Life history and habitat of the endangered dwarf wedgemussel *Alasmidonta heterodon* (Bivalvia:Unionidae)

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Abstract. The reproductive cycle, population demographics, and habitat use of the dwarf wedge-mussel (*Alasmidonta heterodon*) were studied in populations from the Tar River, North Carolina, and Aquia Creek, Virginia, during 1991 and 1992. The mussel is a long-term brooder, spawning in late summer and becoming gravid in fall. Laboratory infestations with glochidia on 15 species of fish confirmed three hosts for *A. heterodon*: tessellated darter (*Etheostoma olmstedi*), Johnny darter (*E. nigrum*), and mottled sculpin (*Cottus bairdi*). Six species of sunfishes, four minnows, one sucker, and one catfish tested in the laboratory did not serve as hosts.

Age and growth characteristics were calculated using a thin sectioning technique on valves collected from the Tar River, Aquia Creek, and Neversink River, New York. As computed by the von Bertalanffy equation, the dwarf wedgemussel reaches a maximum length of 38.70 mm, 45.26 mm, and 45.84 mm in the Tar River, Aquia Creek, and Neversink River, respectively. There were significant differences in growth rates of *A. heterodon* from the Tar River and Aquia Creek and between populations in the Neversink River and Aquia Creek. There was no significant difference in growth rate of populations from the Tar and Neversink rivers.

Age–class distribution of live mussels collected at the three sites was estimated using age–length keys. The Tar River population included year classes from 4 to >6 years. Excessive shell erosion prevented the aging of older individuals and thus, a key to include larger live individuals. The age class distribution of the Aquia Creek population ranged from 2 to 9 years, while the Neversink River population was represented by age 1 to 8 year classes. The von Bertalanffy growth equations for the Tar River, Aquia Creek, and Neversink River populations were as follows: $L_t = 38.70$ mm $(1 - e^{-0.299(t+0.251)})$; $L_t = 45.26$ mm $(1 - e^{-0.260(t+0.244)})$; and $L_t = 46.84$ mm $(1 - e^{-0.207(t+0.335)})$, respectively.

Habitat-suitability experiments were conducted in the laboratory to determine preferred substratum size and water velocity. Dwarf wedgemussels always preferred the finer substratum offered, but little preference was shown for lotic versus lentic flow regimes.

Key words: *Alasmidonta*, Unionidae, freshwater mussels, life history, fish hosts, age and growth analysis, habitat preference.

The dwarf wedgemussel (*Alasmidonta hetero-don*), listed as an endangered species in the United States on 14 March 1990, is primarily confined to Atlantic coastal rivers from North Carolina to New Brunswick (Master 1986, Shelley 1987). Since its description by Lea in 1829, *A. heterodon* has been found at about 70 locations in 15 major drainages; it has been extirpated from all but about 30 locations. In the southern

extent of its range, the species has been reported from the Neuse and Tar River systems (Walter 1956, Johnson 1970, Clarke 1981); however, it has not been found in the Neuse drainage since Walter's survey (Shelley 1987). There is a reproducing population in Aquia Creek, Virginia, and also remnant populations in the South Anna, Nottoway, and Po rivers and Cedar Run, Virginia.

Most of the proposed explanations for the decline of the dwarf wedgemussel stem from human degradation of habitat and water quality where the species occurs. Factors affecting *A. heterodon* populations include agricultural, industrial, commercial, and domestic pollution and runoff. Specifically, these factors can act to lower dissolved oxygen; increase silt loading;

change pH, alkalinity, and hardness levels; and introduce toxicants such as potassium, zinc, copper, chlorine, cadmium, and arsenic (Master 1986).

The dwarf wedgemussel is a relatively small species, seldom reaching its maximum length of 57 mm (Master 1986). The shell outline is subrhomboidal or subtrapezoidal, sometimes rather elongate. As described by its species name, *heterodon*, the dwarf wedgemussel has a unique dentition pattern; the right valve possesses two lateral teeth while the left has only one—a trait opposite to that of all other North American species having lateral teeth (Clarke 1981). Some degree of sexual dimorphism exists within the species. The outline of the female shell is shorter, swollen posteriorly, and more trapezoidal, whereas the male shell is more compressed, ovate, and elongate (Johnson 1970, Clarke 1981).

The reproductive cycle of *A. heterodon* is assumed to be similar to that of other species of Unionidae (Clarke 1981). Gravid females of *A. heterodon* have been reported from February to late August and are thought to be long-term brooders (Johnson 1970).

Bivalves in temperate regions have slow or no shell growth in the winter months and during the spawning season, and these differences in growth patterns appear as annual growth rings (Jones et al. 1978, McCuaig and Green 1993). The use of external growth rings for aging has been criticized as underestimating ages of mussels due to inconsistent annulus formation. External annuli may not necessarily correspond directly with season changes, as several years can pass without annulus formation on some species (Downing et al. 1992, Downing and Downing 1993). We used a thin sectioning technique where false annuli are distinguished from true winter growth rings by being thin and incomplete, different in color and texture, and inconsistent with the spacing of true annuli (Negus 1966, Neves and Moyer 1988). The assumption remained, however, that annuli were formed on a yearly basis.

The objectives of this study were: (1) to describe the reproductive cycle of *A. heterodon*, including determination of fish hosts; (2) to obtain population demographics, such as sex ratio, ages, and size-class structure of populations; and (3) to evaluate preferences for substratum size and water velocity in short-term laboratory experiments.

Study Sites

The Tar River originates in Person County, North Carolina, and flows in a southeasterly direction to the Pamlico River, which empties into Pamlico Sound. The study reach was a 3.5-km stretch of river between Routes 158 and 1141 in Granville County. Sampling was concentrated in a pool about 700 m downstream of the Route 158 bridge crossing because of the relatively high densities of *A. heterodon* here. Most of the catchment basin is forested, but it has some row crops. Other mussel species occurring at this site included the eastern elliptio (*Elliptio complanata*), variable spike (*E. icterina*), squawfoot (*Strophitus undulatus*), and eastern creekshell (*Villosa delumbis*).

Aquia Creek in Stafford County, Virginia, flows east along the Quantico Marine Corps Base and into the Potomac River. Most individuals of *A. heterodon* were found between the confluence of Cannon Creek with Aquia Creek and culverts under old Route 643, about 0.5 km downstream. The surrounding catchment is forested, although a housing development near the study site is planned. *Elliptio complanata, E. icterina, S. undulatus,* and *A. heterodon* occur at this site.

The Neversink River in Orange County, New York, flows south to join the Delaware River at Port Jarvis, New York. One of the healthiest populations of the dwarf wedgemussel was discovered in the lower 12–18 km of this river in 1990. The substratum in this river reach is stony with patches of sand and gravel (Strayer and Ralley 1993).

Methods

Reproductive cycle

Period of gravidity was determined by checking the marsupia of females for glochidia beginning in March 1991 and continuing until gravid females were no longer observed in field collections. Monthly surveys for gravid females were resumed in October 1991 and continued through May 1992. Gravid individuals were identified by swollen and darkened marsupia (Ortmann 1921). Mussels were collected by snorkeling and hand picking, using glass-bottom water scopes during times of high water flow or turbidity. Scuba equipment also was

used occasionally during exceptionally high water in spring. Because sexually dimorphic characters were not readily distinguishable in many individuals, non-gravid mussels during the period of gravidity were assumed to be males in estimating a sex ratio for A. heterodon.

Water temperature was monitored throughout the study using a Ryan thermograph (Ryan Instruments Inc., Redmond, Washington) with a 90-d scroll. By continuously monitoring water temperature, we attempted to correlate glochidial release periods with changes in temperature.

During the period of gravidity, three 0.45-m^2 square-frame drift nets with 130 μm mesh and removable cod ends were set for 2 h, evenly spaced along the 13-m mean width of the Tar River and 4-m mean width of Aquia Creek, immediately downstream of areas containing A. heterodon. Drift samples were collected weekly from 6 April to 4 May 1992 and on three subsequent occasions in May and July. Drift samples were preserved in 10% formalin buffered with sodium borate. The drift samples were filtered through 0.5-mm mesh to eliminate larger debris when necessary. The filtrate was treated with Rose Bengal, a protein-specific stain, to facilitate differentiation of glochidia from sediment and organic debris in the sample.

Fish hosts

Determination of fish hosts was carried out in two phases. During the first phase, all fish species in the study areas were collected and examined for glochidial infestations. Collections were made using dipnets and a backpack electroshocking unit (Coffelt BP-1C, Coffelt Electronics Co., Flagstaff, Arizona 86001). Glochidia with hooked valves, like those of A. heterodon, typically attach to the fins, lips, and other soft scaleless epithelial tissue (Lefevre and Curtis 1910); therefore, only stunned fish with external glochidia were sacrificed, preserved in 10% buffered formalin, and checked under magnification for glochidiosis.

During the second phase, we induced infestation of fish suspected as hosts from results of phase one. To avoid potential immunological responses (Arey 1923), fish to be infested in the laboratory were collected from areas devoid of mussels whenever possible. Fish were collected and taken to the laboratory in an 80-L cooler

filled with chilled river water. At least five fish of each species were collected for use in experiments. Portable fish savers (Marine Metal Products Co., Clearwater, Florida 33575) provided aeration. To reduce stress, 30 g of furacin (9.5% active ingredient) and 50 g of uniodized NaCl were added to the water before transport. The fish were placed in fiberglass Living Streams equipped with chiller units (Frigid Units, Inc., Toledo, Ohio 43613), separated by species, and allowed to acclimate to laboratory conditions for at least 1 wk before experiments.

Gravid females of A. heterodon were collected from the Tar River by snorkeling, placed in cloth bags, and taken to the laboratory in 80 L coolers filled with river water aerated with a portable fish saver. To prevent abortion of glochidia by females, water temperature was kept low by periodically adding an ice pack to the river water. The mussels were kept in a 40-L aquarium placed on top of a Living Stream, with water kept at a constant 15°C. A recirculating water system was created by pumping water into the aquarium from the Living Stream using a submersible pump (Little Giant Corporation, Oklahoma City, Oklahoma) at 1 L/min, for about 36 water turnovers per day. While in captivity, mussels were fed a commercial invertebrate diet (Marine Invertebrate Diet, Hawaiian Marine Imports Inc., Houston, Texas) on alternate days.

Glochidia were removed from gravid females by puncturing the ventral margin of the marsupium with a 3.8-cm 18-gauge sterile hypodermic needle and injecting water from a 10-cc syringe, forcing the glochidia out of the marsupium through the puncture hole into a glass petri dish. This procedure does not appear to injure the mussel (Waller and Holland-Bartels 1988). Richard et al. (1991) showed that the entire ventral edge of the demibranch of at least some gravid mussels ruptures in the process of releasing glochidia, gradually healing after release. Glochidia were first tested for viability by placing a subsample in contact with a few grains of NaCl; viable glochidia immediately snap shut in response to the presence of salt (Zale and Neves 1982).

Test fish were placed in a 4.2-L glass container with water level sufficient only to allow them to remain upright. Two 10-cm airstones were placed in the water to keep glochidia in suspension. Glochidia were then added to the water using a glass Pasteur pipette with a rubber

bulb. Airstones were inadequate for keeping glochidia suspended, so the pipette was used to manually direct settled glochidia to the mouth and gills of test fish. Fish were kept in contact with glochidia for 60 min.

Fish used in infestation experiments were held in three different systems. A recirculating laboratory stream with a capacity of about 7 m³ was used to hold most of the test fish. This system consisted of 13 aquaria (80-L capacity) placed in a partially filled (about 60 cm deep) circular laboratory stream. Water was pumped from the stream into the aquaria at a rate of 1 L/min for 18 turnovers per day. Water temperature was regulated by the ambient air temperature, ranging from 21.0 to 22.5°C.

Because total mortality of mottled sculpins (*Cottus bairdi*) occurred at the warmer temperatures of the recirculating laboratory stream, a second system using cooler water (averaging 15°C) was used to hold them (described earlier for holding gravid mussels). The third system was a static environment consisting of two 40-L aquaria. Both aquaria were aerated with two 10-cm airstones. On alternate days, about 75% of the water was removed by siphoning, then replaced with dechlorinated tap water.

A species of fish was considered a suitable host if attachment, encystment, and development to the juvenile phase occurred on that species. Juveniles were identified by their opaque valves and by foot movements.

Population demographics

During the gravidity period, the incidence of females was recorded. Estimates of sex ratio were based solely on the appearance of the marsupia of individuals examined during this period. Nongravid individuals were assumed to be males, while those individuals with swollen and darkened marsupia were classified as females.

Valves from the Tar River, Aquia Creek, and the Neversink River were used to calculate age and growth characteristics of these dwarf wedgemussel populations. All shells used for analysis were freshly dead valves collected from stream bottoms in 1991 and 1992. The minimum sample size for a site was 21 valves. The sample size for each site depended mainly on the quality (degree of erosion) of the shells collected. At study sites in the Tar River and Aquia Creek, whole valves of *A. heterodon* were collected,

dated, and assigned a number by writing on the shell nacre in waterproof ink. Additional shell material was collected from the Neversink River in Orange County, New York by David Strayer and Jonathan Ralley (Institute of Ecosystem Studies). The length of each shell was recorded to the nearest 0.1 mm using vernier calipers for subsequent length-at-age analysis. Total length was measured as the maximum anteroposterior dimension parallel to the hinge (Ortmann 1920, Ball 1922).

Mussel ages were determined by thin-sectioning valves as described by Neves and Moyer (1988), with one exception. Loctite epoxy (Geoscience Resources, Burlington, North Carolina), an ultraviolet light-sensitive adhesive, was used to cement the thin section to a frosted petrographic slide. When placed in an ultraviolet light box, the bond required only 5 to 10 min to harden. Annuli were enumerated under 50 and 100× magnification to determine age. Growth rings were judged to be annuli only if they extended from the umbonal region to the shell margin. At each point where an annual growth line intersected the margin, we marked the point on the slide with a black felt tip pen. The shell from which the slide was made was then held up to its thin section, and a mark was made on the shell at each point where an annulus was present. The cut section was then placed over the opposite valve from the same mussel, and the annuli were drawn onto the uncut valve. This procedure allowed the determination of back-measured lengths-at-age for subsequent growth analysis. Back-measured lengths were discernible from only a fraction of the sections made. Severe shell erosion rendered the early annuli illegible in most of the larger specimens. A von Bertalanffy growth equation was calculated from the back-measured lengths-at-age using the FISHPARM program (American Fisheries Society, Computer User Section, Tampa, Florida).

Instantaneous rate of mortality (Z) was calculated using the method described by Hoenig et al. (1983). In this method all lengths are transformed to the parameter y using the equation

$$y = -\ln\left(1 - \frac{L_c}{L_\infty}\right)$$

where L_c represents the first fully recruited length and L_∞ is the von Bertalanffy asymptotic growth estimate. The first fully recruited cohort

in our analyses is defined as age 3. Instantaneous rate of mortality was then calculated with the equation

$$Z = \frac{(k)(\ln 2)}{y_m - y_c}$$

where k is the von Bertalanffy growth constant, Y_m is the median y of y's greater than y_c, and y_c is the log-transformed lengths greater than L_c. Instantaneous rate of mortality was then converted to annual mortality rate with the equation $A = 1 - e^{-z}$. Variance of Z was calculated using the following sequence of equations from Hoenig et al. (1983):

$$E(\tilde{x}) = \frac{1}{z}\left[\sum_{i=1}^{(n+1)/2} (n - i + 1)^{-1}\right]$$

$$V(\tilde{x}) = \frac{1}{z^2}\left[\sum_{i=1}^{(n+1)/2} (n - i + 1)^{-2}\right]$$

$$V\left(\frac{1}{\tilde{x}}\right) = \frac{V(\tilde{x})}{[E(\tilde{x})]^4} - \frac{[V(\tilde{x})]^2}{[E(\tilde{x})]^6}$$

$$V(\tilde{z}) = [(k)(\ln 2)]^2\left[V\left(\frac{1}{\tilde{x}}\right)\right]$$

where $E(\tilde{x})$ is the expected value of the median from a sample size n (n being odd), and k is the growth constant in the von Bertalanffy growth equation.

The theoretical maximum age was calculated for each population by solving for t in the von Bertalanffy equation

$$L_t = L_\infty(1 - e^{-k(t-t_0)});$$

by setting $L_t = L_\infty$, t_{max} was calculated using the following equation:

$$t_{max} = \frac{\ln L_\infty + kt_0}{k}.$$

Based on the back-calculated lengths-at-age from thin sectioned valves, an age–length key from total lengths-at-age was constructed for each population to allow subsequent determination of age composition. An age–length key is a double frequency table with age (yr) in columns and shell length increments (mm) in rows (Ricker 1975). The percentages from the keys were applied to live individuals collected during 1991 in the Tar River and 1992 in Aquia Creek. For this study, shells were grouped into 4-mm length classes. Each shell was tallied into the proper age–length cell, which formed a ta-

ble of percentages of ages within a given length class.

Growth curves were compared among sites using a dummy variable model modified from Chism et al. (1992). The model tested for differences in growth by fitting one curve to all length-at-age data and then fitting individual growth curves for specimens at each site. The growth curves among sites were considered to be different if individual curves of the Chism et al. (1992) model described the growth measurements with less error than a single curve. Statistical significance ($p < 0.05$) was determined using an F-test macro-program (Minitab 1985).

Habitat preference experiments

The first phase of the habitat preference study was modeled after a substratum preference experiment on the Asian clam (Belanger et al. 1985). Four $17.5 \times 17.5 \times 4.0$-cm habitat chambers constructed from 3.0-mm-thick Plexiglas were filled with the experimental substrata. Experiments were conducted in two 40-L aquaria with a continuous renewal water source. Water temperature and dissolved oxygen were monitored daily. Sediments and A. heterodon were collected from the Tar River. Sediments were dried at 100°C for 24 h, washed, and dried again at 210°C to remove as much organic matter as possible.

Three grades of substratum were tested: fine (0.063–0.850 mm), intermediate (1.68–3.36 mm), and coarse (3.37–8.00 mm). Preferences for these substrata were compared. A reference test of smooth solid substratum was also created by stacking sheets of Plexiglas to the same level as the experimental substrata. In each preference trial, two substratum types were placed side by side in the habitat chambers with a distinct line of demarcation between them. Three or four dwarf wedgemussels were placed along the line of demarcation between substrata, all facing the same direction, with the umbo and anterior end in the sediment, just deep enough for them to remain upright. Mussels were observed after 1 h, then daily for 7 d, and the number of individuals in each substratum type was noted. Three trials of each experiment were completed.

On completion of the substratum preference studies, an experiment was initiated to deter-

mine whether *A. heterodon* prefers a lotic or lentic environment. Fine (0.063–0.850 mm) substratum was placed in two 17.5 × 35.0 × 4.0-cm boxes constructed of 3.0-mm-thick Plexiglas. Current was generated by two submersible pumps connected to a series of 1.27-cm PVC piping arranged in a tier. Each horizontal row consisted of piping with evenly spaced 0.32-cm holes, which allowed water jets to generate a measurable velocity. The velocity-generating apparatus was placed at the head of a Living Stream. One-half of the Living Stream was isolated from current using a box constructed of 0.64-cm thick plywood. Two square holes (17.5 × 7.0 cm) were cut into the plywood to accommodate the habitat boxes. The midpoint of each habitat box was placed directly under the divider. The upstream box (closer to the pumps) served as the moderate velocity regime, while the box downstream provided the low velocity regime. Five mussels were placed along the midpoint of each habitat box, with the umbo and anterior ends in the sediment deep enough to allow them to remain upright. Movements of the mussels were observed after 1 h and then daily for 7 d. Each experiment was replicated three times. Dissolved oxygen (mg/L) was measured with a YSI model 51B dissolved oxygen meter (Yellow Springs Instrument Co., Inc., Yellow Springs, Ohio), and water velocity (cm/s) was monitored daily with a Marsh McBirney Flo Mate 2000 (Marsh-McBirney, Inc., Frederick, Maryland) at the upstream and downstream end of each habitat box. On the seventh day, after the mussels had been given ample time to burrow into the substratum of a given flow regime, the nose velocity (velocity directly above the substratum in which the mussel was buried) at each mussel was recorded.

The velocity preference experiment was conducted in two flow regimes: moderate ($\bar{x} = 8.9$ cm/s) and low ($\bar{x} = 3.7$ cm/s) velocity. Both sets of experiments were conducted at the same time, and lower velocity was achieved by increasing the distance of the mussels from the pumps. Five mussels were placed in fine sediments in both experiments.

In July and August 1992, nose velocities were measured for *A. heterodon* in the Tar River and Aquia Creek using a Marsh McBirney Flo Mate 2000. A normalized suitability index (NSI) was calculated for velocity occupied by dwarf wedgemussels using a technique similar to that

described by Bovee (1986). The technique assigns the placement of a curve over the range of microhabitat observations for a given variable (e.g., velocity). To calculate curve placement, a normalized weighting factor of 1.0 was given to the range of the variable that included observations between the 25 and 75 percentiles, 0.5 to the points that described the 12.5 and 87.5 percentiles, 0.10 to the points at the 5.0 and 95.0 percentiles, 0.05 to the points at the 2.5 and 97.5 percentiles, and 0 to the points at the 0 and 100 percentiles.

The substratum and velocity preference experiments were analyzed by one-way ANOVA for each sediment and velocity pairing. For each pairing of sediment and velocity (A vs. B), three possible outcomes were compared: (1) mussels moved to sediment A or velocity A, (2) mussels moved to sediment B or velocity B, and (3) mussels remained along the line of demarcation between the two sediments or velocities. If a significant ($p < 0.05$) difference occurred in the ANOVA *F*-test, a Tukey's Multiple Range test was used to determine which group(s) were significantly different at an α-level of 0.05.

Results

Reproductive cycle

When the Tar River was sampled for drifting glochidia in May 1991, and neither glochidia nor gravid females were found, drift sampling was discontinued. Sampling for gravid individuals resumed in October 1991 and continued through the winter and spring months of 1992 at both study sites; but only one partially gravid female was found (14 April, 14°C) among 31 individuals examined. No gravid females were found in Aquia Creek among 26 individuals examined between October 1991 and April 1992. Drift nets were set weekly, however, at both study sites from 6 April to 4 May 1992 and on three subsequent occasions in May and July 1992 to record conditions associated with the potential release of glochidia. Considerable numbers of *Elliptio* sp. glochidia occurred in the drift of both streams, but no *A. heterodon* glochidia were found in the samples.

On 24 September 1992, a fully gravid female of *A. heterodon* was collected, the first since sampling began at the Tar River site; water temperature was 19°C. A small sample of glochidia

TABLE 1. Species tested as potential fish hosts of the dwarf wedgemussel in the Tar River and Aquia Creek.

Scientific name	Common name
Catostomidae	
Catostomus commersoni[c]	white sucker
Centrarchidae	
Ambloplites rupestris[d]	rock bass
Lepomis auritus[c]	redbreast sunfish
Lepomis gibbosus[c]	pumpkinseed
Lepomis macrochirus[c]	bluegill
Micropterus salmoides[c]	largemouth bass
Pomoxis nigromaculatus[c]	black crappie
Cottidae	
Cottus bairdi[d]	mottled sculpin
Cyprinidae	
Clinostomus funduloides[c]	rosyside dace
Nocomis leptocephalus[a]	bluehead chub
Notropis procne[c]	swallowtail shiner
Notemigonus crysoleucas[c]	golden shiner
Ictaluridae	
Noturus insignis[c]	margined madtom
Percidae	
Etheostoma nigrum[a]	Johnny darter
Etheostoma olmstedi[b]	tessellated darter

[a] Tar River.
[b] Aquia Creek.
[c] Inhabits both drainages.
[d] Inhabits neither drainage.

was removed in the laboratory, but they were judged to be immature because they were enclosed in the vitelline membrane and were non-responsive to saline solution. Glochidia remained encased in the vitelline membrane until late October. At this time, glochidia snapped shut when exposed to salt crystals. When the

glochidia reached maturity in the laboratory, we resampled the Tar River and collected an additional 15 gravid females on 5 November 1992; eight were used in host fish experiments. All A. heterodon were returned live to the Tar River following the experiments.

Fish host determination

On 20 May 1992, fish were electroshocked in and below pools with A. heterodon in the Tar River. All fish with signs of attached glochidia were preserved and later examined under magnification in the laboratory. However, none of the fish had A. heterodon glochidia attached. Immediately after the first gravid female was found, potential fish host species were collected from sites devoid of mussels whenever possible. Most of the fishes were collected from rivers near Blacksburg, Virginia. Of the fish species (17) common to Aquia Creek and the Tar River, 10 were used in fish host experiments. In addition, 5 species that occurred in only one stream or neither were tested (Table 1).

Laboratory infestations of fish began on 25 November 1992 and were completed by 12 January 1993. Glochidia metamorphosed to juveniles on mottled sculpin (Cottus bairdi), Johnny darter (Etheostoma nigrum), and tessellated darter (E. olmstedi) (Table 2). The remaining 12 species sloughed glochidia within 4 d (Table 3).

Glochidia responded very differently to fish that later proved to be hosts versus non-hosts. With the exception of rock bass (Ambloplites rupestris), all of the non-hosts had very low initial infestation rates. All fish were infested in the same manner with comparable numbers of mature and viable glochidia; however, glochidia did not attach nearly as densely on fishes that were not hosts. In the rock bass exception, A.

TABLE 2. Fish species that served as hosts for the glochidia of the dwarf wedgemussel.

Infested species	Number infested	Period of metamorphosis (d)	Peak day of excystment	Temperature range (°C)	Number of juveniles recovered
Cottidae					
Cottus bairdi	14	16–38	30	15.0–20.0	479
Percidae					
Etheostoma nigrum	5	10–22	18	21.0–22.0	16
Etheostoma olmstedi	5	12–26	16	19.0–21.5	33

heterodon glochidia attached mostly to the gills rather than the fin margins. The area of the gills surrounding individual glochidia turned opaque and white within 2 d of infestation. No glochidia remained attached after 48 h of this reaction. The two darter species and the mottled sculpin acquired very high infestations of glochidia.

Population demographics

On 24 and 30 September 1992, 39 dwarf wedgemussels were checked for gravidity at the Tar River site; 23 (59%) were not gravid and were assumed to be males. The remaining 16 (41%) had swollen and darkened marsupia, indicative of the gravid condition. There was no significant deviation from a 1:1 sex ratio (χ^2 = 1.26).

Total length-at-age data were highly variable, partly due to differences in the timing of mortality. For example, a mussel dying in June would be of greater length than a mussel of the same age that had died the previous fall or winter, yet it would be included within the same age class. Because the lengths of mussels varied greatly within year classes, back-measured lengths at annuli were used for determining age and growth patterns, rather than total lengths-at-age.

A model using a set of dummy variables was used to test for differences in growth curves of mussels among the three study sites; the growth curves for all sites were not the same ($p = 0.017$). There were significant differences between the growth curves of *A. heterodon* from the Tar River and Aquia Creek ($p = 0.010$) and between those of the Neversink River and Aquia Creek ($p = 0.015$). There was no significant difference between the growth curves of dwarf wedgemussels from the Tar and Neversink rivers ($p = 0.109$). Growth curves for the Tar River and Neversink River populations were similar in younger mussels (<4 yr), diverging only at later ages. Sizes of mussels at Aquia Creek were consistently shifted toward greater lengths-at-age, explaining the significantly different growth curve for this population.

Tar River population characteristics

One hundred valves from the Tar River were thin-sectioned; however, annuli on only 28

TABLE 3. Fish species that did not serve as hosts for glochidia of the dwarf wedgemussel.

Infested species	Number infested	Temperature range (°C)	Last day of observed attachment
Catostomidae			
Catostomus commersoni	5	21.0–21.5	1
Centrarchidae			
Ambloplites rupestris	5	21.0–21.5	4
Lepomis auritus	2	21.0–21.5	2
Lepomis gibbosus	5	21.0–21.5	2
Lepomis macrochirus	5	21.0–21.5	4
Micropterus salmoides	2	21.0–21.5	3
Pomoxis nigromaculatus	6	21.0–21.5	4
Cyprinidae			
Clinostomus funduloides	5	15.0–19.0	2
Nocomis leptocephalus	2	21.0–22.0	3
Notemigonus crysoleucas	6	21.0–22.0	3
Notropis procne	5	21.0–22.0	1
Ictaluridae			
Noturus insignis	5	21.0–22.0	1

specimens ranging from 25.5 to 34.3 mm were confidently identified. The ages of mussels sectioned ranged from 2 to 6 yr. Larger and presumably older mussels were collected, but because of excessive shell erosion, they could not be aged.

An age–length key was used to estimate the age distribution of the Tar River population by assigning ages to all live dwarf wedgemussels ($n = 58$) measured to the nearest 0.1 mm. Ages assigned to live *A. heterodon* collected at the Tar River and Aquia Creek were based on the highest percentage in a length increment for a given year class. Most specimens collected from the Tar River were age 6 or older (Fig. 1). Instantaneous rate of mortality was calculated to be 0.59, with a variance of 0.017 ($n = 43$). Annual mortality rate was 44%.

The growth pattern of *A. heterodon* in the Tar River was asymptotic, with growth rate (mm/yr) highest in the first year, gradually declining with age (Fig. 2). Severe shell erosion in the older individuals prevented aging of mussels older than 6 yr. This lack of an age–length relation for older specimens limited our ability
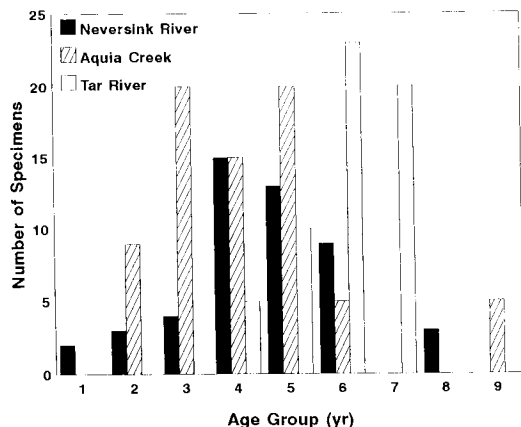
FIG. 1. Age class composition of live *Alasmidonta heterodon* collected in the Tar River, North Carolina ($n = 58$); Aquia Creek, Virginia ($n = 72$); and Neversink River, New York ($n = 45$). Age 7 cohort in the Tar River includes age 7 and older mussels that could not be accurately aged because of excessive shell erosion.

to determine at what age the asymptote was approached.

The von Bertalanffy growth equation for the Tar River population was as follows:

$$L_t = 38.70 \text{ mm } (1 - e^{-0.299(t + 0.251)})$$

$$(n = 43; \quad \text{MSE} = 4.05).$$

The maximum theoretical age (t_{max}) was 12 yr. The equation predicted a maximum length of 38.70 mm; however, the largest live individual found was 44.5 mm. There was little disparity between the observed mean length at each annulus and the von Bertalanffy predicted lengths at age (Table 4).

Aquia Creek population characteristics

Seventy-nine specimens were thin-sectioned from shells collected in Aquia Creek, and 40 were usable for age and growth analyses. The ages of sectioned shells ranged from 2 to 9 yr. Age class distribution of live animals was estimated using an age–length key derived from thin-sections. Most live *A. heterodon* collected in Aquia Creek were between 3 and 5 yr old (Fig. 1). Instantaneous rate of mortality was 0.42, with a variance of 0.0002 ($n = 90$). Annual mortality rate was 34% at the Aquia Creek site.

The growth pattern of individuals from Aquia Creek also was asymptotic, and growth rate (mm/yr) was highest for ages 1 and 2. Length began approaching an asymptote at about age 6 (Fig. 3).

The von Bertalanffy equation describing the growth pattern for the Aquia Creek population was as follows:

$$L_t = 45.26 \text{ mm } (1 - e^{-0.260(t + 0.244)})$$

$$(n = 90; \quad \text{MSE} = 10.58).$$

The maximum theoretical age (t_{max}) was 14 yr. The equation predicted a maximum length of nearly 45.3 mm. The largest live individual found at this site was 43.1 mm, while the largest shell found in the stream was 45.7 mm. The predicted lengths-at-age calculated by the von Bertalanffy equation agreed closely with the observed mean lengths for the earlier ages. The slight underestimation of the lengths at older ages could be attributed to the very low number of sections available from older mussels (Table 4).

Neversink River population characteristics

Thin-sections were made from 24 dwarf wedgemussel shells from the Neversink River; 21 of the specimens could be aged. The ages of mussels ranged from 3 to 10 yr. An age–length key was made for this population. Lengths from 45 live *A. heterodon* were used to estimate the age distribution of the population in the Neversink River, based on the age–length key. Most
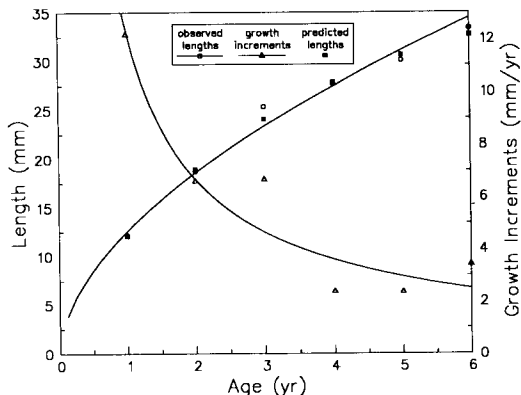

FIG. 2. Mean growth in length of *Alasmidonta heterodon* in the Tar River, observed and predicted by the von Bertalanffy growth equation.
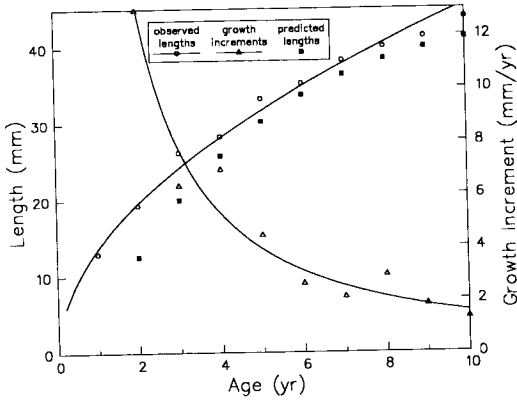
FIG. 3.   Mean growth in length of *Alasmidonta heterodon* in Aquia Creek, observed and predicted by the von Bertalanffy growth equation.

live *A. heterodon* collected in the Neversink River were 4 to 6 yr old (Fig. 1). Instantaneous rate of mortality was calculated to be 0.27 ($n = 41$), with a variance of 0.0001 for *A. heterodon* at this site. Annual mortality was 24%.

The growth of *A. heterodon* in the Neversink River is also asymptotic, approaching an asymptote at age 6 (Fig. 4). With the exception of the oldest observed individual, which was overestimated, the lengths-at-age predicted by the von Bertalanffy equation agreed closely with the observed mean lengths-at-age for this site (Table 4).

The von Bertalanffy equation describing the Neversink population was as follows:

$$L_t = 46.84 \text{ mm } (1 - e^{-0.207(t+0.335)})$$

$$(n = 41; \quad MSE = 6.04).$$

The maximum theoretical age (t_{max}) was 18 yr. The equation predicted a maximum length of 46.8 mm, whereas the largest specimen received was 42.6 mm.

Habitat preference experiments

Temperature and dissolved oxygen were monitored daily during the substratum and velocity preference studies. The Frigid Unit thermostat was set at 15°C, but temperature varied from 13.5 to 18.0°C ($\bar{x} = 14.7 \pm 0.93$). Dissolved oxygen levels ranged from 7.9 to 10.0 mg/L ($\bar{x} = 9.2 \pm 0.54$).

Dwarf wedgemussels collected from the Tar River preferred all mineral substratum types

TABLE 4. Observed and predicted (von Bertalanffy growth equation) lengths (mm) at annuli of dwarf wedgemussels in the Tar River, North Carolina; Aquia Creek, Virginia; and Neversink River, New York.

|	Tar River				Aquia Creek				Neversink River			
	Observed lengths		Predicted lengths		Observed lengths		Predicted lengths		Observed lengths		Predicted lengths	
Annulus	Mean	Range	Mean	n^a	Mean	Range	Mean	n^a	Mean	Range	Mean	n^a
1	12.16	8.4–15.7	12.07	7	12.96	9.2–15.6	12.51	7	12.75	11.3–14.2	11.33	2
2	18.73	12.2–21.5	18.95	12	19.28	11.7–25.7	20.01	25	17.35	14.3–19.2	17.99	6
3	25.36	21.9–26.7	24.06	10	26.21	19.4–32.2	25.79	22	22.99	18.9–26.5	23.40	8
4	27.73	25.8–30.0	27.84	8	28.29	24.8–37.5	30.25	17	28.29	23.4–33.9	27.79	7
5	30.08	28.1–31.4	30.65	4	33.22	28.4–37.9	33.69	11	31.38	27.8–36.0	31.36	6
6	33.40	32.5–34.3	32.73	2	35.20	32.4–41.0	36.34	4	34.66	31.4–38.3	34.26	5
7					38.20	38.2	38.40	1	36.83	35.9–37.9	36.62	3
8					40.0	40.0	39.96	1	38.47	37.7–39.6	38.54	3
9					41.3	41.3	41.17	1	38.30	38.3	40.09	1
10					43.8	43.8	42.11	1				

^{a} Number of observations at that annulus.
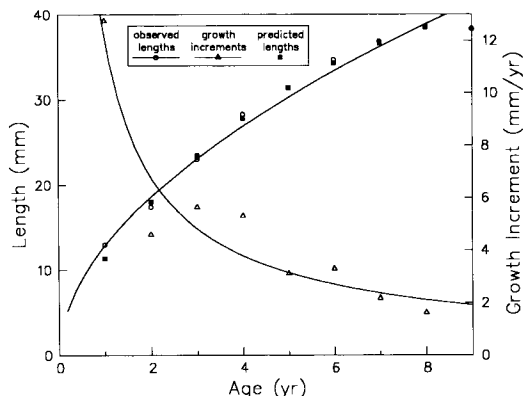
FIG. 4. Mean growth in length of *Alasmidonta heterodon* in the Neversink River, observed and predicted by the von Bertalanffy growth equation.

over the reference test of Plexiglas substratum. Most mussels moved readily into the substratum, although a few remained along the line of demarcation well into the experiment. When fine substratum was tested, all mussels were buried by day 4 of the experiment. When intermediate substratum was tested, it took the full 7 days before all the individuals were buried. When coarse substrate was tested, all but one mussel were buried in the sediment by day 4; the remaining mussel moved to the Plexiglas substratum on day 4 and stayed there for the duration of the experiment.

Dwarf wedgemussels preferred fine over coarse substratum. By day 4 of the experiment, the choice was statistically significant ($p = 0.002$). By day 7, all individuals were buried in the fine substratum. Nearly 67% chose fine over intermediate substratum, and 75% chose intermediate over coarse substratum. Although most specimens of *A. heterodon* moved to the finer substratum in each experiment, there was no significant preference by day 7 between fine and intermediate particle sizes ($p = 0.2499$) or between intermediate and coarse substrata ($p = 0.4286$).

The mussels were fairly immobile in the moderate velocity experiment, and several buried themselves at the line of demarcation. No significant difference in mussel locations occurred until day 7 of the experiment. At this time, significantly more mussels ($p = 0.0110$) were present in the side of the tank that offered a refuge from flow than in the free-flowing side. There

was no difference in the number of mussels along the line of demarcation versus the number in the lotic and lentic areas.

Mussels in the low flow experiment moved more than those held in moderate flow. None remained along the line of demarcation for more than 24 h after day 3. After all mussels had moved away from the line of demarcation, there was little movement between the two velocities. Most of the mussels, however, moved within one side of the tank, but they seldom moved between flow regimes. A significant choice of lotic versus lentic velocity was never established in the low velocity experiment.

Nose velocity was measured on day 7 of the experiments for each of three trials. Mean nose velocity was 2.3 cm/s for mussels in the moderate flow experiment and 1.7 cm/s for mussels in the low flow experiment (Table 5).

Nose velocities measured at the Tar River were zero or below the sensitivity of the current meter during the sampling time. Nose velocities were measured for 69 dwarf wedgemussels at Aquia Creek, which was a lotic environment, with water velocities at mussel locations ranging from 0 to 29 cm/s ($\bar{x} = 6.8$ cm/s). The velocities occurring within the highest suitability range were calculated to be 2 to 10 cm/s.

Discussion

Reproductive cycle

Although we were unable to define the release period for *A. heterodon* at field sites, the species seemingly follows a reproductive time frame similar to those of others in the subfamily Anodontinae (Coker et al. 1921). Based on anecdotal evidence, such as dates when gravid

TABLE 5. Nose velocities recorded on day 7 of the velocity preference experiment.

Trial	n	$\bar{x}$ (range cm/s)
Moderate velocity		
1	5	1.2 (0–6)
2	5	3.8 (0–12)
3	5	1.8 (0–9)
Low velocity		
1	5	0.8 (0–2)
2	5	2.8 (0–5)
3	5	1.6 (0–3)

females were present or absent, release of glochidia probably occurs primarily in April in North Carolina.

Release of glochidia has been linked to a number of environmental cues, including water temperature (e.g., Matteson 1955, Bruenderman and Neves 1993), and discharge or flow rates (Hynes 1970, Kitchel 1985). Release of glochidia triggered by a temperature threshold would coincide with certain fishes entering river headwaters to spawn (Pflieger 1975). Spring flow rates would be especially important for *A. heterodon* to release glochidia in the Tar River because flows approach zero during summer. Anodontine mussels produce some of the largest glochidia (Kat 1984), which have a propensity to sink (Wood 1974a). Higher flows during glochidial release may aid in keeping glochidia suspended in the water column for longer periods, thus increasing their probability of encountering host fishes.

Based on histological evidence, *A. heterodon* undergoes gametogenesis from May to July in New England (J. Nicholson and D. Smith, University of Massachusetts, personal communication), and is gravid as early as late August in North Carolina (J. Alderman, North Carolina Wildlife Resources Commission, personal communication) or late September (our study). However, we did not search for gravid females during summer 1992. Ortmann (1919) reported finding gravid *A. heterodon* during the months of February through April in Pennsylvania, whereas Clarke (1981) found gravid dwarf wedgemussels during June in Massachusetts.

The Tar River and Aquia Creek populations had seemingly poor reproductive success in 1991. Matteson (1948) observed a similar phenomenon in *Elliptio complanata* in 1945 due to a very cool spring and summer at his site. In a related study, Matteson (1955) noted that sexual activity varied temporally among years in *E. complanata* and attributed this variation to temperature. Unfortunately, this explanation does not describe the conditions recorded in the Tar River. The 1991 summer water temperatures were not lower than in previous years, as judged by USGS gauging station data. Periodic weak year classes probably occur in this species as in others (Negus 1966, Haukioja and Hakala 1978). Other factors may have influenced the apparent reproductive failure. Dwarf wedgemussels may have spawned and released glochidia in 1991

during times when no sampling was conducted (July through September). Female dwarf wedgemussels may also be more prone than males to burrow below the substratum in response to low temperature. Consequently, females would have been much less likely to be found and examined for gravidity during the winter months. Although drift nets were placed in areas downstream of dwarf wedgemussel assemblages during months when long-term brooders are known to release, the nets were set only once per week, and release may not have coincided with the sampling of drift.

Fish host determination

Because no *A. heterodon* glochidia were collected in spring 1992, no inferences were made on natural host fishes in the Tar River. Obtaining glochidia from the marsupium using water forced through a hypodermic needle was effective and did not appear to harm the animal. We knew that stressing the mussels by raising the temperature, lowering dissolved oxygen levels, starvation, and "rough handling" could cause premature release of glochidia (Matteson 1948, 1955), but we used none of these procedures because relatively long-term stressors might have been more harmful than the few seconds required with a hypodermic needle.

Glochidia of the dwarf wedgemussel did not remain in suspension even when airstones provided extreme turbulence. Other researchers have reported similar observations with anodontine glochidia. Wood (1974a) observed that the glochidium of *Anodonta cygnea* remained in suspension only 2 s if it was open with the byssal thread extended, and only 1 s if it was closed. Howard and Anson (1922) made similar observations and stated that hooked glochidia do not rely on the current to keep them in suspension. Because hooked glochidia are more prone to attach to fins (Lefevre and Curtis 1910, Dartnall and Walkey 1979), they may rely on the movements of host fishes to agitate the bottom, bringing them in proximity to a fin margin or gill (Howard and Anson 1922). These observations would be consistent with the behaviors of the darters and sculpins, which serve as hosts for *A. heterodon*. Lefevre and Curtis (1910) stated that darters are readily infested on the fins and gills, with highest glochidial densities occurring on the fin margins. In four *Alasmidonta*

TABLE 6. Known host fishes for the genus *Alasmidonta*.

Mussel	Host	Source
Alasmidonta viridis	*Etheostoma nigrum*	Clarke (1981)
	Cottus bairdi	Clarke (1981)
	Cottus carolinae	Clarke (1981)
A. minor[a]	*Cottus carolinae*	Zale and Neves (1982)
A. calceolus[a]	*Etheostoma nigrum*	Zale and Neves (1982)
	Cottus bairdi	Zale and Neves (1982)
A. marginata	*Catostomus commersoni*	Clarke (1981)
	Hypentelium nigricans	Clarke (1981)
	Moxostoma macrolepidotum	Clarke (1981)
	Ambloplites rupestris	Clarke (1981)
	Lepomis gulosus	Clarke (1981)
A. atropurpurea	*Hypentelium nigricans*	Gordon and Layzer (1993)
A. heterodon	*Etheostoma nigrum*	our study
	Etheostoma olmstedi	our study
	Cottus bairdi	our study

[a] Now considered to be synonyms of *A. viridis* (Turgeon et al. 1988).

species for which host fishes are known, all but two host species are benthic dwellers (Table 6). Wood (1974b) concluded that glochidia may possess the ability to discriminate among fish species during the initial stages of attachment by recognizing certain substances on the surface of the fish. This phenomenon could explain why host fishes had higher degrees of infestation than non-host species.

Determination of sex ratio

As documented in the literature, the sex ratio of a mussel species can vary from population to population (e.g., van der Schalie and van der Schalie 1963, Smith 1979, Zale 1980, Bauer 1987). Most of the previous studies used histological analysis to sex mussels. Because we based the sex ratio of *A. heterodon* strictly on the condition of marsupia (gravid versus nongravid), the number of females present may have been underrepresented because of the possibility of nongravid females in the sample. Similarly, Bauer (1987), comparing the number of gravid females with the sex ratio, calculated that only 64% of female *Margaritifera margaritifera* reproduce in any given year.

Population demographics

Growth was asymptotic in each of the three populations, with growth rate highest early in life (ages 1 and 2) and slowing markedly throughout the life span to an upper limit. An inflection point in the growth plot mentioned by Moyer (1984), possibly marking the commencement of reproduction, was not observed, probably because we pooled sexes when computing the growth curves.

The dummy variable model calculated that the lengths-at-age growth curve of *A. heterodon* in Aquia Creek was significantly different from those for the Tar River and Neversink River populations. This model has had limited use, so its susceptibility to Type I error is not known. Because of higher water temperatures and longer growing season associated with differences in latitude, the Tar River population would presumably have the highest growth rates, while the Neversink River population would have the lowest (Bauer 1992).

The parameter k is the growth constant in the von Bertalanffy growth function. As k increases, the rate at which the asymptote is approached also increases. The variable k also has been described as a "coefficient of catabolism" by von Bertalanffy (1938) and Beverton and Holt (1959), implying that it is linked with rate of metabolism. Although the model calculated that *A. heterodon* in Aquia Creek had a growth curve significantly different from those at the other sites, the values of k and L_∞ in all three populations were consistent with Bauer's (1992) observations that k and L_∞ are correlated with latitude. As latitude increases, k decreases because of the colder temperatures and reduced metabolic rate.

However, L_∞ and maximum age increase with latitude. The Tar River population, lowest in latitude, had the highest k and lowest L_∞, whereas the Neversink River population, highest in latitude, had the lowest k and highest L_∞. The Aquia Creek population had k and L_∞ values between those of the other sites.

That significant differences in growth rate did not occur between the Tar River and Neversink River is somewhat surprising, based on the asymptotic lengths (L_∞) and growth constants (k) of the populations. The von Bertalanffy parameters follow the predictable gradation associated with latitude, as described by Bauer (1992). Statistical differences in growth curves do not, however, follow the same pattern. This phenomenon can be partly explained by the differences in the models used to describe growth among populations. The parameters of the von Bertalanffy growth function, L_∞ and k, are integrally linked and cannot be used by themselves to explain growth rates of populations (Bernard 1981). These parameters describe the endpoint of the growth curve, not necessarily growth during the life of the animal. In the statistical comparison using the dummy variable model, growth is considered throughout the entire life of the animals in each population. The difference between growth of individuals of the Aquia Creek population and growth of the others was statistically significant. However, growth in the later years of the Aquia Creek population slowed, resulting in the von Bertalanffy parameters conforming to the expected latitudinal gradient.

The maximum ages of A. heterodon observed in this study lie within the ranges of other anodontine species. Genera in the subfamily Anodontinae are typically fast-growing mussels with relatively short life spans and maximum ages often <15 yr (Crowley 1957, Negus 1966, Haukioja and Hakala 1978). We found no A. heterodon younger than age 4 at the Tar River site. The Aquia Creek and Neversink River populations, however, appeared to have young individuals present (<age 3), indicating that the population is reproducing. The relatively small sample sizes of A. heterodon under age 3 at all sites is probably due to sampling bias rather than an absence of mussels in those age-classes. Several researchers have documented difficulty in finding young mussels, resulting in a skewed age class representation toward older animals

(Chamberlain 1931, Stober 1972, Yokley 1972, Fisher and Tevesz 1976, Coon et al. 1977). The collection of juvenile mussels requires prescribed sampling (Neves and Widlak 1987).

Missing year classes were evident at all three sites surveyed, but irregular recruitment has been documented in many other species of freshwater mussels. Negus (1966) observed weak year classes in populations of Anodonta anatina and Unio pictorum. Haukioja and Hakala (1978) also reported annual variation in breeding success, with some age classes absent, whereas others accounted for 80% of the population.

The mortality rate estimate for the Tar River was very high (A = 44%) compared with the other sites. Length measurements used in estimating mortality rate probably influenced this calculated value. As mentioned earlier, older specimens from the Tar River could not be aged because of shell erosion. Therefore, the length distribution used in the computation of mortality was skewed toward the smaller (younger) individuals. The method of Hoenig et al. (1983) used median lengths in estimating mortality; thus, a smaller median length for a data set would result in a higher mortality estimate, other factors in the equation being equal. Because there were different age-class distributions and length measurements for the three populations, mortality rate estimations would not be directly comparable. Direct comparisons would be appropriate if age–length categories are equally represented among populations.

Habitat preference

Dwarf wedgemussels consistently chose the finer substratum offered in preference trials, although the results were only statistically significant in the experiment of coarse versus fine sediments. Substratum size chosen by mussels corresponded to the median diameter of substratum samples taken in the field. Strayer and Ralley (1993) observed that A. heterodon in the Neversink River occurred frequently in quadrats containing patches of fine sediment. There are possible adaptive values associated with mussels occupying fine substratum. Swan (1952) observed that softshell clams (Mya arenaria) exhibited higher growth rates in sand than in mud or gravel. Kat (1982) reported similar findings in the eastern elliptio (Elliptio complanata) and hypothesized that reduced growth rate by

mussels occupying muddy substrata may be linked to impeded filtration systems, irritation of the mantle, and constant energy expenditures necessary to keep the mussel upright in the mud (see also Lewis and Riebel 1984). Firmly packed substratum enables mussels to remain upright in a feeding position with no energy expended to maintain position. In addition, consolidated substratum allows the foot to anchor, enabling the mussel to pull itself vertically (Trueman et al. 1966).

Dwarf wedgemussels showed no obvious preference for a particular current velocity. When a significant preference was exhibited at the end of the experiment, it was in favor of the lentic environment. When nose velocities were measured on day 7 of each trial, they were consistent with the lowest values in the maximum suitability range of the normalized suitability index calculated for the Aquia Creek site. Therefore, dwarf wedgemussels from the Tar River used in these experiments may merely be tolerant of the standing water conditions of summer, but prefer a slow to moderate flow.

Conclusion

Few young dwarf wedgemussels were found at the Tar River site, possibly suggesting poor reproductive success in recent years. Dwarf wedgemussels, being relatively short-lived, have a shorter reproductive life and fewer cohorts to reproduce than most other mussel species. The diversity of size classes at the Aquia Creek and Neversink River sites may indicate a higher rate of recruitment there than in the Tar River.

Prior studies of the species noted that dwarf wedgemussel populations no longer inhabit river reaches after impoundment (Master 1986). Master (1986) hypothesized that dams exclude diadromous fishes, thought to be hosts at that time, from entering habitats occupied by *A. heterodon*. Johnny darters typically inhabit slow-moving pools in small creeks (Pflieger 1975) and have even been reported in impounded bodies of water (Scott and Crossman 1973, Becker 1983). Less is known of the effects of standing-water habitats on the tessellated darter. Mottled sculpins are found in spring branches or streams kept cool by spring flow and are intolerant of heavy siltation (Pflieger 1975), thus it may be uncommon for this species to occur in proximity with *A. heterodon*. The two darter

species, the most likely natural hosts of the dwarf wedgemussel, are widespread and tolerant of low flow, suggesting that the dwarf wedgemussel's decline is not intricately linked with a problematic fish host relationship.

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