variation in the number of juveniles produced during each trial was due primarily to differences in the initial number of attached glochidia. Ten of the 11 tested fish families were unsuitable as hosts of *P. collina* glochidia (Table 6). Other cyprinid species in the upper James River drainage, although untested, also may be suitable hosts.

Relatively few glochidia were collected from the aquaria with white suckers and northern hog suckers the day after inoculation. The suckers quickly sloughed the glochidia and apparently consumed them. These observations lead us to believe that suckers and other benthic feeders may ingest glochidia incidentally in streams.

Several nonhost fish species retained glochidia for a longer period of time than other nonhost fish, but only empty valves identical to those of living juveniles were collected. Kitchel (1985) described this phenomenon and called the embryonic mussels pre-metamorphosed juveniles. In our study, pre-metamorphosed juveniles were occasionally produced by host species, and by fish species which did not produce viable juveniles. Because of delayed metamorphosis of glochidia at colder water temperatures, the pre-metamorphosed juveniles observed in our study may have been due in part to the relatively cold water temperatures (13-15° C) of the 1989 host fish experiments. Due to the lengthy periods of attachment to these species, a repeat of these infestations seems warranted to confirm their nonhost designations.

POPULATION CHARACTERISTICS

On 28 July and 2 December 1989, ten of 23 *Pleurobema collina* marked on 20 June 1988 were recovered and examined for annulus formation. The recovered specimens were between six and ten years old, and two to eight mm of growth were added to the margin of each valve. One of the six mussels had a second thin growth check between the 1988 annulus and the margin; however, all others exhibited only one annulus.

Age class structure of 100 specimens of *Pleurobema collina* collected from muskrat middens along Johns and Dicks Creeks ranged from three to 19 years, with a mean age of eight years (Fig. 3). The age distribution is slightly bimodal but indicated that sufficient recruitment is sustaining these populations. The presence of dominant year-classes, such as age 11, was evident. The estimated mean annual mortality rate was 15.6 ± 1.4% for adult mussels (ages 4-19).

The growth pattern in valve length of *Pleurobema collina* from Johns and Dicks Creeks was asymptotic. The predicted annual growth increments declined gradually

Table 5. Cyprinid fish species that served as hosts for *Pleurobema collina* glochidia in laboratory experiments.

Fish species	Number of fish infested	Number of survivors	Juvenile[1] mussels collected	Days to metamorphosis	Temperature range ($^{\circ}$C)
Nocomis leptocephalus (Girard)	11	0	—	0	16-21
(bluehead chub)	7	4	41	48	15-18
Clinostomus funduloides Girard	13	11	—	13	15-18
(rosyside dace)	9	0	—	7	15-18
	3	14	14	30	15-18
Cyprinella analostana (Girard) (satinfin shiner)	15	10	44	34	15-18
Lythrurus ardens (Cope)	5	0	—	0	15-18
(rosefin shiner)	17	5	2	40	15-18
	5	5	8	36	15-18
Campostoma anomalum (Rafinesque) (central stoneroller)	16	1	13	26	16-23
Rhinichthys atratulus (Hermann)	15	12	3	23	16-23
(blacknose dace)	14	9	6	50	15-18
Phoxinus oreas (Cope)	9	1	1	29	16-23
(mountain redbelly dace)	17	13	8	44	15-18

[1]Includes pre-metamorphosed juveniles.

Table 6. Fish species that did not serve as hosts for *Pleurobema collina* glochidia in laboratory experiments.

Fish species	Number of fish infested	Number of survivors	Period of attachment (days)	Number of premetamorphosed juveniles	Temperature range (°C)
1988					
Catostomidae					
Catostomus commersoni (Lacepède) (white sucker)	15	15	1	—	16
Hypentelium nigricans (Lesueur) (northern hog sucker)	11	11	2	—	20
Ictaluridae					
Noturus insignis (Richardson) (margined madtom)	18	18	8	—	22-23
Percidae					
Etheostoma flabellare Rafinesque (fantail darter)	8	6	10	—	15-18
Centrarchidae					
Lepomis auritus (Linné) (redbreast sunfish)	13	11	12	—	15-18
Cyprinidae					
Notropis procne (Cope) (swallowtail shiner)	10	6	31	—	13
1989					
Percidae					
Etheostoma olmstedi Storer (tessellated darter)	1	1	6	—	13-15
Percina notogramma (Raney and Hubbs) (stripeback darter)	8	8	8	—	13-15
Centrarchidae					
Ambloplites rupestris (Rafinesque) (rock bass)	6	6	6	—	13-15
Cyprinidae					
Notropis procne (Cope) (swallowtail shiner)	4	4	55	—[1]	13
Catostomidae					
Erimyzon oblongus (Mitchill) (creek chubsucker)	8	8	2	—	13-15
Cyprinidae					
Pimephales notatus (Rafinesque) (bluntnose minnow)	9	9	12	—	13-15
Notemigonus crysoleucas (Mitchill) (golden shiner)	6	5	41	4	13-15
Umbridae					
Umbra pygmaea (DeKay) (eastern mudminnow)	6	6	12	—	13-15
Aphredoderidae					
Aphredoderus sayanus (Gilliams) (pirate perch)	7	7	37	—	13-15
Anguillidae					
Anguilla rostrata (Lesueur) (American eel)	9	8	44	1	13-15
Poeciliidae					
Gambusia affinis (Baird and Girard) (western mosquitofish)	9	9	45	119	13-15
Esocidae					
Esox niger Lesueur (chain pickerel)	9	8	25	22	13-15
Salmonidae					
Salvelinus fontinalis (Mitchill) (brook trout)	6	6	15	—	13-15

[1]Not enumerated.

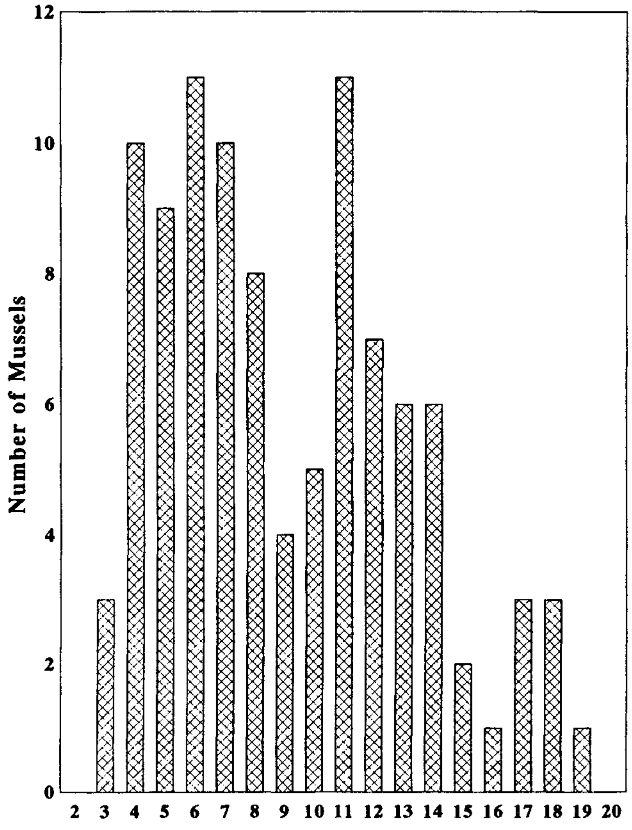

Fig. 3. Age structure of *Pleurobema collina* in Johns and Dicks creeks, based on shells collected in muskrat middens.

from 7.04 mm/yr for age 1 individuals to 0.88 mm/yr for age 19 mussels (Table 7). The von Bertalanffy growth equation that described growth of *P. collina* is as follows:

$$L_t = (74.439)(1 - e^{(-0.11556(t+1.2436))})$$
$$(N = 100, MSE = 4.48)$$

The growth equation predicted a maximum length of 74.4 mm, and the largest valve collected was 75.2 mm. Observed mean length-at-annulus measurements fit most predicted values extremely well, especially the younger cohorts (Table 7). The small sample sizes of older age groups likely resulted in the poorer fit between observed and predicted values for these cohorts.

The occurrence and location of spines on *Pleurobema collina* varied considerably among populations and individuals within populations (Fig. 4). The incidence of spines differed significantly among the five populations ($p = 0.05$). Incidence of spines was significantly lower in Dicks Creek and higher in Catawba Creek than in the other three streams, which were not significantly different ($p = 0.05$). Most valves and live mussels from these populations lacked spines, or evidence of spines at younger ages such as nubs or erosive scars where spines should have been visible. The presence of spines in juvenile and adult mussels in most headwater populations was the exception rather than the rule.

DISCUSSION

The habitat requirements of the James spinymussel are seemingly nonspecific. The mussel was found in 1.5 to 20 m wide second and third order streams at water depths of 0.3 to 2 m. *Pleurobema collina* was found in a variety of substrata ranging from sand and silt mixtures to gravel and sand mixed with embedded rubble. Specimens occurred in a variety of flow regimes, near stagnancy in some pools to swift water in riffles and runs. These occupied habitats are similar to those described by Clarke and Neves (1984).

The microhabitat requirements of the other species of spinymussels seem to be more restrictive than those of the James spinymussel. The Altamaha spinymussel [*Elliptio spinosa* (Lea, 1836)] has been found only on sandbars of very coarse to fine sand (Sickel, 1981). The Tar spinymussel (*E. steinstansana* R. I. Johnson and Clarke, 1983) also lives in hard-packed, fine to coarse sand substrata and is occasionally found in soft sand (Clarke, 1983; Widlak 1987). Although the James spinymussel was often found in sandy habitats, it also resided in gravel and embedded rubble. The James spinymussel is somewhat nonspecific in its habitat requirements and now occurs primarily in headwater streams. Habitats occupied by the Altamaha and Tar spinymussels might also include coarser substrata in the headwaters of their respective drainages, but these two species are seemingly adapted only to finer

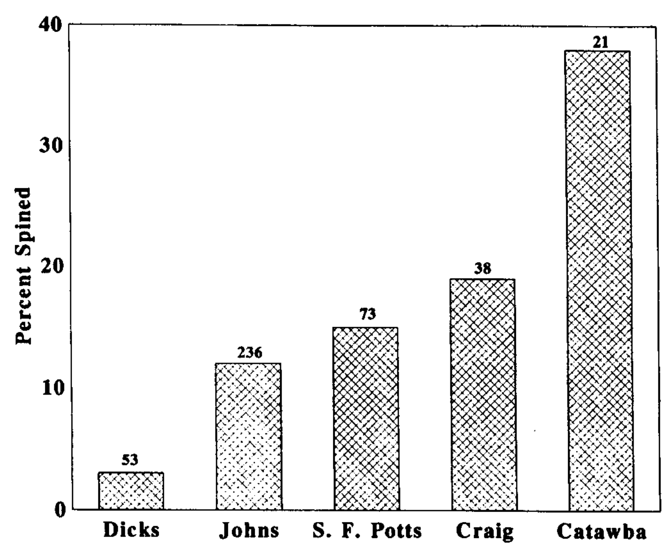

Fig. 4. Incidence of spines on *Pleurobema collina* from five populations in the upper James River watershed. Number on histogram is sample size for each population.

Table 7. Observed and predicted lengths-at-annuli (mm) of *Pleurobema collina* from Johns and Dicks Creeks, Craig County, Virginia, 1988 and 1989.

Annulus	Number of individuals	Observed length Mean	Range	Predicted length	Growth increment
0	0	—	—	9.96	
1	0	—	—	17.00	7.04
2	0	—	—	23.27	6.27
3	3	28.68	25.00-34.40	28.85	5.58
4	10	33.83	27.35-39.25	33.83	4.98
5	9	39.30	35.25-42.70	38.26	4.43
6	11	42.60	37.45-48.90	42.21	3.95
7	10	43.80	40.35-48.75	45.73	3.52
8	8	49.36	44.40-56.20	48.86	3.13
9	4	49.29	43.60-53.30	51.65	2.79
10	5	54.41	47.55-58.20	54.14	2.49
11	11	57.81	50.55-65.55	56.35	2.21
12	7	60.31	53.10-75.20	58.33	1.98
13	6	61.47	7.80-64.25	60.08	1.75
14	6	61.98	58.25-65.70	61.65	1.57
15	2	64.20	61.25-67.15	63.05	1.40
16	1	60.85	60.85	64.29	1.24
17	3	61.83	58.15-64.30	65.40	1.11
18	3	65.27	62.15-68.80	66.38	0.98
19	1	71.35	71.35	67.26	0.88

substrata. The spines of the Altamaha and Tar spinymussels are generally more developed than those of the James spinymussel, and if they act as stabilizers in shifting substrata such as loose sand (Johnson, 1970), the spines may be morphological evidence of their habitat specificity.

GLOCHIDIAL RELEASE AND GRAVIDITY PERIODS

Like the other members of its genus, *Pleurobema collina* is a short-term brooder that releases glochidia from early June through late July. Weaver (1981) reported glochidia of *P. oviforme* (Conrad, 1834) and *Fusconaia barnesiana* (Lea, 1838) in drift samples from mid-May through late July 1980 in Big Moccasin Creek, Virginia, and Kitchel (1985) recorded gravid *P. oviforme* from mid-June through late August in the North Fork Holston River, Virginia. Yokley (1972) reported the glochidial release period of *P. cordatum* (Rafinesque, 1820) from late April through early July, with peak glochidial densities in June in the upper Tennessee River.

Water temperature and stream discharge are thought to be important environmental variables that influence the glochidial release and gravidity periods. The peak of the glochidial release period of *Pleurobema* spp. occurs when mean daily water temperatures are between 21° and 29° C in late spring and early summer (Yokley, 1972; Kitchel, 1985). Peak densities of *P. collina* glochidia were found in South Fork Potts Creek after stream temperatures reached 23° C. This finding is similar to that reported for other congeneric mussels. Glochidial density of *P. cordatum* peaked in the Tennessee River in June after the water temperature averaged 21° C (Yokley, 1972). *Pleurobema oviforme* glochidia reached peak densities at 24° C in Big Moccasin Creek, Virginia (Weaver, 1981). In the North Fork Holston River, *P. oviforme* glochidia reached peak densities in mid- and late July when temperatures were between 25° and 29° C (Kitchel, 1985).

Stream discharge could have influenced the glochidial release period because glochidial densities peaked three days after the spring discharge dropped to near-normal summer levels in South Fork Potts Creek. A seasonal rise in discharge and a subsequent increase in nutrient levels were described by Hynes (1970) to initiate reproductive activity in many aquatic animals. Kitchel (1985) suggested that discharge could influence the abundance of glochidia of various unionids in stream drift in the North Fork Holston River, Virginia. However, we collected insufficient data to correlate stream discharge with densities of glochidia.

The glochidia of all members of the genus *Pleurobema* are spineless, subovate, and of medium size (Utterback, 1915-1916; Baker, 1928; Oesch, 1984). Glochidia of *P. collina* were similar in size and shape to other members of the genus, ranging from 0.18 to 0.22 mm in length and from 0.14 to 0.20 mm in height. Glochidia of *P. oviforme* range from 0.15 mm to 0.17 mm in length and height (Weaver, 1981; Kitchel, 1985). The length and height of glochidia of *P. cordatum* are 0.15 to 0.18 mm (Utterback, 1915-1916), and the glochidia of *P. coccineum* (Conrad, 1834) are 0.15 to 0.16 mm in length and height (Utterback, 1915-1916; Baker, 1928; Clarke, 1981).

Conglutinates released by gravid females of *Pleurobema collina* were unlike those described for congeneric species. Mature conglutinates were subcylindrical and compressed, and glochidia were arranged along the perimeter of each conglutinate. Pigmentation consisted of a thin ribbon of tan color in the center of the conglutinate, although some conglutinates were colorless. The conglutinates of other *Pleurobema* spp. are thin, lanceolate, or leaf-shaped, varying in color from white to yellow or orange (Oesch, 1984), and glochidia typically are spread throughout the conglutinate. Because the James spinymussel is the only species of *Pleurobema* on the Atlantic slope, placement of the species in this genus could need to be re-evaluated. The evolutionary significance of conglutinates is unknown, although some researchers suggested that they could mimic food items of fishes when released (Chamberlain, 1934; Kat, 1984; Gordon and Layzer, 1989).

The average fecundity of *Pleurobema collina* is lower than that of females of most other freshwater mussels. Freshwater mussels usually produce between 75,000 and 3,000,000 glochidia/female (Coker *et al.*, 1921). Females of *Quadrula cylindrica strigillata* (Wright, 1898) produce about 114,246 (± 5368) embryos/female (Yeager and Neves, 1986), and *Margaritifera margaritifera* (Linné, 1758) has an average fecundity of 4.2 million glochidia/female (Bauer, 1987). A female *Unio crassus* Retzius, 1788, produces between 9,500 and 100,000 glochidia, depending on its size (Engel and Hannover, 1989). Gravid *P. collina*, however, brood roughly 13,400 glochidia/female.

FISH HOSTS

Species of the genus *Pleurobema* parasitize a relatively small percentage of the fish assemblage in their respective streams. Of 14 species of fishes collected from South Fork Potts Creek, only common shiners, rosyside daces, bluehead chubs, pumpkinseeds, and fantail darters had *P. collina* glochidia attached to their gills. Although no glochidia were observed on central stonerollers, this species was identified as a fish host in laboratory experiments. A possible reason for this discrepancy is the inaccessibility of their gills. The central stoneroller has an extended connection between its gill and isthmus, and only the outermost gill and distal edges are visible when viewed through the opercular opening. Because of limited access to the gills, our observations may have overlooked infestation of this species. Among the 21 species inhabiting the South Fork Potts Creek, the incidence of infestation was 19.6% (N = 286). Similar results were obtained by an investigation of *P. oviforme* in the North Fork Holston River, Virginia. Twelve of 41 species of fishes were parasitized by glochidia of *P. oviforme* (see Kitchel, 1985). Of the fish species infested with glochidia, 12.3% (N = 1738) bore *P. oviforme* glochidia. Most of the fish species that serve as hosts of *P. collina* are common throughout the drainage, such that the extirpation of this mussel from limited host abundance or distribution is unlikely. Cyprinids seem to be a suitable family of host fishes because they are one of the most diverse and successful lineages in North America and were probably more abundant before the introduction of non-native piscivores in the James River drainage.

POPULATION CHARACTERISTICS

The age class structure of most mussel species seemingly indicates that younger mussels are often underrepresented in population samples (Yokley, 1972; Coon *et al.*, 1977), perhaps because of sampling bias (Chamberlain, 1931; Coon *et al.*, 1977). Zale (1980) found that quadrat sampling was effective for collecting young mussels, although other researchers found this technique inadequate for rare species (Neves *et al.*, 1980; Kovalak *et al.*, 1986; Neves and Odom, 1989). Quadrat sampling would probably be suitable for obtaining young *Pleurobema collina* because we documented their occurrence in most extensively surveyed streams. We used valves from muskrat middens to assess age class composition, which may have resulted in some bias against the youngest age groups (Neves and Odom, 1989; Hanson *et al.*, 1989). However, in spite of any sampling bias in valve sizes, we documented healthy recruitment in the populations sampled.

Aging of valves from thin sections was effective for *Pleurobema collina.* The valves of this species are relatively small and thin and easily sectioned in ten to 35 min. Most annuli were easy to identify from the thin sections. Examination of six *P. collina* collected in 1989 (from the 23 marked in 1988) revealed that this species formed yearly primary growth rings. Neves and Moyer (1988) also demonstrated annual growth line formation in *P. oviforme, Medionidus conradicus* (Lea, 1834), *Villosa vanuxemensis* (Lea, 1838), and *Lasmigona subviridis* (Conrad, 1835) in southwestern Virginia.

The von Bertalanffy growth equation adequately described the growth of *Pleurobema collina* from the Johns and Dicks Creeks. The predicted values agreed well with observed values when N/age class was fairly large. For ages three to 15, the differences between predicted and observed values ranged from zero to 1.93 mm (N = 92), but for ages 16 to 19 (N = 8), the differences ranged from 1.11 to 4.09 mm.

The growth of *Pleurobema collina* is characteristic of other species of the subfamily Ambleminae. Members of Ambleminae usually have thick shells and grow slowly relative to thin-shelled species (Isely, 1914; Coker *et al.*, 1921; Coon *et al.*, 1977). Thick-shelled species grow most rapidly early in life, and later growth slows to a few mm/yr (Scruggs, 1960; Negus, 1966; Moyer, 1984). This is the pattern of growth in the James spinymussel; annual growth increment decreased steadily from 7.04 to 0.88 mm/yr with age.

There are several anthropogenic and natural threats to the James spinymussel's continued existence. Nearly all the riparian lands bordering streams with the James spinymussel are privately owned. With more intensive use of the land, it is probable that water quality and habitat suitability will deteriorate. At present, the most detrimental activities include road construction, cattle grazing, and feed lots that often introduce excessive silt and nutrients into the stream.

The introduced Asian clam [*Corbicula fluminea* (Müller, 1774)] is beginning to invade several sites where *P. collina* is found. This exotic bivalve is believed by many to be a threat to native unionids, especially in Atlantic coastal rivers (Fuller and Richardson, 1977; Kraemer, 1979; Clarke, 1986, 1988).

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