REPRODUCTIVE BIOLOGY AND COMPARATIVE GROWTH RATES OF SELECTED SPECIES OF FRESHWATER MUSSELS (BIVALVIA: UNIONIDAE) IN THE NEW AND GREENBRIER RIVERS, VIRGINIA AND WEST VIRGINIA

by

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Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE
in
Fisheries and Wildlife Sciences

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June, 1986

Blacksburg, Virginia

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(ABSTRACT)

The reproductive biology of four unionid mussels, Actinonaias carinata, Elliptio dilatata, Cyclonaias tuberculata, and Tritogonia verrucosa, from the New River in Virginia and West Virginia was investigated. The gametogenic cycle, length and timing of spawning and glochidial release periods, and age at sexual maturity were described for each species. Comparisons of growth rates of C. tuberculata subpopulations from the Greenbrier River and three locations downstream of Bluestone Dam on the New River in West Virginia were also made to determine the effect of the dam on growth of mussels downstream.

A. carinata is bradytictic, spawning in mid-summer, brooding glochidia throughout the fall and winter, and releasing them in the spring. E. dilatata, C. tuberculata, and T. verrucosa are tachytictic. Spawning began in mid-March for these three species and continued into May for T. verrucosa, into June for C. tuberculata, and into July for E. dilatata. Glochidia were released upon maturation, beginning in mid-April and continuing through June for T. verrucosa, and into August for E. dilatata. C. tuberculata released glochidia from March through June. All four

species appeared to reach sexual maturity between the ages of 4 and 6, depending upon the species.

Growth in shell length in the four subpopulations of C. tuberculata was asymptotic. Growth rate, described by the parameter w from a reparameterization of the von Bertalanffy growth equation, was significantly higher immediately below Bluestone Dam compared to the site furthest downstream. Growth of this species did not differ significantly among the other sites; however, a trend of decreasing growth rate with increasing distance from the dam was apparent. Observed differences in growth were attributed to differences in food availability and quality resulting from the operation of Bluestone Dam.

ACKNOWLEDGEMENTS

Completion of this thesis would not have been possible without the support and assistance of many people other than myself. I owe a debt of thanks to many individuals, and though I cannot express all of my gratitude in these short acknowledgements, I hope those people will realize how fully I appreciate their help and concern.

I would first like to thank Dr. Richard J. Neves for having me as a student and introducing me to a fascinating group of animals, freshwater mussels. His support and guidance were instrumental in the completion of my work, and the financial support I received during my stay at Virginia Tech was duly appreciated. I would also like to thank the other members of my committee, Dr. Donald J. Orth and Dr. Jackson R. Webster. Dr. Orth was especially helpful with the analytical aspects of my research and giving of his time whenever I needed it. I thank Dr. Webster for his advice and willingness to discuss my work whenever I asked it of him.

I cannot begin to thank all of my fellow graduate students that made my tenure at Virginia Tech an enjoyable one. I would first like to extend my thanks to those people who assisted me in the field. These include the members of the , , , , and , as well as , , , , and . I also received a great deal of help in the laboratory from , , , , , , and . These people have my gratitude.

I would like to extend a special thanks to a few individuals that contributed not only to my work, but also to my everyday well-being. I thank for her encouragement, thoughtfulness, and companionship. I am also deeply indebted to the members of the , my officemates , , , and . These people not only created an atmosphere in which I was comfortable and productive, but also provided me with insights into many facets of life through their experiences and opinions. They were always there to listen and always willing to assist me with my problems.

I owe my greatest thanks to my family for their constant encouragement and support. I thank them for accepting me for who I am and encouraging me to be what I desire. Finally, I want to thank my fiance, . She, more than any other person, is responsible for my finishing this work. She was there when I needed her, and I cannot thank her enough.

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INTRODUCTION

The Mussel Resource

The rivers, streams, and lakes of North America harbor over 200 species of freshwater mussels (Pelecypoda: Unionacea), which constitute the richest fauna of its kind in the world (Burch 1975). Especially diverse mussel assemblages exist in the Mississippi, Tennessee, and Ohio River drainages, with some waters historically containing upwards of 60 species (Ortmann 1925). Some mussel beds in these rivers at one time supported millions of naiades and provided an important resource to inhabitants of these river basins (Carlander 1954). North American Indians harvested mussels as a food source as well as for use in constructing tools and ornaments. Such practices were evidently widespread, but had little impact on the fauna. In the late 1800's, freshwater mussels became a resource of economic significance, as the basis of a booming pearl button industry along the major rivers of the Midwest. Although the button industry was short-lived, mussels are still harvested today to provide shell for use as nuclei in the Japanese cultured-pearl industry (Isom 1969).

Aside from their economic value, freshwater mussels are important biological and ecological components of aquatic ecosystems. Filter-feeding by mussels removes organic detritus from the water column and may significantly reduce downstream losses of energy in lotic systems (Wallace et al. 1977). Suspended solids not utilized by mussels are excreted as pseudofeces, providing a valuable source of nutrition for

other detritivores (Stansbery and Stein 1971). In many streams, mussels make up the bulk of the biomass of the bottom fauna. Negus (1966) found the standing stock of mussels in one reach of the Thames River, England, to be 2922 kg/ha, constituting over 90 percent of the benthic biomass. Mussel production in this same river reach was 205 kg/ha/yr. Turnover of such production provides a significant amount of energy to other detritivores. Live mussels also serve as important food sources for some fishes, birds, raccoons, muskrats, and other furbearers (Fuller 1974).

Because of their longevity and sedentary nature, mussels can function as indicators of environmental quality. Growth patterns and chemical composition of unionid shells are reflective of environmental conditions, and analysis of these characteristics can provide information on short and long-term changes in aquatic environments (Tevesz and Carter 1980). Naiades also bioaccumulate many organic pollutants in their tissues and therefore may serve as monitors of ecosystem health and recovery following contamination by pesticides and other toxicants (Stansbery and Stein 1971). The presence of an abundant mussel fauna is usually indicative of a healthy fish fauna, since most mussel species depend on at least one species of fish in order to complete their life cycle. Most mussels are also intolerant of prolonged exposure to degraded environmental conditions, and thus the health of an existent mussel assemblage is usually indicative of the health of the aquatic ecosystem as a whole.

Mussel Declines

The mussel fauna of North America has been greatly reduced in abundance and diversity in the past century due to a variety of anthropogenic factors. In the late 1800's, mussel stocks began experiencing severe depletions from overharvest by commercial musselers (Carlander 1954). Even today there is considerable harvesting pressure on some remaining stocks as demand for shell to support the cultured-pearl industry increases (Waters 1980).

Environmental impacts resulting from the impoundment of the major river systems of the United States have had dramatic consequences on local mussel assemblages. The extensively dammed Tennessee River drainage has experienced a reduction in excess of 50 species since impoundment was begun in the 1930's (Isom 1969). Coon et al. (1977) reported the loss of eight mussel species and dramatic shifts in the relative abundances of remaining species in the upper Mississippi following impoundment of the river in the 1930's. Such changes in the fauna are a result of siltation, alterations of the flow regime, elimination of riffle habitats, changes in water quality, and disruption of the reproductive cycle caused by the damming of free-flowing rivers (Fuller 1974). Heavy barge traffic and associated channelization and dredging activities have also contributed to mussel declines in many navigable rivers (Coon et al. 1977).

Poor land use practices have rendered many streams unsuitable for mussels. Erosion of farmlands and cutover forests probably had a significant role in eliminating mussels from many areas through siltation

due to excessive runoff (Fuller 1974). Mussels have also declined as a result of industrial and domestic pollution. Strayer (1980) attributed reductions in mussel diversity in reaches of the Clinton River, Michigan, to considerable pollution from urban areas. Mining and wood processing operations, as well as introductions of pesticides and heavy metals, have also been cited as factors in the demise of many mussel populations (Stansbery 1969; Fuller 1974; Stansbery and Clench 1975). The introduced Asiatic clam, Corbicula fluminea (Muller, 1774), may also be adversely affecting mussel populations through competition for food and substrate, though this has yet to be fully substantiated (Sickel 1973; Gardner et al. 1976).

Despite these anthropogenic influences, healthy mussel populations still exist in some rivers throughout North America. These populations provide an avenue for biologists to gather essential information about the life histories and habitat requirements of these molluscs that is necessary to ensure the continued existence of this unique fauna.

Life Histories of Mussels

Much is known about the general life histories of freshwater mussels; however, detailed studies for the majority of species are lacking. In general, the sexes are separate, although hermaphroditism is common in some species (van der Schalie 1970). Eggs are produced in the ovaries and released into the suprabranchial chamber where fertilization by sperm, released concurrently by males, occurs. Embryos are released into the marsupial gills where they develop into parasitic larval forms called

glochidia. Species characterized as short-term (tachytictic) breeders usually spawn in spring and release glochidia soon after they become fully developed (Lefevre and Curtis 1912). Long-term (bradytictic) breeders may spawn in the late spring and summer, with glochidia overwintering in the marsupia to be released in the spring. Once released, glochidia must attach to specific fish hosts, usually on the gills or fins, where they metamorphose for a short time before dropping off and settling to the bottom as juveniles (Coker et al. 1921).

Required fish hosts and the timing and duration of gametogenesis, spawning, and glochidial release periods vary among mussel species, and details are known for few taxa. Considerable research was done early in this century on the life histories of many important commercial mussel species (Lefevre and Curtis 1910, 1912; Coker et al. 1921). These studies were concerned mainly with identifying fish hosts for various species and developing propagation techniques in order to replenish diminishing mussel stocks. Consequently, identification of glochidia and their phases of parasitism received attention in early research efforts (Surber 1912, 1913; Howard and Anson 1922). Ortmann (1909) and Utterback (1916) addressed the breeding seasons of naiades in Pennsylvania and Missouri, respectively, but they provided only cursory information on the life history of any given species.

More detailed investigations of at least portions of the life histories of many species have been conducted since these early studies. Matteson (1948) thoroughly described gametogenesis, fertilization, and glochidial development in Elliptio complanata. Similar information has been gathered on Actinonaias ellipsiformis and Anodonta cygnea (van der

Schalie and van der Schalie 1963; Wood 1974). Van der Schalie (1970) studied the incidence of hermaphroditism in nearly 100 species of Nearctic mussels, reporting that the majority of species are principally dioecious. Yokley (1972) summarized the gametogenic cycle, glochidial development and fish host relationships of Pleurobema cordatum. Biannual gametogenesis in Margaritifera margaritifera was investigated by Smith (1978). Spawning, glochidial release periods and glochidial infestations of fish by this species were also reported (Smith 1976). Similar information is also known for several species of Anodonta (Heard 1975). More recently, Weaver (1981) and Zale and Neves (1982a) have conducted detailed life history studies on several mussel species in southwestern Virginia.

Knowledge of the fish hosts of most naiad species is lacking. Fuller (1974) summarized the glochidia-fish host relationships recognized prior to 1972, and few subsequent studies have been conducted. Wiles (1975) investigated fish host relationships for Elliptio complanata, Lampsilis radiata radiata, and three species of Anodonta in Nova Scotia. Fish hosts have also been described for Margaritifera margaritifera and Lasmigona compressa, and several unionids from southwestern Virginia (Smith 1976; Tompa 1979; Weaver 1981; Zale and Neves 1982b). Investigations into the physiological aspects of glochidia-fish host associations to determine the chemical components of fish serum that control host suitability have recently been undertaken (Isom and Hudson 1984; Neves et al. 1985). This work was aimed at providing a means of culturing mussels to the juvenile stage while by-passing the parasitic stage and need for specific hosts.

Despite recent research, a great deal is unknown about the biology, ecology, and specific life histories of the majority of freshwater mussel

species. This knowledge is necessary for effective management of existing mussel stocks and to restore and augment depleted stocks. Effective recovery plans for endangered mussel species cannot be implemented until the reproductive biology of these species is known. It is clear that much basic research on the life history of freshwater naiades remains to be done and is necessary if the decline of these organisms is to be reversed.

Age and Growth Studies

Studies on the age and growth characteristics of freshwater mussels are scarce and often of questionable accuracy. A common fault of many studies is lack of validation of aging techniques. Methods of aging in past studies have usually involved counting growth rings on the external surface of the shell, with the assumption that the rings were deposited annually. Erosion of the shell surface and the deposition of false annuli by mussels undergoing stressful conditions can significantly affect the accuracy of such studies, and thus makes this method of aging suspect if validation procedures are omitted (Moyer 1984).

Research on mussel growth has centered mainly on describing growth patterns of selected species at specific locations. Chamberlain (1931) studied the growth of four commercially important species in three geographic regions of the United States and developed mean length-at-age models for each species by region. Similar relationships were developed by Stansbery (1961) for several Lake Erie unionids. Correlations of growth rates of these species with habitat variables were made to determine factors associated with stunting in these lake forms. Negus (1966)

used external growth rings to devise growth curves for a unionid assemblage in the Thames River, England, as part of a larger study assessing the effect of a thermal discharge into the river on mussel growth and production.

The relationship between shell weight and age in several molluscs has been investigated and found to be essentially linear for a considerable proportion of the life span for most unionids studied (Sheldon 1967). Coon et al. (1977) developed power functions to describe growth in twelve species of naiades from the Mississippi River. Growth equations for six additional species, including an endangered species, Fusconaia edgariana, were developed for populations from southwestern Virginia (Zale 1980; Weaver 1981; Kitchel 1985). Haukioja and Hakala (1978, 1979) studied growth characteristics of Anodonta piscinalis, testing four asymptotic growth equations for predicting length-age relationships in 15 populations of this species. Taking a more applied approach, McCuaig and Green (1983) developed Ford-Walford plots and von Bertalanffy growth curves relating shell growth in length to age for two Lake Erie mussel species and illustrated how such models may be used in detecting long-term environmental impacts.

Recently, Moyer (1984) evaluated the accuracy of four methods of aging freshwater mussel shells: shell ashing, use of acetate peels, external ring counts, and shell thin-sectioning. He concluded that shell thin-sectioning was the most accurate method, particularly for older specimens on which external lines are ill-defined. More importantly, through the use of a mark-recovery study spanning three years, Moyer (1984) validated the deposition of annular rings on the shell both internally and ex-

ternally. Such validation supports the use of aging methods based on growth increment counts, particularly thin-sectioning, by which both true and false annuli are easily detected.

Impacts of Dams

Documentation is lacking on the impact of most anthropogenic activities on freshwater mussel populations. The most significant human impact on the fauna, the damming of free-flowing rivers, has received the most attention in the literature. The majority of the information addresses faunal changes resulting from destruction of riverine habitats through impoundment, but little is known on the effects of dams on downstream naiad populations. Responses of aquatic invertebrate communities to upstream impoundments are well documented (Baxter 1977; Walburg et al. 1981; Petts 1984), but in most cases, effects on mussels have been overlooked. Stansbery (1964) surveyed the naiad fauna below Wilson Dam on the Tennessee River in 1963, reporting a reduction in the fauna from 63 to 30 species since pre-impoundment days. Loss of mussel species in the tailwaters below dams on the Tennessee River has been attributed, in part, to seasonally low oxygen tensions associated with hypolimnial releases (Isom 1969). Fisher and Lavoy (1972) documented losses of unionids from an "intertidal" zone created by water level fluctuation below a dam on the Connecticut River.

Perhaps the most damaging effect of dams to mussels is the disruption of the glochidia-fish host relationship. Operational procedures of hydroelectric dams can significantly alter downstream fish populations by

creating conditions unsuitable for certain life history stages, eliminating prey items, and displacing or stranding individual fish (Radford and Hartland-Rowe 1971; Petts 1984). Dams may also eliminate spawning migrations, effectively extirpating some fish species. Loss of potential fish hosts can lead to reproductive failure of mussels and has been cited as a cause of poor mussel recruitment below some dams (Sickel 1982).

Other detrimental impacts on mussel populations resulting from upstream impoundment include elimination of suitable substrates through excessive siltation and/or river bed scouring, disruption of spawning cycles through alterations in the thermal regime, and impairment of feeding and growth. These impacts have been realized for other aquatic invertebrates (Lehmkuhl 1979; Petts 1984), but they have yet to be adequately addressed for mussels. Knowledge of the types and magnitude of impacts on mussel populations that would be expected from upstream impoundment and related dam operations is needed to assess the environmental impacts of such activities.

New River Mussel Fauna

The New River is a sixth-order stream originating in the Blue Ridge Mountains near Blowing Rock, North Carolina, flowing generally northward through Virginia into West Virginia, and eventually merging with the Gauley to form the Kanawha River. The New-Kanawha River system is considered to be the oldest river system in North America, occupying the same river channel established by the ancient Teays River that flowed across the eastern half of the continent during the Tertiary period (Addair

1944). The extreme age of the New River basin makes this river unique among major rivers of the eastern United States. The river is characteristically montane with much of the relatively narrow channel consisting of bedrock, boulders, and large cobbles (Hocutt et al. 1978). The majority of the river in West Virginia flows through the New River Gorge, over a series of large rapids, cascades, and low falls. Less than 2.0 km downstream of its confluence with the Gauley River is the 7.3 m high Kanawha Falls. Two dams are situated on the river: Claytor Dam near Newbern, Virginia, operated by Appalachian Power Company for the production of hydroelectric power, and Bluestone Dam, a U.S. Army Corps of Engineers flood-control dam located at Hinton, West Virginia. Bluestone Dam is an epilimnial-release dam located 1.3 km upstream of the confluence of the New and its largest tributary, the Greenbrier River, and is presently under consideration for conversion to a hydroelectric facility.

The prominent physical features of the New River have had a profound influence on its naiad fauna. The fauna is strikingly depauperate when compared to the high diversity (34 species) presently found in the Kanawha River (Stansbery 1980; Clarke 1982; Taylor 1983). The lack of diversity in the New River is related to the physical features of the river that served to limit mussel colonization, the effects of Pleistocene glaciation on the drainage, and possibly stream captures by other drainages (Jirka and Neves 1985). Only eleven species of mussels have been reported from the New River, with species composition and abundance varying greatly throughout its length (Jirka and Neves 1985). The greatest densities and diversity of naiades are found in the reach of river in West Virginia below Bluestone Dam known as the New River Gorge.

Ten species have been reported from this area, with mussels being extremely abundant throughout the first several miles of the river below the dam.

Existing information on the life histories and age and growth characteristics of the mussel species in the New River Gorge is cursory for all species except Lampsilis fasciola (Zale 1980). Lefevre and Curtis (1912), Utterback (1915), Coker (1919), and Ortmann (1919) described the glochidia, gravid periods, and glochidial release periods of many of these species, but detailed studies on the gametogenic cycles and other life history parameters remain to be done. The importance of and the need for such information in managing and protecting the existing mussel fauna of the New River is clear. Information on the influence of Bluestone Dam on the downstream populations is also necessary to assess possible impacts on the mussel resources of the river that might occur with changes in operational procedures of this structure. The goal of this study was therefore to provide information on the life histories of four mussel species in the New River, and to assess the influence of Bluestone Dam on growth characteristics of mussels below the dam. Specifically, the objectives were as follows:

1. To describe the reproductive biology of four freshwater mussel species, Actinonaias carinata, Cyclonaias tuberculata, Elliptio dilatata, and Tritogonia verrucosa, in the New River, Virginia and West Virginia.
2. To compare the growth rates of Cyclonaias tuberculata subpopulations from the Greenbrier River and various locations downstream of Bluestone Dam on the New River, West Virginia.

The four species studied under the first objective were chosen because of their ample abundance in the New River and the lack of information on the reproductive cycles of these species. Cyclonaias tuberculata was chosen for study in the second objective because adequate numbers of this species could be found for several miles downstream of Bluestone Dam and in the Greenbrier River.

METHODS AND MATERIALS

Study Areas

Mussels used in this study were collected from the New River in Montgomery County, Virginia, and Raleigh and Summers Counties, West Virginia, and the Greenbrier River in Summers County, West Virginia. Water in this section of the New River is relatively hard (>50 mg/L $CaCO_3$), with a pH ranging from approximately 6.5 to 8.1, and alkalinities ranging from approximately 34 to 73 mg/L HCO_3^- (Klarberg 1977). Water chemistry of the Greenbrier River is similar to that of the New River below Bluestone Dam (Hocutt et al. 1978). Ten of the eleven mussel species known to exist in the New River occur in the study areas (Table 1). The mussel fauna of the Greenbrier River is essentially the same as that in the New River (Zeto and Schmidt 1984; Jirka, unpublished records). Two collection sites for mussels used in the reproductive component of this study were located in the New River (Figure 1). The primary study area (R1) (latitude 37°42'N, longitude 80°53'W) was a 120 x 30 m section of river located approximately 7.2 km below Bluestone Dam near Hinton, West Virginia. Substrate in this section consisted of cobble mixed with gravel and small boulders. Depth ranged from 0.4 to 1.2 m. A second site (R2) (latitude 37° 14'N, longitude 80°38'W) was a 300 x 200 m section of the river located off of State Route 652 near McCoy, Virginia (Figure 2). Depth ranged from 0.3 to 0.6 m depending on water releases at Claytor Dam,

Table 1. Mussel species reported from the New River in North Carolina, Virginia, and West Virginia.

Scientific Name	Common Name
Actinonaias carinata (Barnes, 1823)	Mucket
Alasmidonta marginata (Say, 1818)	Elktoe
Anodonta grandis (Say, 1829)	Common Floater
Cyclonaias tuberculata (Rafinesque, 1820)	Purple Wartyback
Elliptio dilatata (Rafinesque, 1820)	Spike
Lampsilis fasciola (Rafinesque, 1820)	Wavy-rayed Lampmussel
Lampsilis ovata (Say, 1817)	Pocketbook
Lasmigona subviridis (Conrad, 1835)	Green Floater
Quadrula quadrula (Rafinesque, 1820)	Mapleleaf
Toxolasma parvus (Barnes, 1823)*	Lilliput
Tritogonia verrucosa (Rafinesque, 1820)	Buckhorn

* - Not reported from study areas

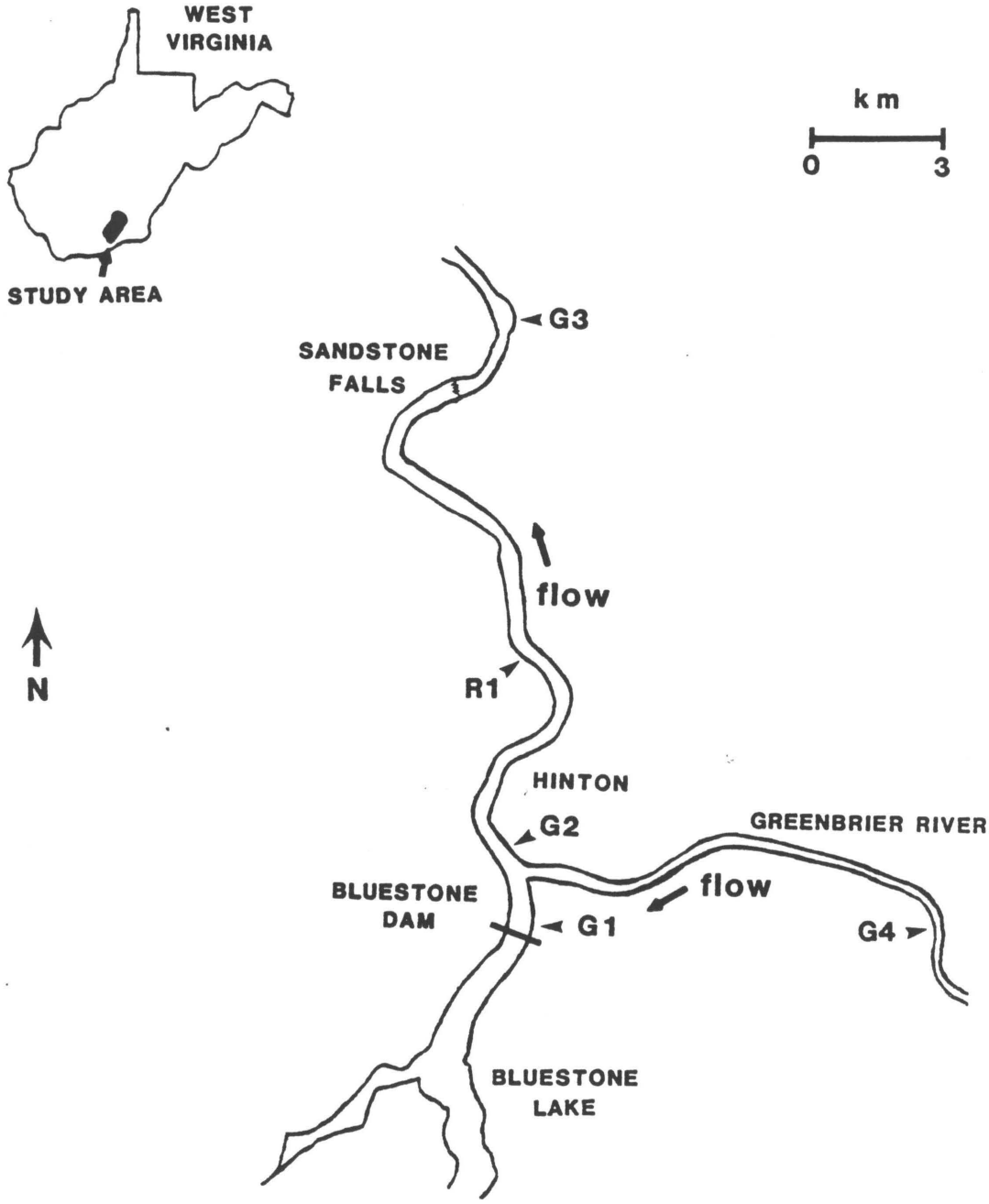


Figure 1. Collection sites fo specimens used for descriptions of reproductive biology (R) and growth comparisons (G) in the New River and Greenbrier, West Virginia.

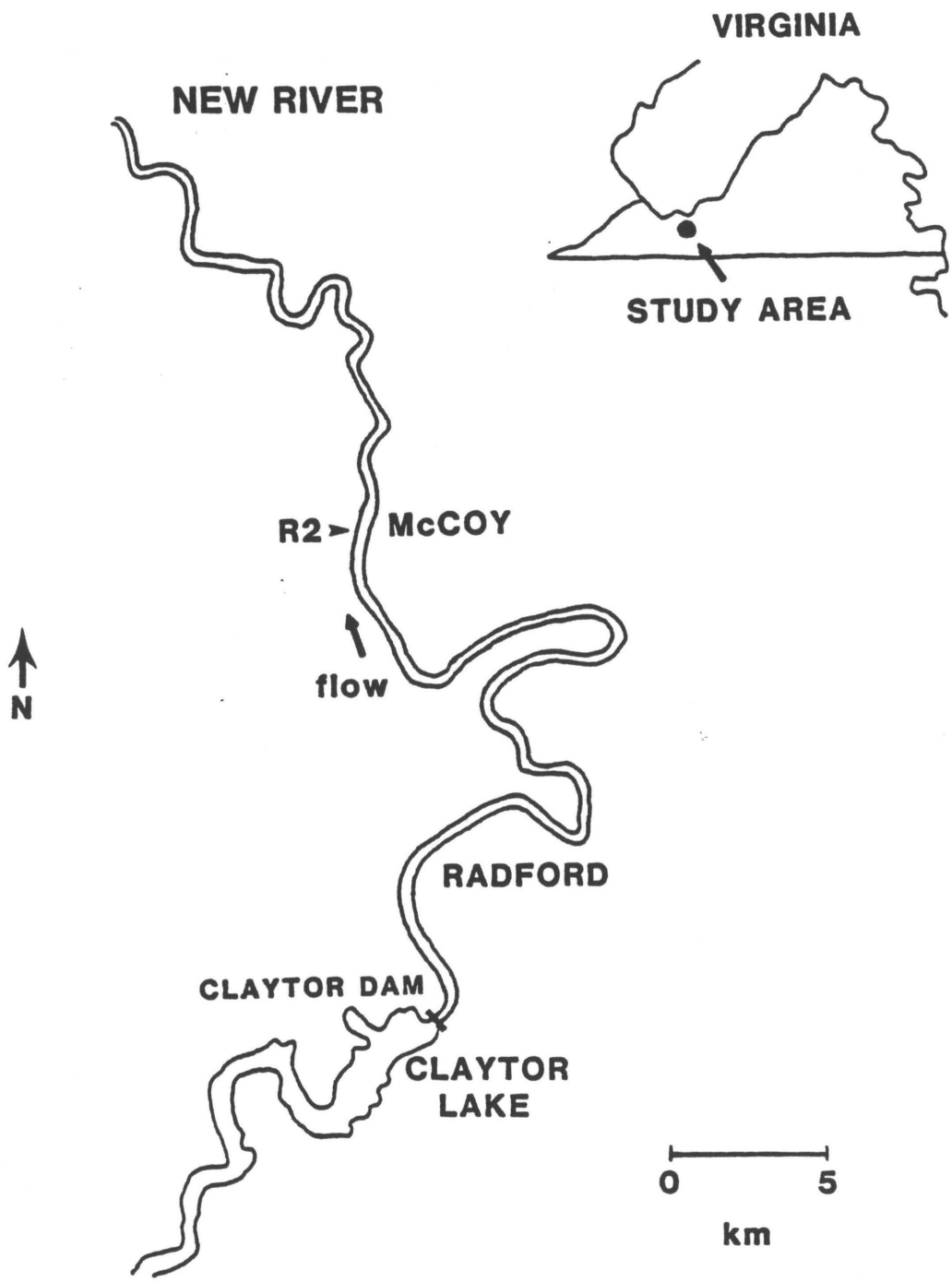


Figure 2. Collection site of specimens used for reproductive biology descriptions in the New River, Virginia.

and the substrate was predominantly sand and gravel interspersed with bedrock. Collections were only made at this site when adequate samples could not be obtained from the site in West Virginia.

Three collection sites associated with the growth component of this study also were located in the New River (Figure 1). One site (G1) (latitude 37°40'N, longitude 80°53'W) consisted of a 700 x 200 m area located immediately below Bluestone Dam and adjacent to the Army Corps of Engineers Park at the base of the dam. Substrate consisted primarily of bedrock interspersed with gravel and cobble. Depth ranged from 0.2 to 0.5 m. Another site (G2) (latitude 37° 40'N, longitude 80°54'W) was situated along the east bank approximately 3.2 km downstream of Bluestone Dam and consisted of a 70 x 30 m section of river with a sand-gravel substrate and a depth of 0.3 to 0.7 m. A third site (G3) (latitude 37° 46'N, longitude 80°53'W) was located approximately 18.5 km below Bluestone Dam. This site was roughly 200 x 50 m, with a substrate of gravel and cobble interspersed with small boulders and a depth of 0.4 m. One collection site (G4) (latitude 37°38'N, longitude 80°48'W), associated with the growth component of this study, was located in the Greenbrier River, approximately 8.0 km above its confluence with the New River. This site consisted of a 1.0 km long section of river with a substrate of gravel, cobble, and sand, and a depth of 0.3 to 0.6 m.

Reproductive Biology

The reproductive biology of four mussel species, Actinonaias carinata, Cyclonaias tuberculata, Elliptio dilatata, and Tritogonia

verrucosa, was described with respect to gametogenic activity, timing and length of spawning and glochidial release periods, and age at sexual maturity. Collections of six mussels of each species were made monthly from August 1984 through February 1985, and approximately every two weeks from March 1985 to July 1985 (Table 2). All collections were made at R1 in the New River in West Virginia, with the exception of those made from December through March. During this period, insufficient numbers of some species were collected at this site, and the balance of the samples was taken from R2 in Virginia. Specimens were collected by snorkeling or by handpicking with the use of waterscopes. An attempt was made to collect equal numbers of each sex and represent as wide a range of size classes as possible. Mussels were transported to the laboratory in mesh bags immersed in river water or packed in crushed ice. Water temperatures below Bluestone Dam for the period of 30 August 1984 through 5 July 1985 were obtained from J. R. Voshell, Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia. These data were used to determine the range of temperatures during which spawning and glochidial releases occurred.

Gametogenic Cycle

Methods for describing gametogenesis and early life history phases closely followed those of Zale and Neves (1982a) and Weaver (1981). Mussels brought into the lab were placed in plastic tubs of water containing the relaxant propylene phenoxitol (Inolex Corp., Philadelphia,

Table 2. Collection sites, dates, and numbers of mussels obtained for histological examination from the New River, Virginia and West Virginia.

		No. of Specimens			
Date	Site	A. carinata	C. tuberculata	E. dilatata	I. verrucosa
8-3-84	R1	6	6	6	6
9-3-84	R1	6	6	6	6
10-7-84	R1	6	6	6	6
11-2-84	R1	6	6	6	6
12-7-84	R1	6	-	-	-
12-10-84	R2	-	6	1	6
1-16-85	R1	6	2	-	2
1-19-85	R2	-	-	6	4
1-25-85	R1	-	4	-	-
2-17-85	R1	6	3	1	2
2-18-85	R2	-	-	-	4
2-21-85	R2	-	3	5	-
3-17-85	R1	6	-	1	-
3-20-85	R2	-	6	5	6
3-30-85	R1	6	6	2	1
3-31-85	R2	-	-	4	5
4-15-85	R1	6	6	6	6
4-29-85	R1	6	6	6	6
5-12-85	R1	6	6	6	6
6-3-85	R1	6	6	6	6
6-14-85	R1	6	6	6	6
7-3-85	R1	6	6	6	6
Total		90	90	85	90

PA 19148). Once relaxed, specimens were fixed in 10 percent buffered (sodium borate) formalin and preserved in 70 percent ethyl alcohol. A portion of gonadal material from each mussel was excised with a scalpel, dehydrated in a series of alcohol baths, cleared with xylene, and imbedded in paraffin (Humason 1979). Serial sections 7-µm thick were cut from each gonadal mass with a microtome and affixed to glass slides. Slides were stained with Heidenhain's iron hematoxylin and eosin-orange G using standard staining procedures (Humason 1979). Prepared slides were examined under a compound microscope at 40 to 200x to determine the sex and state of gametogenic development of each mussel. Timing and length of spawning period for each species were determined by identifying the period between the first collection of mussels containing mature gametes and the last collection of mussels lacking sex products, indicating release of gametes.

The age at which individuals of each species become reproductively active was estimated by determining the age of the youngest individual of each species that exhibited development of gametic material, based on histological examinations. Ages of the smallest (assumed to be the youngest) specimens of each species were determined by counting growth rings on the exterior of the shell. External growth ring counts were used in place of shell thin-sectioning since counting external lines is less time consuming and comparable in accuracy to thin-sectioning estimates for mussels less than ten years old (Moyer 1984).

Differentiation of Glochidia

Differentiation of the glochidia of mussel species in the New River was necessary in order to determine periods of glochidial release for the different species. Measurements of length, width, and hinge length of the glochidia of A. carinata, E. dilatata, C. tuberculata, T. verrucosa, Lampsilis ovata, and L. fasciola were made on 50 glochidia removed from gravid females of each species to describe morphometrics and identify the glochidia of each species (Figure 3). Glochidia of the anodontines Lasmigona subviridis, Anodonta grandis, and Alasmidonta marginata were not included in this analysis, since the glochidia of this subfamily are easily distinguished from those of other subfamilies by their size and shape. Quadrula quadrula was ignored since the report of this species from the New River is likely erroneous. A Kruskal-Wallis test was performed to test for differences among species, and an LSD procedure using ranks was used to determine which species differed from the others.

Glochidial Release

Timing and length of the glochidial release period for each mussel species were determined in two ways. Stream drift samples were taken concurrently with mussel collections, except that no drift samples were collected from December 1984 through February 1985. All drift samples were collected at site R1 in West Virginia between 10:00 a.m. and 4:00 p.m.. A square-framed drift net (45 cm/side) of 130 micron mesh with a

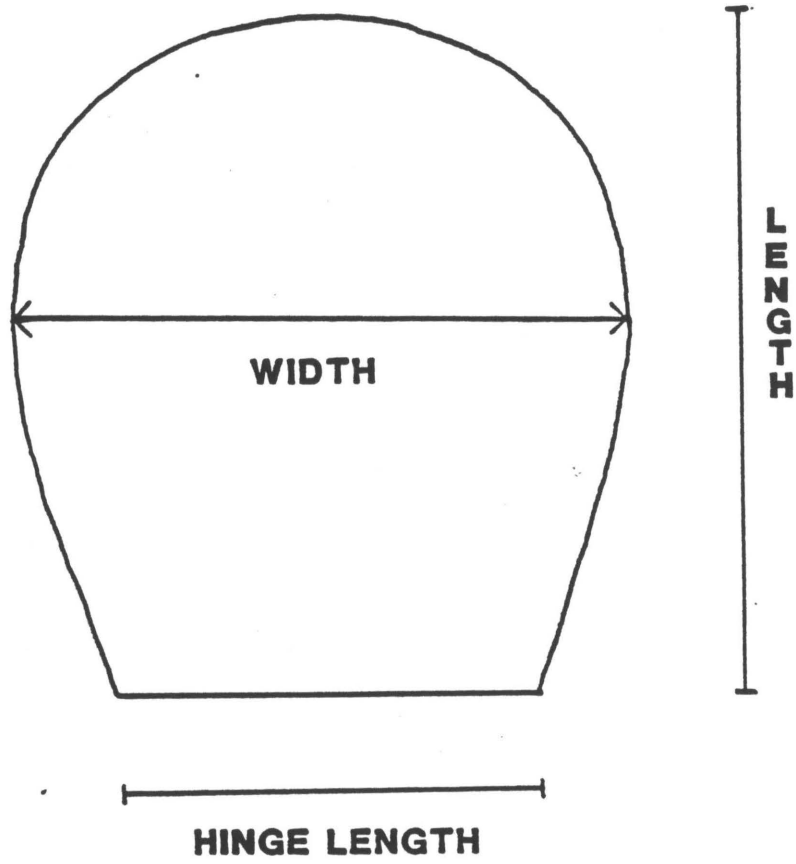


Figure 3. Length, width, and hinge length dimensions of a glochidium.

removable cod end was placed below the collection site for 30 to 45 minutes. Drift samples were preserved in 10 percent buffered formalin, with rose bengal added to facilitate sorting of glochidia from other material. Large particulate matter was removed by filtering the samples through a 0.5 mm nylon mesh. The remainder of each sample was examined using a dissecting microscope, and glochidia were removed with a capillary tube, identified to species, and enumerated. Current velocities at the mouth of the drift net were recorded using a pygmy current meter to determine volume filtered and hence the density of glochidia per m^3 of water filtered. Periods of glochidial release were identified in part by noting the presence or absence of species in the drift.

Glochidial release periods were also monitored by inspecting the marsupial gills of collected mussels. Gills that appeared gravid (indicated by swelling or beading) were punctured with a sharp probe, and the contents were removed and examined microscopically. Stage of glochidial development was recorded for each gravid female. The period of time between the first collection of gravid females with fully developed glochidia and the last collection of such females was identified for each species. An estimate of the timing and length of glochidial release was made by integrating this information with results obtained from drift samples.

An attempt was made to identify potential fish hosts for the different mussel species by examining the gills of fish for glochidial infestations. Fish were collected via electrofishing in the vicinity of mussel beds during times of the year when glochidia were known to be in the drift. Collected fish were either anesthetized with benzocaine (4% ethyl p-amino

benzoate in acetone) and inspected visually at the site or were preserved in 10 percent buffered formalin and inspected visually in the laboratory.

Growth Comparisons

Three collection sites were established below Bluestone Dam to obtain specimens of *C. tuberculata* for comparison of growth characteristics of downstream subpopulations. A fourth site was situated in the Greenbrier River to determine possible influences of this river on growth of mussels below its confluence with the New. Thirty specimens were collected from each site and transported to the laboratory in mesh bags immersed in river water. Collections were made in August and September 1985, well after the period of annulus formation (Moyer 1984); lengths of collected specimens spanned the size ranges at each site. In the lab, mussels were sacrificed, the visceral mass was removed, and debris was cleaned from the shell surface. Length of each shell, defined here as the longest anterior to posterior axis of the shell, was measured to the nearest tenth of a millimeter. Weight of air-dried shells (both valves) was measured to the nearest tenth of a gram.

Shell Aging

Shells were aged using thin-sectioning techniques similar to those described by Clark (1980) and Moyer (1984). Shells were thin-sectioned using a Buehler Isomet low speed diamond-tipped saw (Buehler Ltd., Evanston, IL 60204). On smaller shells, an initial cut was made along

the longest axis from the umbo to the shell margin and perpendicular to the external growth lines to obtain a shell cross-section containing all internal growth increments (Figure 4). Cross-sections were mounted on petrographic micro-slides (27 x 46 mm) using epoxy cement (Buehler epo-kwick). Mounted shells were secured on a vacuum-sealed chuck connected to a movable arm on the saw and sectioned to a thickness of 0.28 mm (0.011 in). Thin-sections were viewed under a compound microscope at 40x and 100x, and annual growth lines were counted to determine the age of each specimen (Figure 5).

Shells that were too large to fit on 27 x 46 mm petrographic slides required additional processing before cross-sections were cut. For these shells, initial cuts were made with a hacksaw and/or chisel to a size that would allow them to fit in the chuck for cross-sectioning. Thin-sections of these shells did not contain all internal growth lines in their entirety; however, at least a portion of all internal growth increments was present within each thin-section.

Growth Determination

Growth was described using weight-at-age and length-at-age data. Weight-at-age data consisted of dry weight of both valves at age of death. Length-at-age data consisted of total length-at-age data (length of shell at age of death) and back-measured length-at-age data. Back-measured lengths-at-age were obtained using the thin-section of a shell to identify external annuli on the cross-sectioned valve. The cross-sectioned valve was then overlayed on the uncut valve to locate each external annulus on

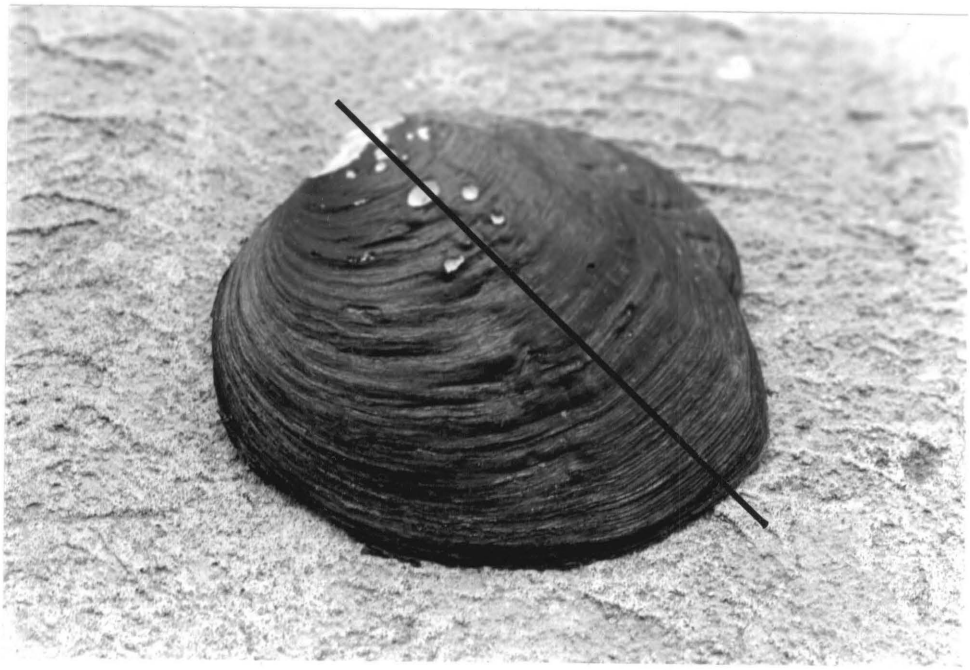


Figure 4. Photograph illustrating axis along which shell thin-sections were made.

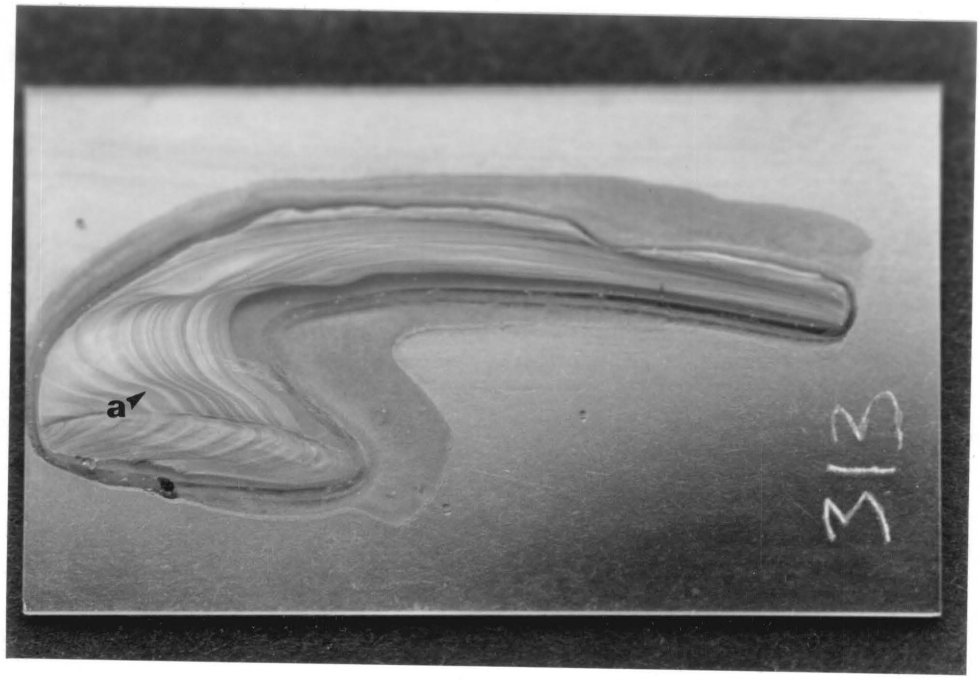


Figure 5. Example of a shell thin-section showing annuli (a) within the shell.

the whole valve. The maximum anterior to posterior length at each annulus was recorded to the nearest tenth of a millimeter. Back-measured lengths were recorded for seven to ten specimens from each study site, depending on the number of specimens in suitable condition. Back-measured lengths were not taken on highly eroded specimens with obliterated external growth increments, and were taken only for annuli that were easily distinguished, usually those representing the first ten years of growth.

Linear correlation procedures were used to describe weight-age relationships. Growth rates of the subpopulations, as described by mean annual increment of shell weight (g/yr) for all specimens collected from each site, were compared statistically using a Kruskal-Wallis test for differences among sites, and an LSD procedure using ranks was used to determine site differences. Length-age relationships were described by fitting the data to a modified version of the von Bertalanffy growth equation:

$$L_t = (w/k)(1-e^{-k(t-t_o)})$$

where t is a given time in years, t_o is the theoretical time when length is zero, k is a growth coefficient describing the rate at which length (L) approaches the theoretical maximum length (L_∞), and w corresponds to the growth rate near t_o (Gallucci and Quinn 1979). The parameter w is equal to the product of k and L_∞ and is used in the equation in place of L_∞ to eliminate the effect of the interdependency of the parameters k and L_∞. This parameter (w) is more robust statistically than either of the

individual parameters and therefore is more suitable for statistical comparisons (Gallucci and Quinn 1979).

Non-linear statistical procedures of the Statistical Analysis System (SAS Institute 1982) were used to derive estimates, approximate standard errors, and 95 percent confidence intervals for w, k, and t_0 for each subpopulation. Based on these values, estimates and 95 percent confidence intervals were calculated for L_∞. Confidence intervals of the three parameters for each subpopulation were compared for overlap to test for differences in growth characteristics between subpopulations.

Data describing the quantity and quality of seston in the Greenbrier River and at several locations in the New River below Bluestone Dam were obtained from the literature (Voshell 1985a). These data were used to determine if any observed patterns in mussel growth were correlated with food abundance. Collection of seston data was conducted at stations close to sites G1 to G4, and are believed to be representative of seston availability at the four sites.

RESULTS

Gametogenic Cycle

Histological sections of gonadal material were made from tissues of 90 Actinonaias carinata, 85 Elliptio dilatata, 90 Cyclonaias tuberculata, and 90 Tritogonia verrucosa. Sex ratios were approximately 1:1 for A. carinata and E. dilatata (Table 3). Males constituted a much greater proportion of the sample than females for C. tuberculata and T. verrucosa. Several specimens of E. dilatata and T. verrucosa collected during the winter could not be sexed confidently due to the absence of well-defined reproductive structures. The majority of these specimens were collected at site R2 in Virginia. Since their condition was not synchronous with that of other individuals collected from this site or R1 in West Virginia, these specimens were considered atypical and were not included in descriptions of reproductive cycles.

Onset of gametogenesis in both sexes of Actinonaias carinata occurs in the early fall. By November, male acini had enlarged, and proliferation of spermatogonia was evident (Figure 6). Males with acini containing predominantly spermatogonia, spermatids, and nutritive structures were collected in December (Figure 7). This condition persisted in all males collected through May. Spermatids were numerous in the testes by early June, and by late June, sperm were present in all males collected. Sperm dominated acini of males collected in July (Figure 8), and spawning

Table 3. Numbers and sex of mussel species collected from the New River, Virginia and West Virginia, for histological examination of gonads.

Species	Males	Females	Unknown	Total
Actinonaias carinata	48	41	1	90
Elliptio dilatata	37	40	8	85
Cyclonaias tuberculata	54	34	2	90
Tritogonia verrucosa	43	33	14	90

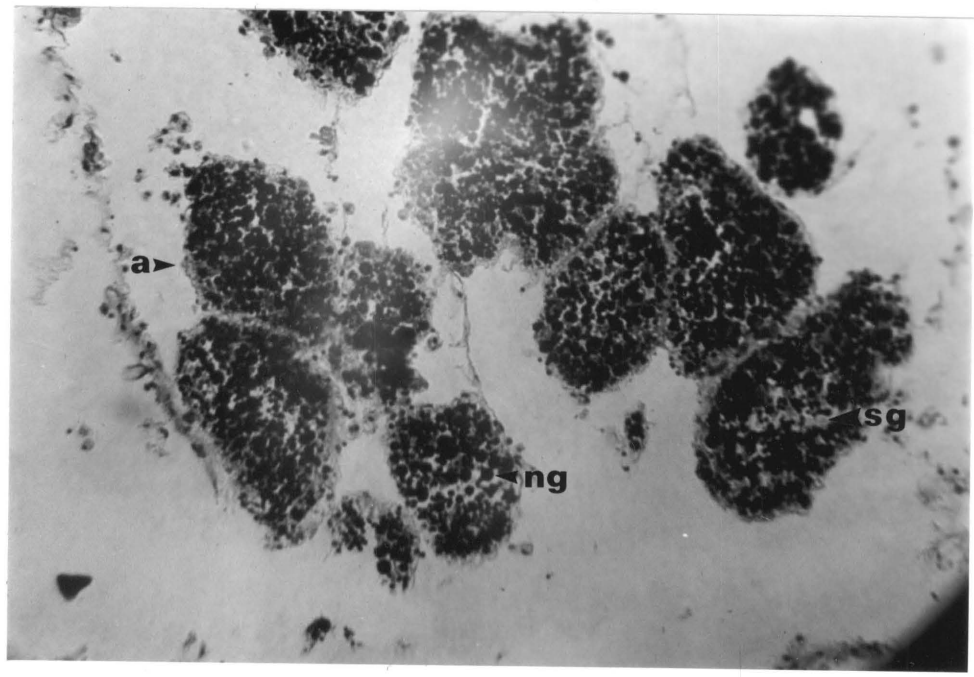


Figure 6. Gonadal section of a male Actinonaias carinata with acini (a) containing nutritive granules (ng) and spermatogonia (sg).

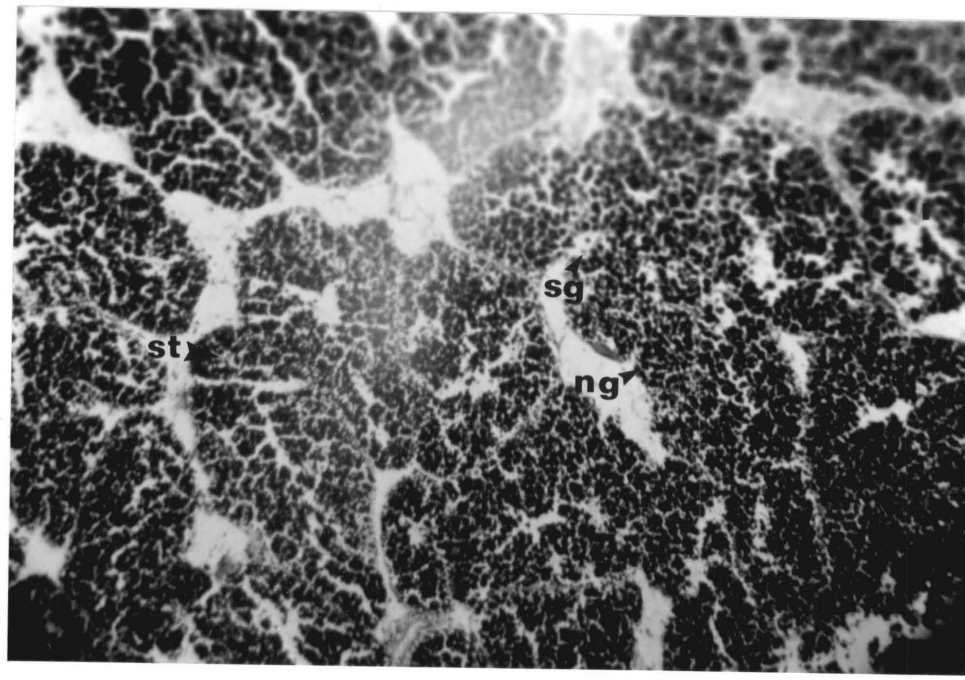


Figure 7. Gonadal section of a male Actinonaias carinata showing spermatids (st), spermatogonia (sg), and nutritive granules (ng).

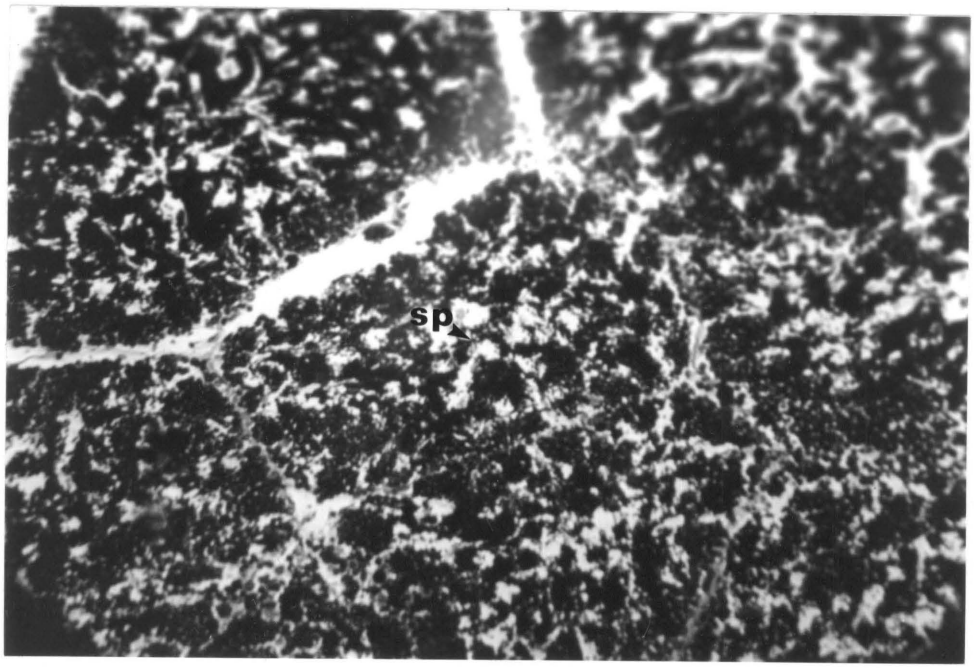


Figure 8. Gonadal section of a male Actinonaias carinata showing sperm (sp) occupying the acini.

and spawned males, indicated by a reduction or near total lack of sperm in the acini, were collected in August (Figure 9). Water temperatures during spawning ranged from 22 to 25 ^{o}C (Figure 10). By September, acini were constricted and widely spaced, containing predominantly nutritive granules and few, if any, residual sperm (Figure 11).

Oogenesis in female Actinonaias carinata began in early October with reformation of widely spaced alveoli containing rudimentary eggs (Figure 12). Ovarian tissues remained in this state from October until June. By late June, alveoli had enlarged, and ova were better defined, though nutritive structures still constituted the bulk of the material within the alveoli (Figure 13). Alveolar walls became thin, and large, mature ova occupied the lumina by July (Figure 14). Spawning in females began once water temperatures reached 22^{o}C. Release of eggs was evident in females collected in July and August, as indicated by alveoli largely devoid of ova and wide spaces between those alveoli still containing eggs in the lumina (Figure 15). Release of eggs was usually not complete. Alveoli in females collected in September were constricted and widely spaced, with many containing remnants of unreleased ova (Figure 16).

Gonadal activity in Elliptio dilatata, Cyclonaias tuberculata, and Tritogonia verrucosa differed from that observed for Actinonaias carinata. Spermatogenesis in E. dilatata began with the reformation of acini in August. Gametogenesis proceeded rapidly, and by September, sperm were abundant in the acini of a portion of the males collected. Other males collected during this period had well-developed acini exhibiting proliferation of spermatogonia. Testes of E. dilatata collected in October and November were characterized by closely packed acini crowded with

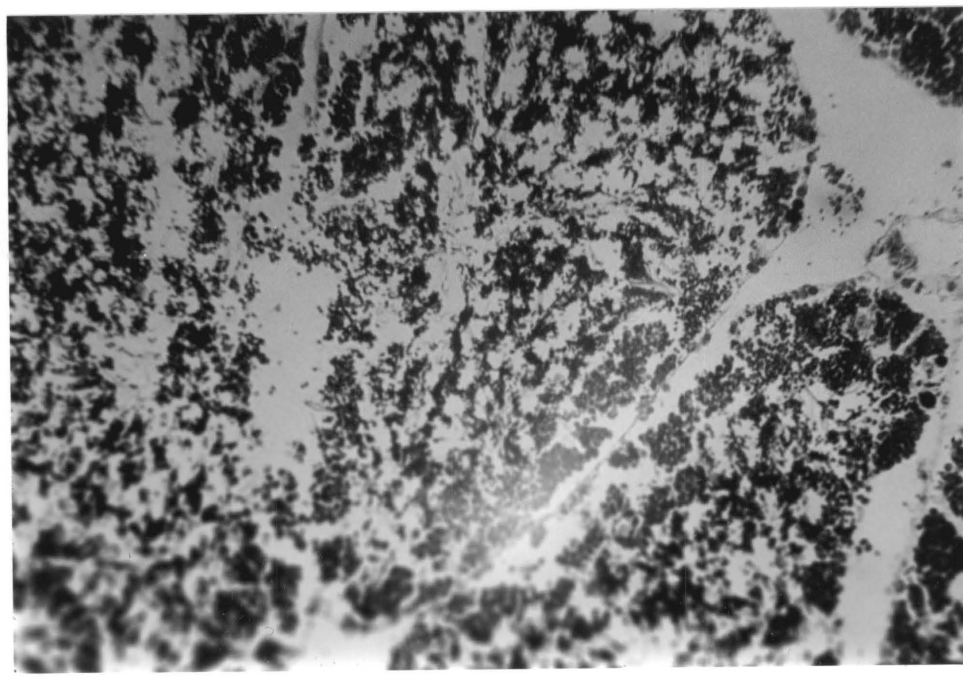


Figure 9. Gonadal section of a spawning male Actinonaias carinata as indicated by reduction in the density of sperm within the acini.

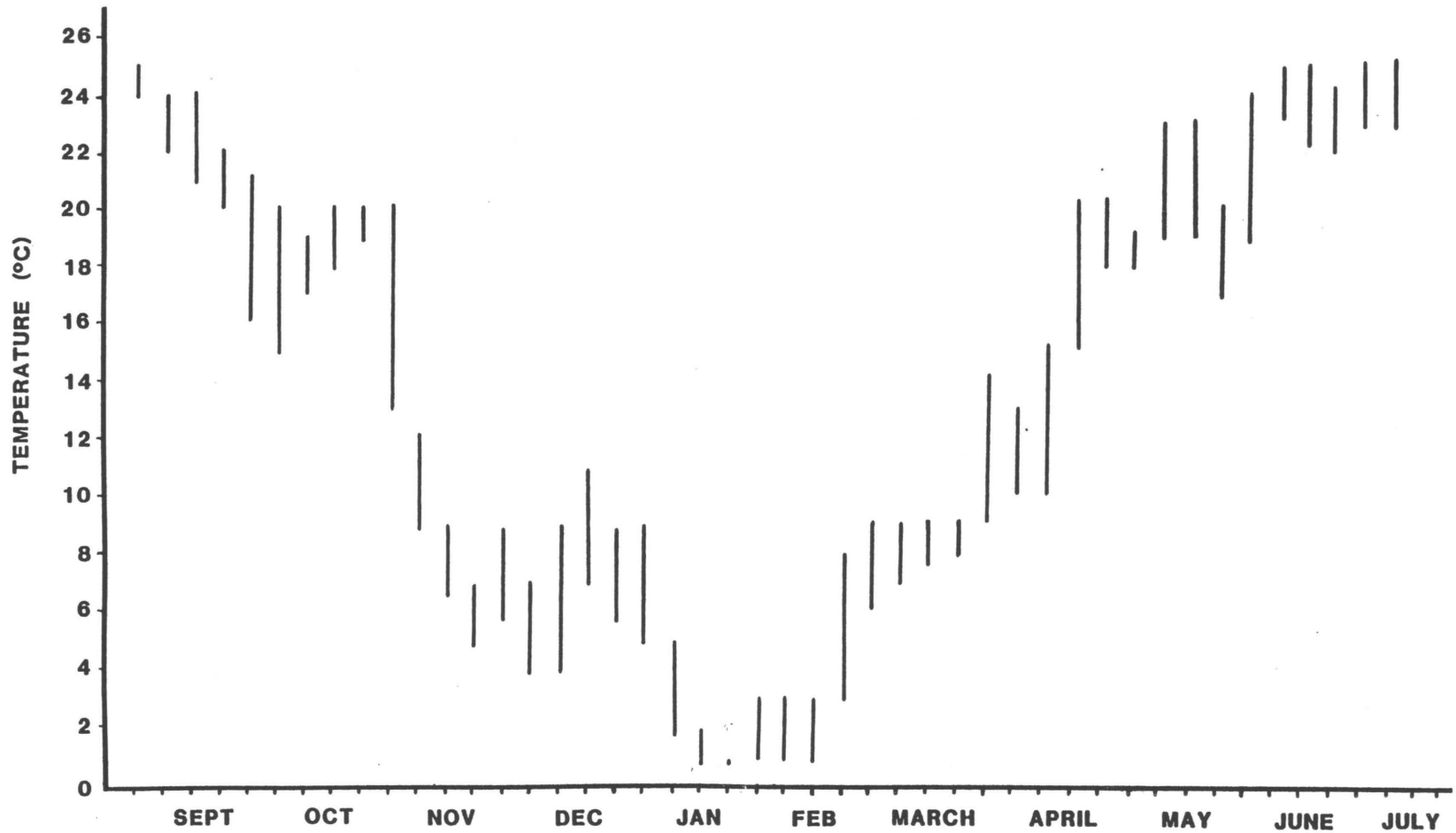


Figure 10. Weekly water temperature ranges (°C) in the New River below Bluestone Dam from August 31, 1984 to July 5, 1985.

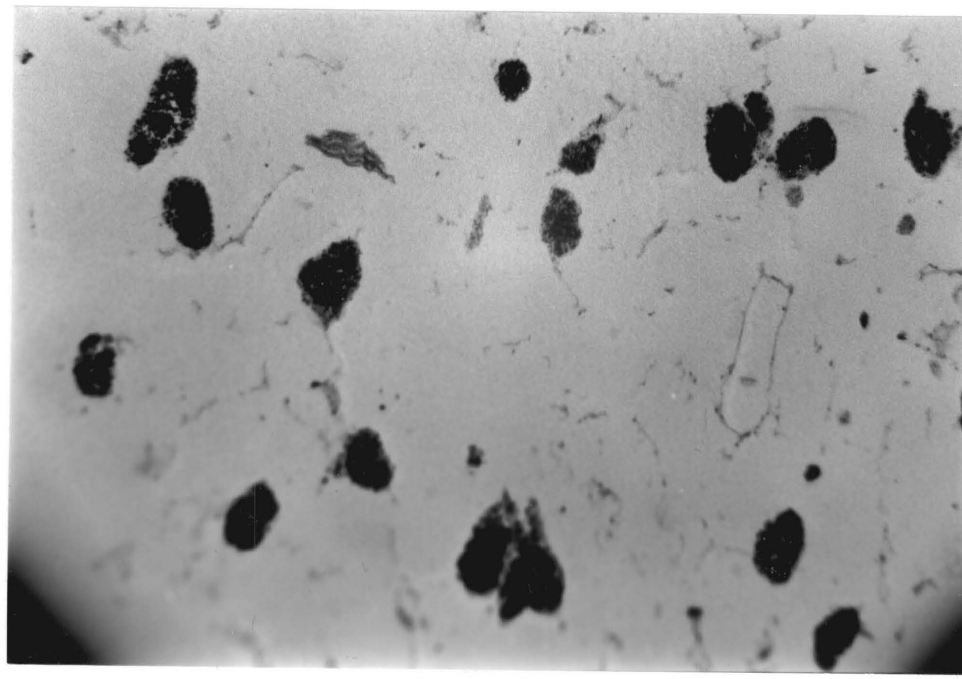


Figure 11. Gonadal section of a male Actinonaias carinata in a post-spawn, reproductively inactive condition.

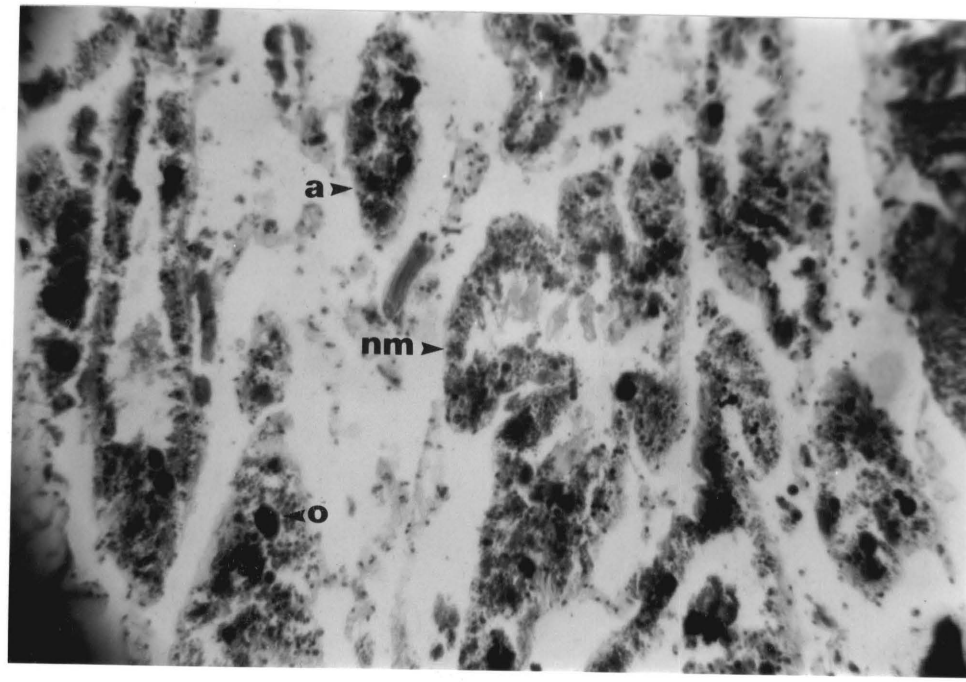


Figure 12. Gonadal section of a female Actinonaias carinata with alveoli (a) containing rudimentary ova (o) and nutritive material (nm).

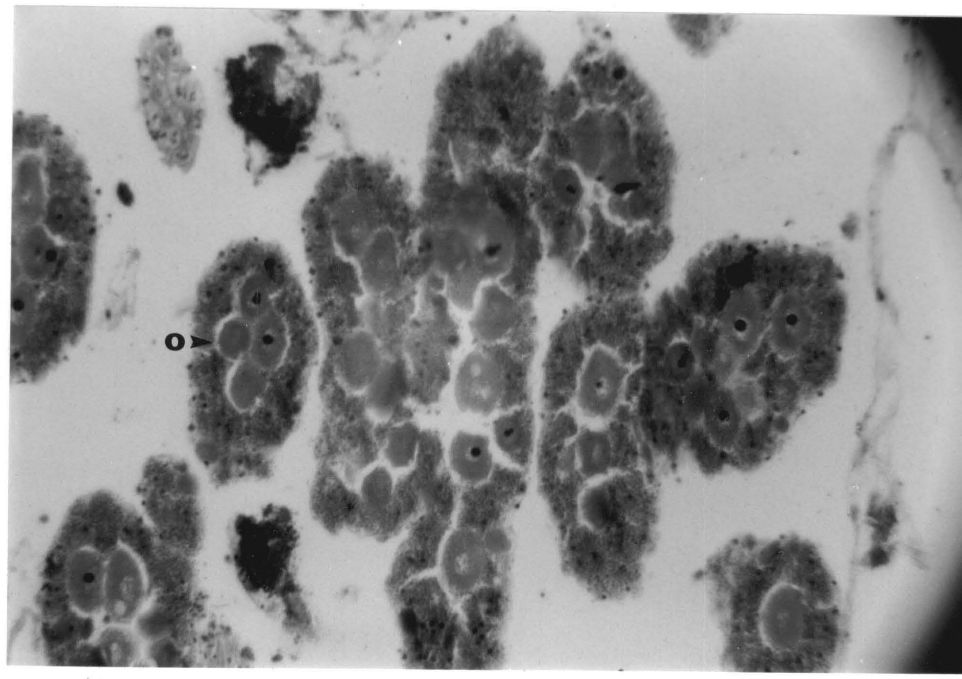


Figure 13. Gonadal section of a female Actinonaias carinata with alveoli containing enlarged ova (o).

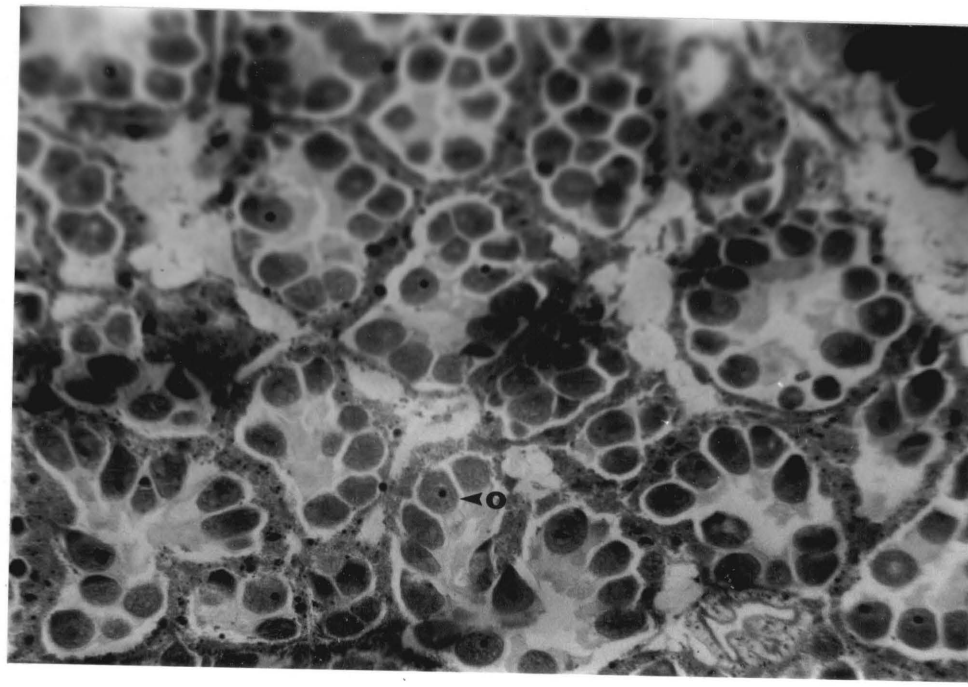


Figure 14. Gonadal section of a female Actinonaias carinata with tightly packed alveoli containing fully developed ova (o).

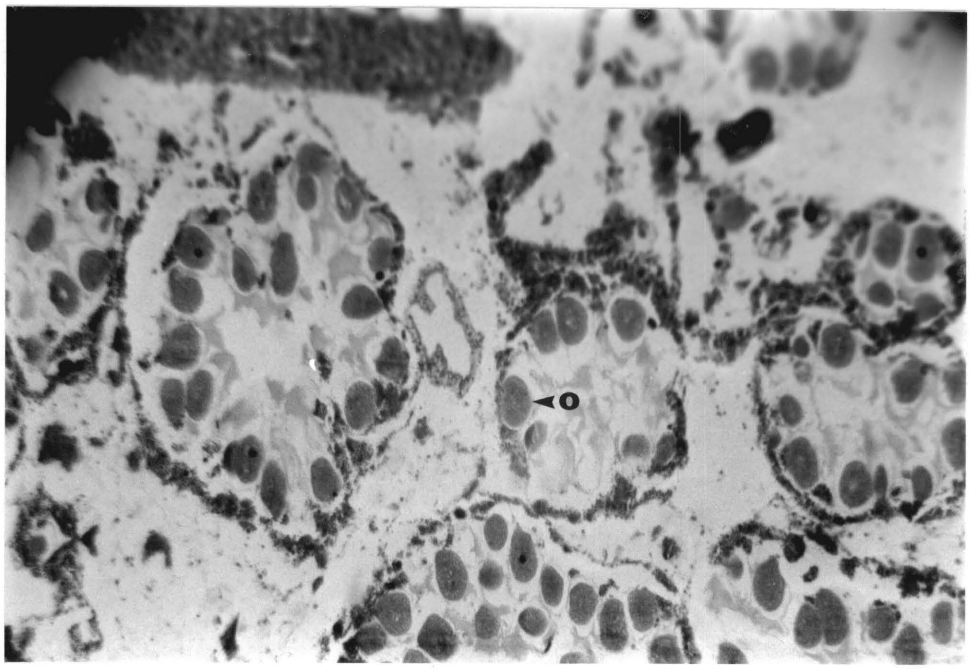


Figure 15. Gonadal section of a spawning female Actinonaias carinata showing a reduction in the density of ova (o) within the alveoli and increased spacing among alveoli.

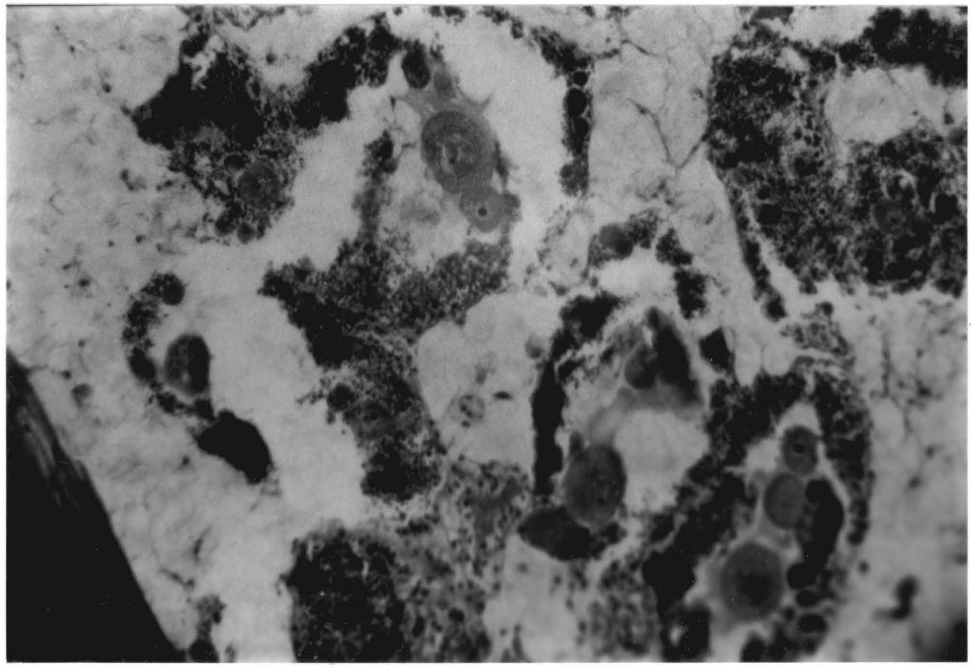


Figure 16. Gonadal section of a spawned, reproductively inactive female Actinonaias carinata.

apparently mature sperm. A lack of suitable male specimens for December through February precludes definitive descriptions of gametic activity for this period; however, male E. dilatata collected in March were similar in gonadal condition to specimens collected in November. Apparently, gonadal activity was suspended during the winter, and males overwintered with acini packed with mature sperm. Males with acini containing numerous sperm were collected into July. Acini largely devoid of sperm, indicating spawning had occurred, were first observed in males collected in late March when water temperatures reached 9 °C. Males in this spent condition were collected into July. By August, acini in males again were widely spaced and constricted, containing few unreleased sperm.

The onset of gonadal activity in female Elliptio dilatata occurred in August and September with enlargement of alveoli and development of rudimentary ova within the alveolar walls. By October, alveolar walls had degenerated, nutritive material was reduced in abundance, and nearly mature ova occupied the lumina. Fully developed eggs were present in the lumina as early as November. Suitable specimens of female E. dilatata were not obtained for December and January, but females collected in February were in a condition similar to that observed in November, and apparently overwintered in this state. Females with thin-walled alveoli filled with mature ova were collected into June. Spawning in females began when water temperatures reached 10° C. Spawning was evident from early April through June, as indicated by increased spacing between alveoli and a reduction and/or lack of mature ova in the alveolar lumina. In most cases, spawning was incomplete, with several gravid females being collected that still contained numerous alveoli filled with apparently

mature ova. By July, alveolar walls had collapsed, and remaining ova appeared to be in the process of resorption.

Gonadal activity in Tritogonia verrucosa and Cyclonaias tuberculata paralleled that observed in Elliptio dilatata with only minor differences in spawning periods. T. verrucosa began spawning in March and continued through May. Spawning in C. tuberculata occurred from early March through June. Development of ova in C. tuberculata proceeded more slowly than in the other two species in the fall, but reached the same condition found in E. dilatata and T. verrucosa by February.

Sexual maturity was reached between the third and fifth years of life in both sexes of A. carinata. One age 2 (in its third year of life) specimen, 26.1 mm in length, was collected and showed no evidence of gonadal activity. Two age 4 specimens (58.5 mm and 64.1 mm), one of each sex, were found to be reproductively active. The youngest E. dilatata collected (age 4, 49.7 mm) was a reproductively active female. No males of similar age were collected, but all males older than this specimen had reached sexual maturity. One age 3 (37.3 mm) T. verrucosa was collected and showed no evidence of gametogenic activity. The youngest reproductively active individual of this species was age 6 and 53.5 mm long. Two age 5 T. verrucosa, one of each sex, were collected in December and were just beginning to show signs of sexual differentiation. The youngest specimens of C. tuberculata collected were a sexually mature age 6 female (58.6 mm) and a sexually mature age 10 male (69.8 mm).

Trematode infestations of the gonads were observed in several specimens of A. carinata and E. dilatata (Figure 17). Nearly 16 percent of the A. carinata and 5 percent of the E. dilatata collected were

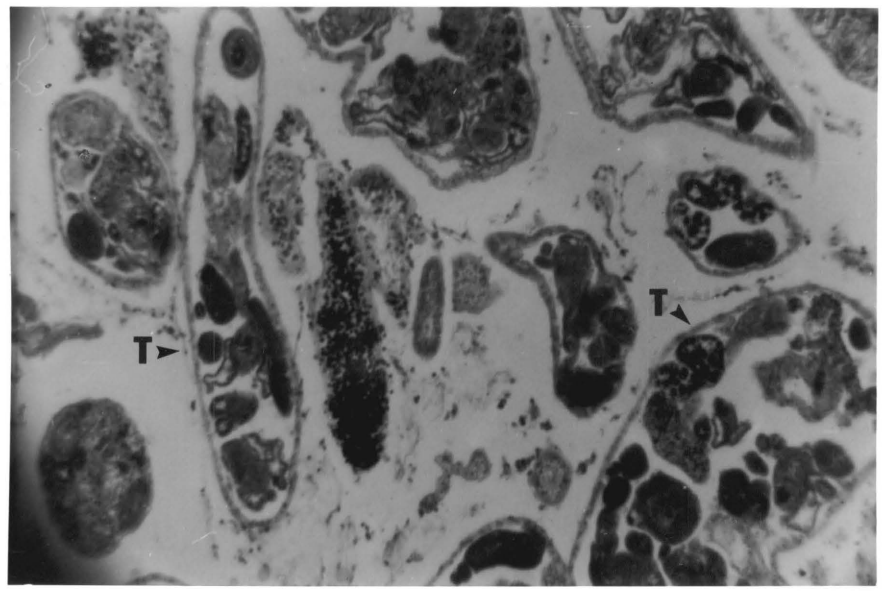


Figure 17. Gonadal section of a male Actinonaias carinata showing trematode (T) infestation.

parasitized. Infestations were usually severe, with the majority of the visceral mass being occupied by parasites and little gonadal material remaining in most affected specimens. Remaining gonadal material appeared to be functioning normally in most affected individuals, though an occasional specimen was reproductively atypical compared to the rest of the population. Generally, infestations were associated with A. carinata greater than 100 mm in length and E. dilatata greater than 80 mm; however, the majority of specimens exceeding these lengths were not parasitized. No trematode infestations were observed in C. tuberculata or T. verrucosa.

Hermaphroditism was observed in one specimen of E. dilatata. Gonadal examination revealed this specimen was functionally male, with occasional ova imbedded in typically male acini. No hermaphroditism was observed in A. carinata, C. tuberculata, or T. verrucosa

Differentiation of Glochidia

A Kruskal-Wallis test and LSD procedure using ranks indicated that measurements of length, width, and hinge length of glochidia all differed significantly ($p<0.001$ for all comparisons) among Actinonaias carinata, Cyclonaias tuberculata, Elliptio dilatata, and Tritogonia verrucosa (Table 4). Glochidia of these species were also statistically different from Lampsilis ovata and Lampsilis fasciola ($p<0.001$). Glochidia of T. verrucosa were easily distinguished from the other species based on size alone, since they were less than one half the size of the other species

Table 4. Dimensions (means and standard deviations) in millimeters of glochidia of selected species of freshwater mussels collected from the New River, West Virginia.

Species	n	Length		Width		Hinge Length	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
Actinonaias carinata	50	0.254	0.009	0.228	0.007	0.129	0.006
Elliptio dilatata	50	0.249	0.007	0.235	0.004	0.160	0.004
Cyclonaias tuberculata	50	0.355	0.007	0.294	0.006	0.133	0.006
Tritogonia verrucosa	50	0.122	0.003	0.109	0.003	0.049	0.003
Lampsilis fasciola	50	0.316	0.004	0.262	0.006	0.118	0.003
Lampsilis ovata	50	0.309	0.006	0.264	0.007	0.121	0.004

(Figure 18). C. tuberculata had the largest glochidia (Figure 19),and their relatively greater length to hinge length ratio and smoothly rounded outline allowed them to be easily distinguished from A. carinata and E. dilatata glochidia. The general shape and size of glochidia of A. carinata and E. dilatata were quite similar (Figures 20, 21); and differentiation of glochidia of these two species was difficult without taking measurements. Glochidia of these two species were most easily distinguished from one another on the basis of hinge length.

Glochidial Release

Glochidia were present in drift samples from August to September 1984, and from late March into July 1985 (Table 5). A. carinata glochidia were collected in the drift from March 30 to May 12, 1985, with the highest densities (64.4/100 m^3) occurring in late March. Glochidia of E. dilatata were present in drift samples collected in August and September 1984, and again from April 29 through July 3, 1985, with the exception of the May sample. Highest densities occurred in early June (56.3/100 m^3) and early July (19.8/100 m^3). T. verrucosa and C. tuberculata glochidia were collected only once in drift samples, in May and March, respectively. Pediveliger larvae of the Asiatic clam were also collected in the drift and were extremely abundant throughout most of the year.

Gravid females of Actinonaias carinata were collected from September 1984 through April 1985. Only the outer gill of this species was used for brooding purposes, and often only the posterior half of the gill

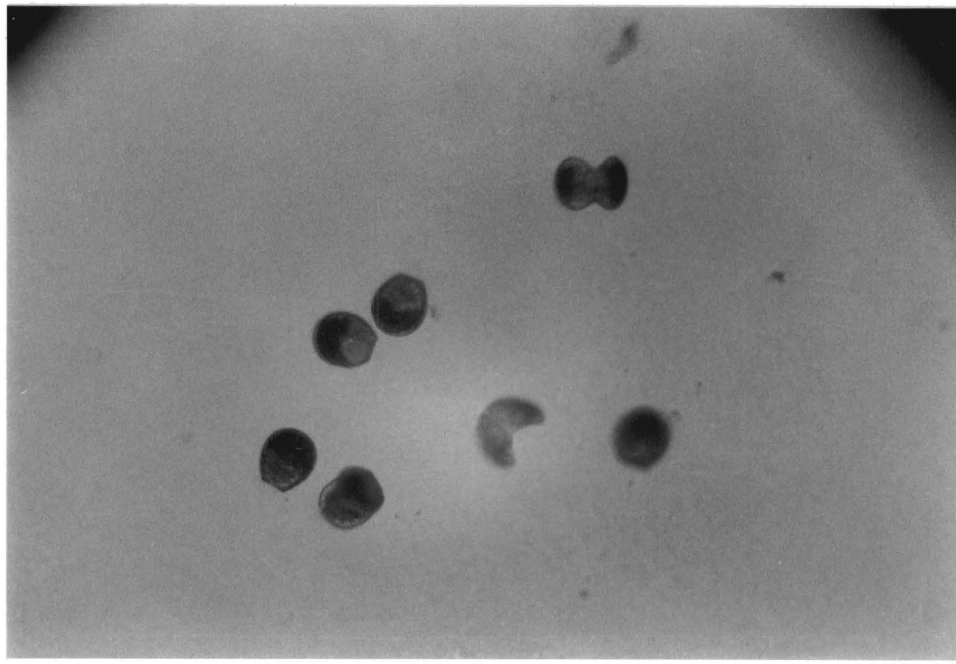


Figure 18. Glochidia of Tritogonia verrucosa.

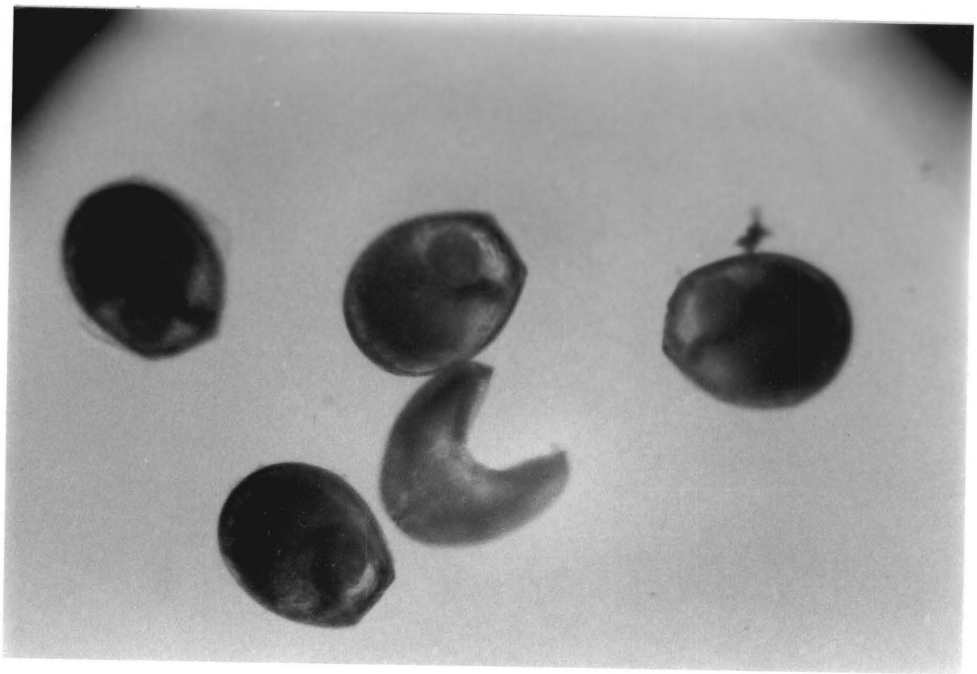


Figure 19. Glochidia of Cyclonaias tuberculata.

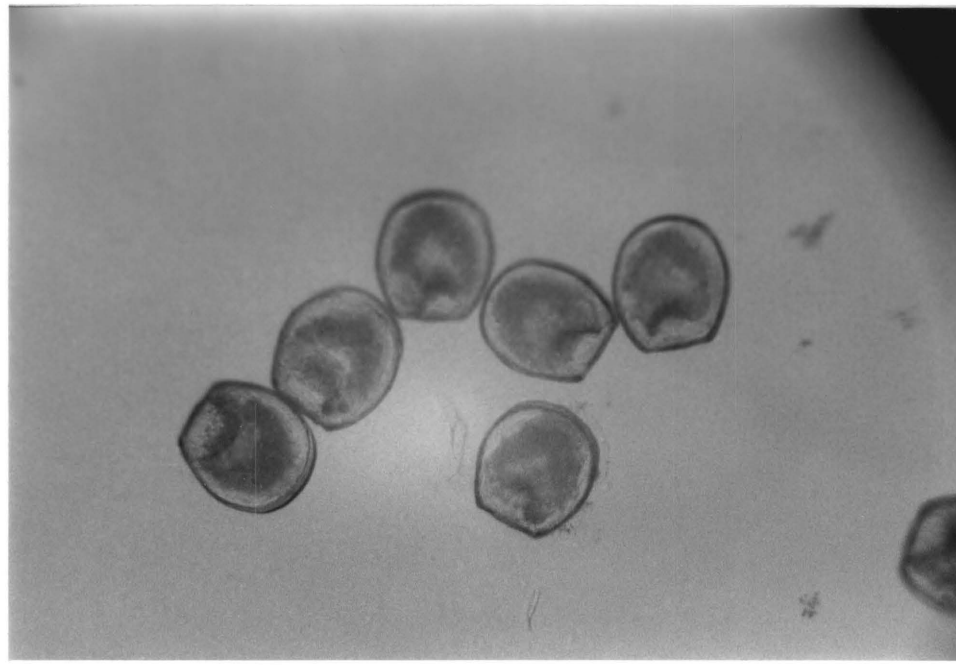
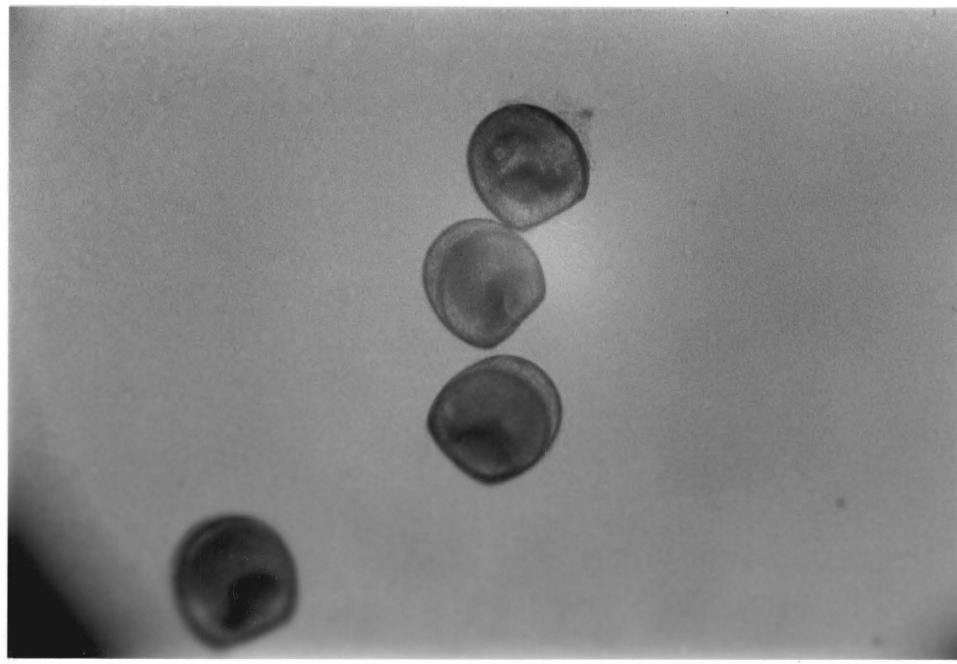


Figure 20. Glochidia of Actinonaias carinata.



200 µm

Figure 21. Glochidia of Elliptio dilatata.

Table 5. Densities (No./100 m^3) of glochidia of Actinonaias carinata, Elliptio dilatata, Cyclonaias tuberculata, and Tritogonia verrucosa and pediveligers of Corbicula fluminea in drift samples collected from the New River, West Virginia.

Date	Actinonaias carinata	Elliptio dilatata	Cyclonaias tuberculata	Tritogonia verrucosa	Corbicula fluminea
8/3/84	0.0	4.2	0.0	0.0	4170.5
9/3/84	0.0	0.5	0.0	0.0	5413.9
10/7/84	0.0	0.0	0.0	0.0	427.2
11/2/84	0.0	0.0	0.0	0.0	45.7
3/17/85	0.0	0.0	0.0	0.0	0.0
3/30/85	64.4	0.0	0.0	1.8	0.6
4/15/85	3.0	0.0	0.0	0.0	0.7
4/29/85	18.3	2.7	0.0	0.0	668.5
5/12/85	14.7	0.0	1.0	0.0	608.5
6/3/85	0.0	56.3	0.0	0.0	47.6
6/14/85	0.0	1.2	0.0	0.0	112.8
7/3/85	0.0	19.8	0.0	0.0	354.5

contained glochidia. Glochidia were not mature in females collected in September, but by October, marsupia contained fully developed glochidia. Marsupia of all female A. carinata collected from May through July were inflated and exhibited beading characteristic of gravid conditions. However, these marsupia were empty, indicating that glochidial release was relatively recent.

Elliptio dilatata females with inflated but empty marsupia were collected in mid-April, suggesting glochidial release had already occurred for these individuals. Gravid E. dilatata were collected from late April through early July, with mature glochidia present in the marsupia from May through July. Eggs and developing glochidia were found in the marsupia of some females as late as mid-June. Only the outer gills were used as marsupia in this species. Periods of gravidity of C. tuberculata and T. verrucosa were similar to that of E. dilatata. Females of these two species with swollen but empty marsupia were collected in mid-April, suggesting some glochidial release had already occurred. Gravid (outer gills only) C. tuberculata, containing eggs and developing glochidia, were collected from late April through June, and females brooding mature glochidia were first collected in May. T. verrucosa used both sets of gills as brooding chambers, and females with mature glochidia were found from late April through early June.

The onset of glochidial releases was associated with rising water temperatures. All four species began releasing glochidia once water temperatures reached 9° C in the spring, and continued releasing as temperatures increased. No releases of glochidia occurred while temperatures were dropping in the fall, though Actinonaias carinata contained

mature glochidia during this period. Though water temperatures began to increase from winter lows as early as mid-February, no glochidial releases were evident until late March when temperatures reached 9°C.

Fish collections made to identify species with natural infestations of glochidia proved unsuccessful. Several sampling efforts were conducted, but only one fish was collected with glochidia on its gills. Glochidia on this fish, a smallmouth bass (Micropterus dolomieui), were either A. carinata or E. dilatata, but a definitive identification could not be made. It is likely that these glochidia were A. carinata, since smallmouth bass are a known host for this species (Fuller 1974). Collection dates, species, and numbers of fish inspected are summarized in Appendix A.

Growth Comparisons

Age group distributions of specimens of C. tuberculata collected from sites G1 to G4 are presented in Figures 22 to 25. Specimens from G1 ranged in age from 17 to 61 years. Ages of specimens from G2 and G3 ranged from 11 to 37 and 14 to 36 years, respectively. The broadest range of ages, including the youngest (10 years) and the oldest (91 years) specimens, was collected at G4.

Linear correlation analyses of mean shell weight versus age for the four sites showed that the relationship is approximately linear over the range of ages sampled, except at G1 where the great variability exhibited by the data resulted in a regression line with a slope not significantly different from zero (Figures 26 to 29). Comparisons of annual increment

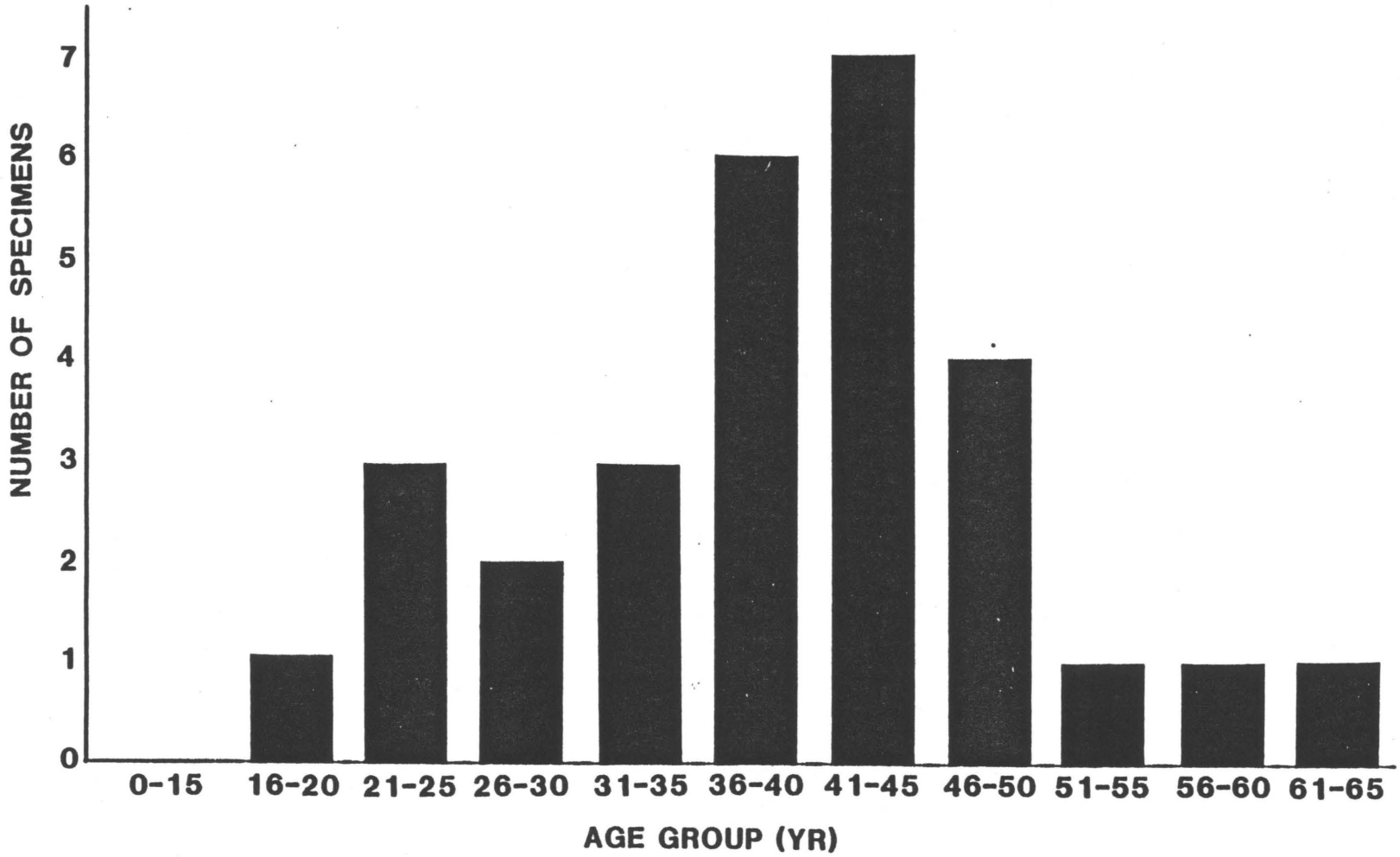


Figure 22. Age group distribution of Cyclonaias tuberculata collected at site G1 in the New River, West Virginia (N = 29).

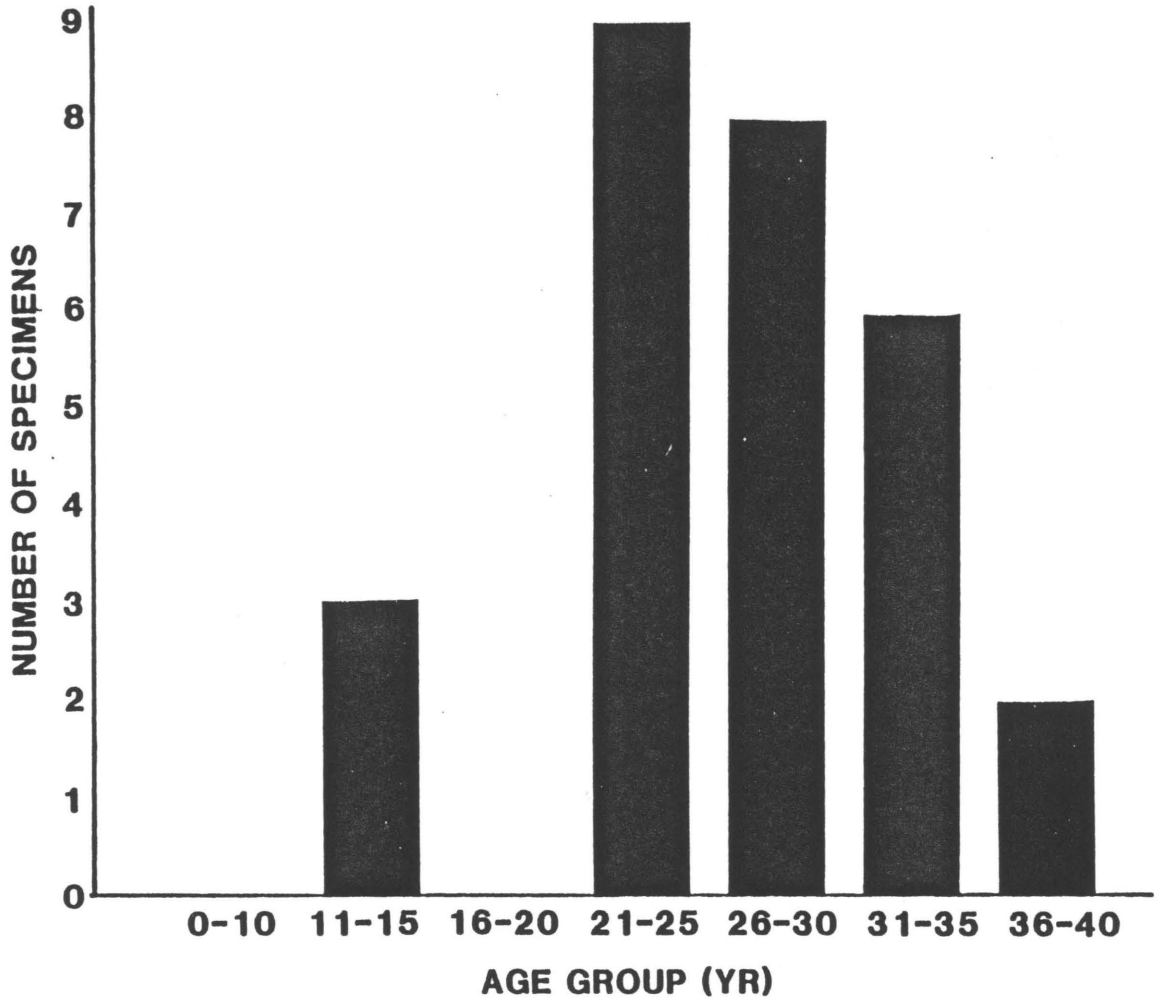


Figure 23. Age group distribution of Cyclonaias tuberculata collected at site G2 in the New River, West Virginia (N = 28).

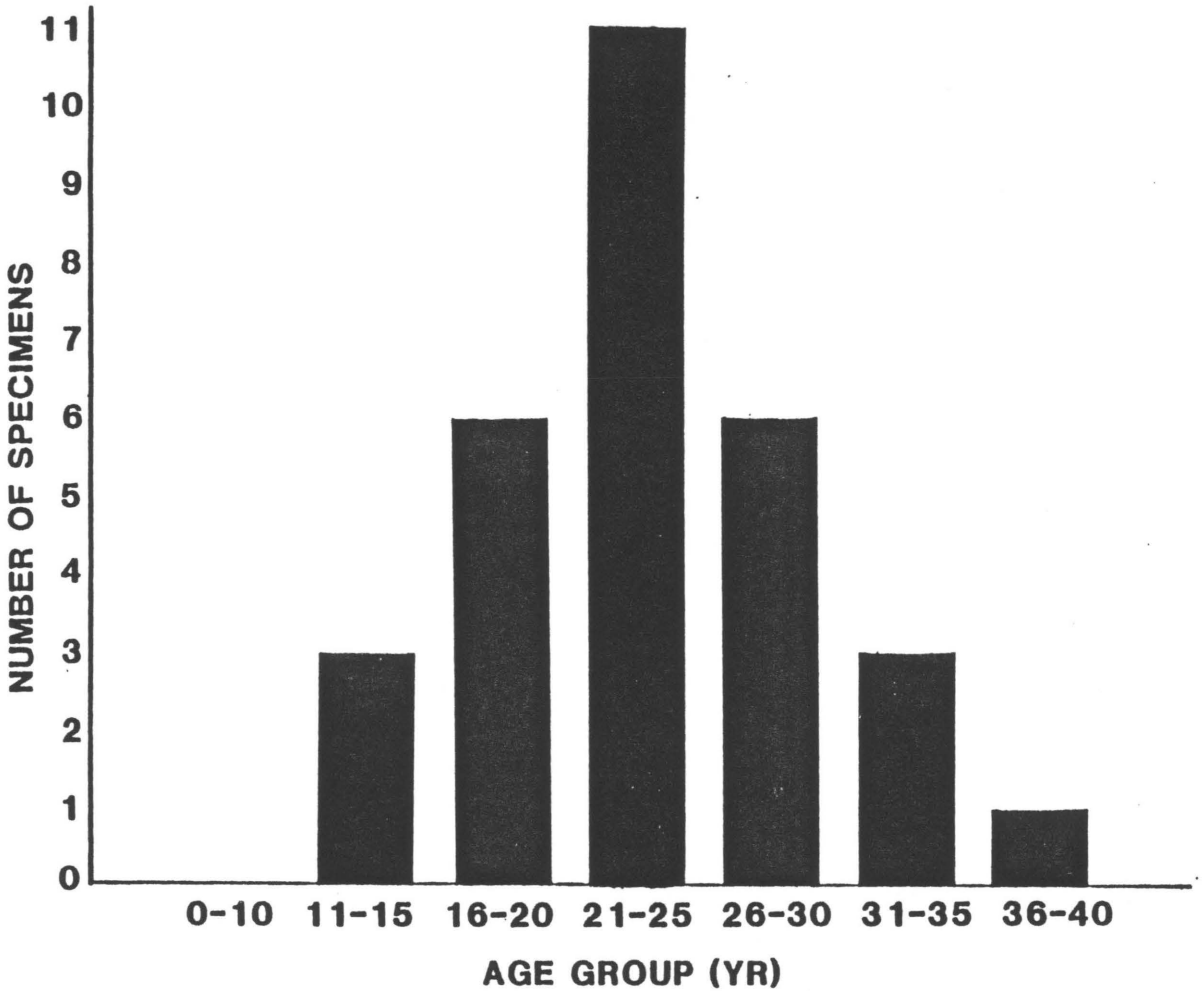


Figure 24. Age group distribution of Cyclonaias tuberculata collected at site G3 in the New River, West Virginia (N = 30).

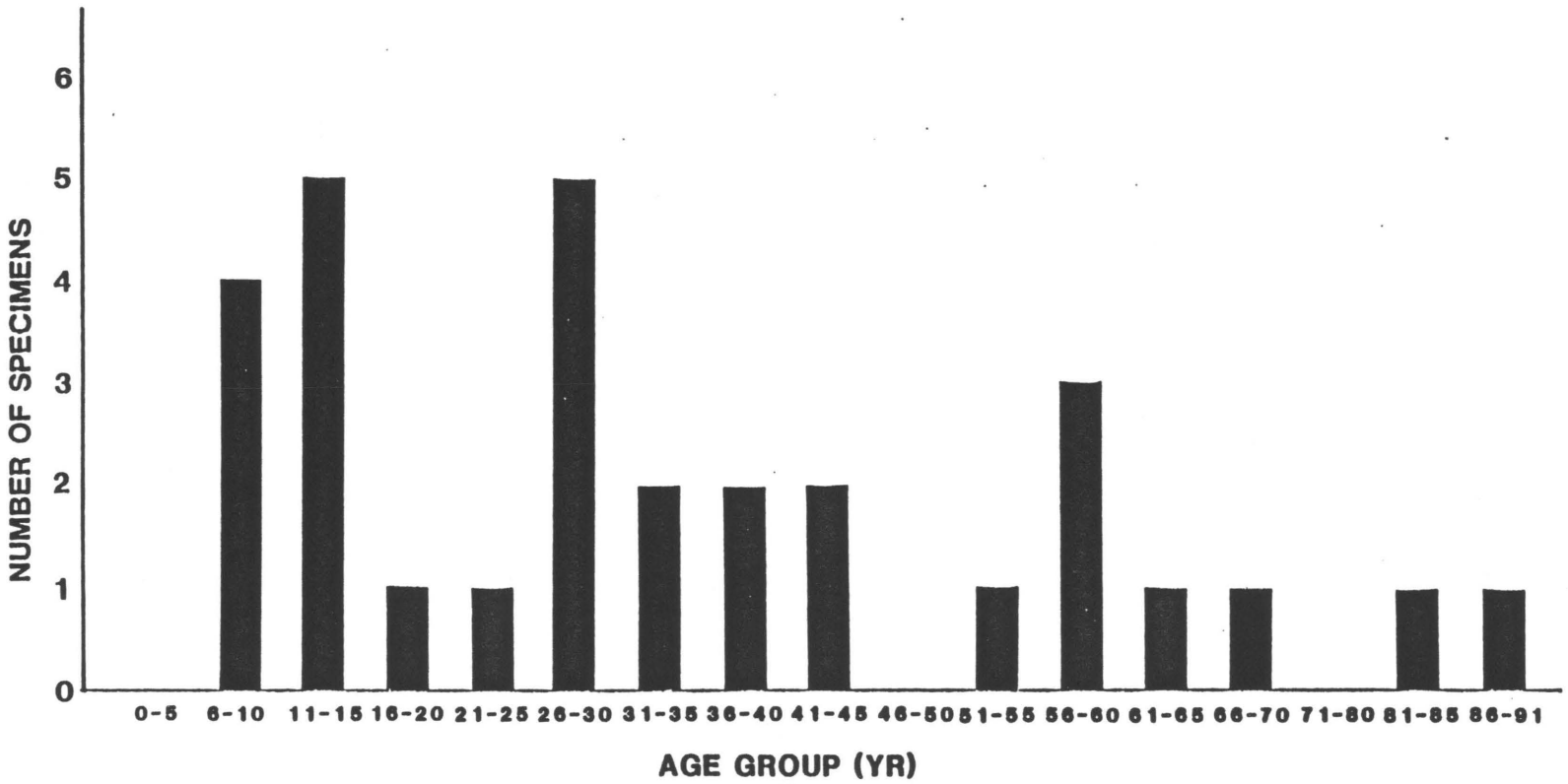


Figure 25. Age group distribution of Cyclonaias tuberculata collected at site G4 in the Greenbrier River, West Virginia (N = 30).

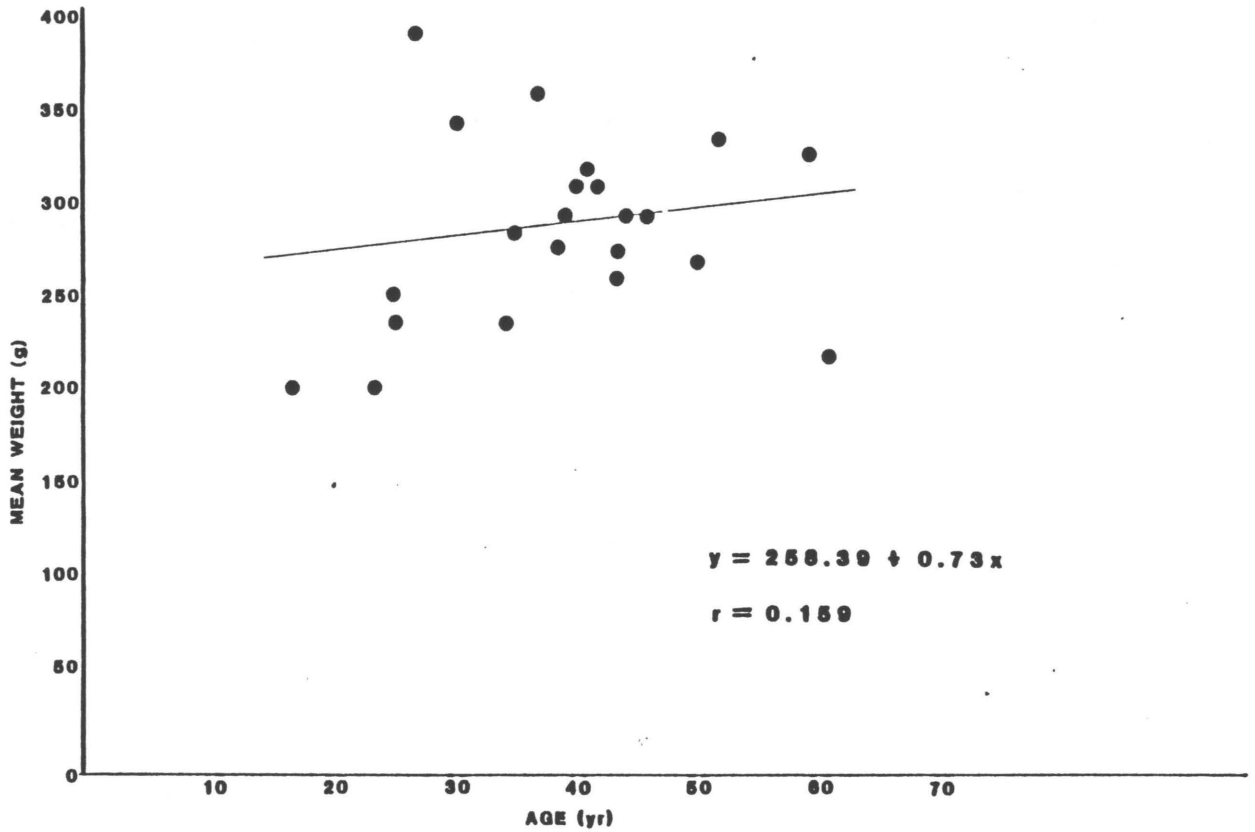


Figure 26. Mean shell weight versus age for Cyclonaias tuberculata collected from site G1 in the New River, West Virginia.

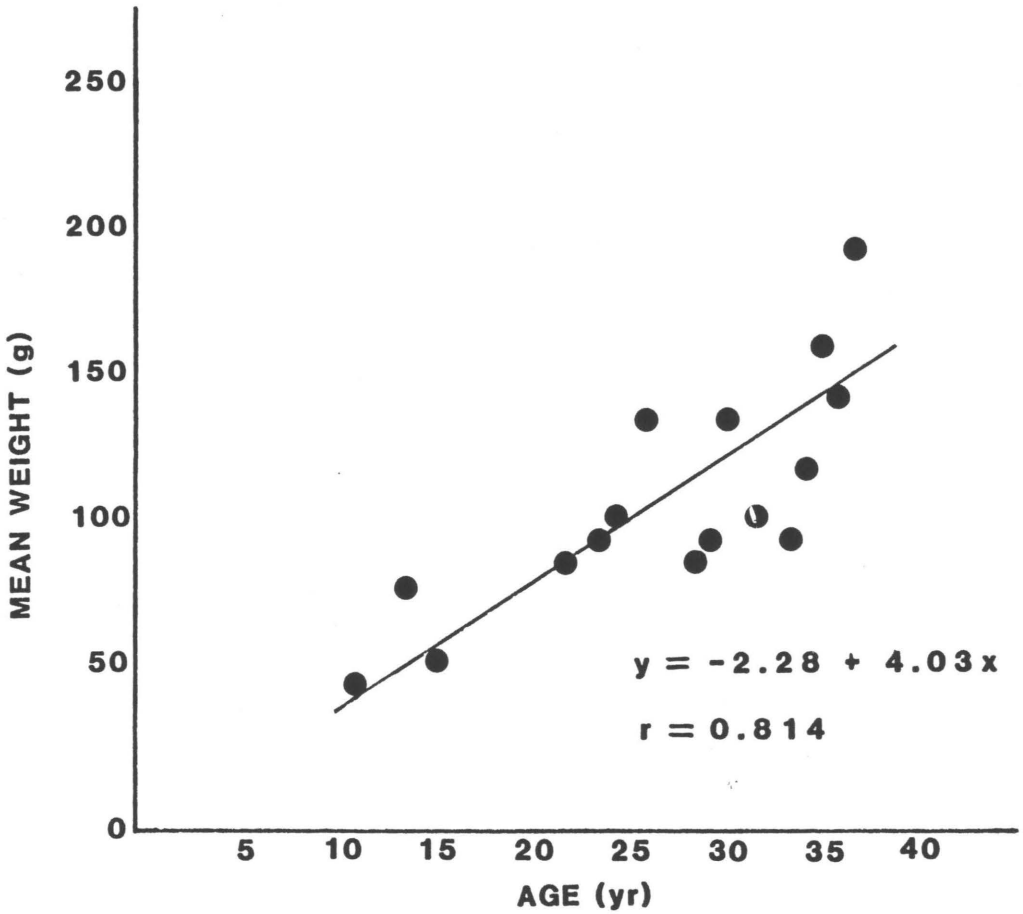


Figure 27. Mean shell weight versus age for Cyclonaias tuberculata collected from site G2 in the New River, West Virginia.

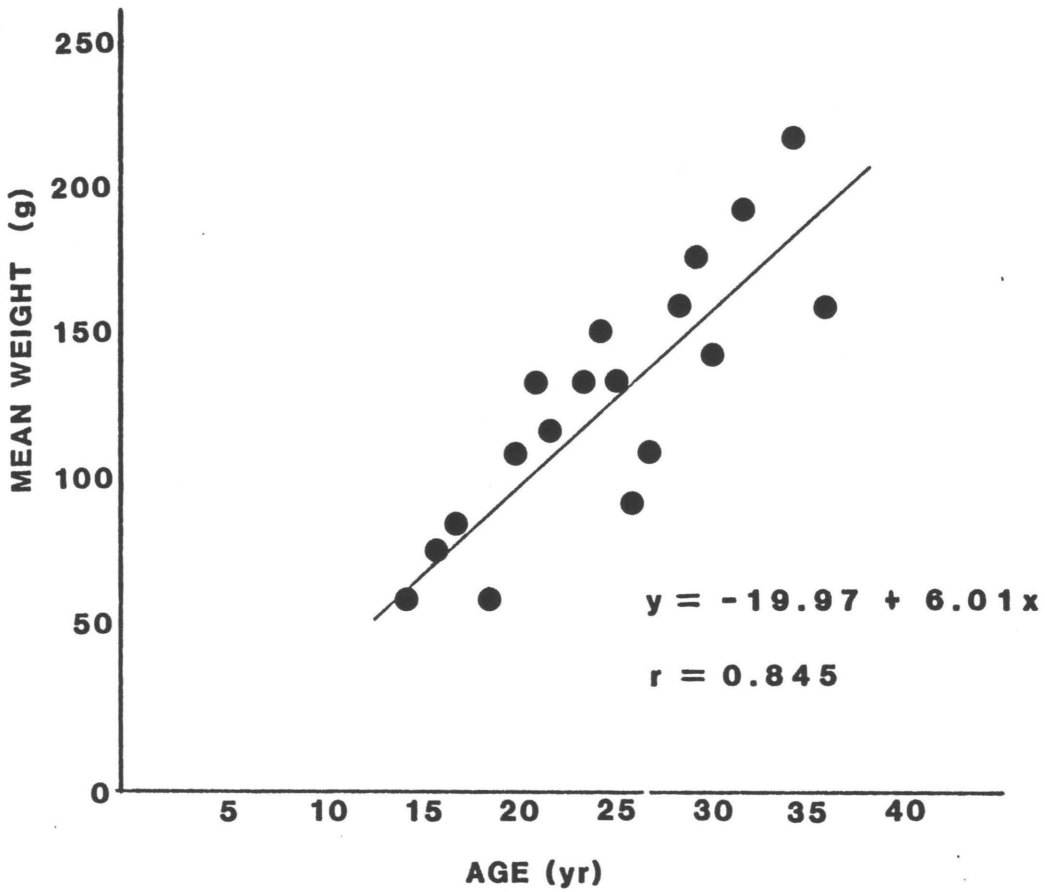


Figure 28. Mean shell weight versus age for Cyclonaias tuberculata collected from site G3 in the New River, West Virginia.

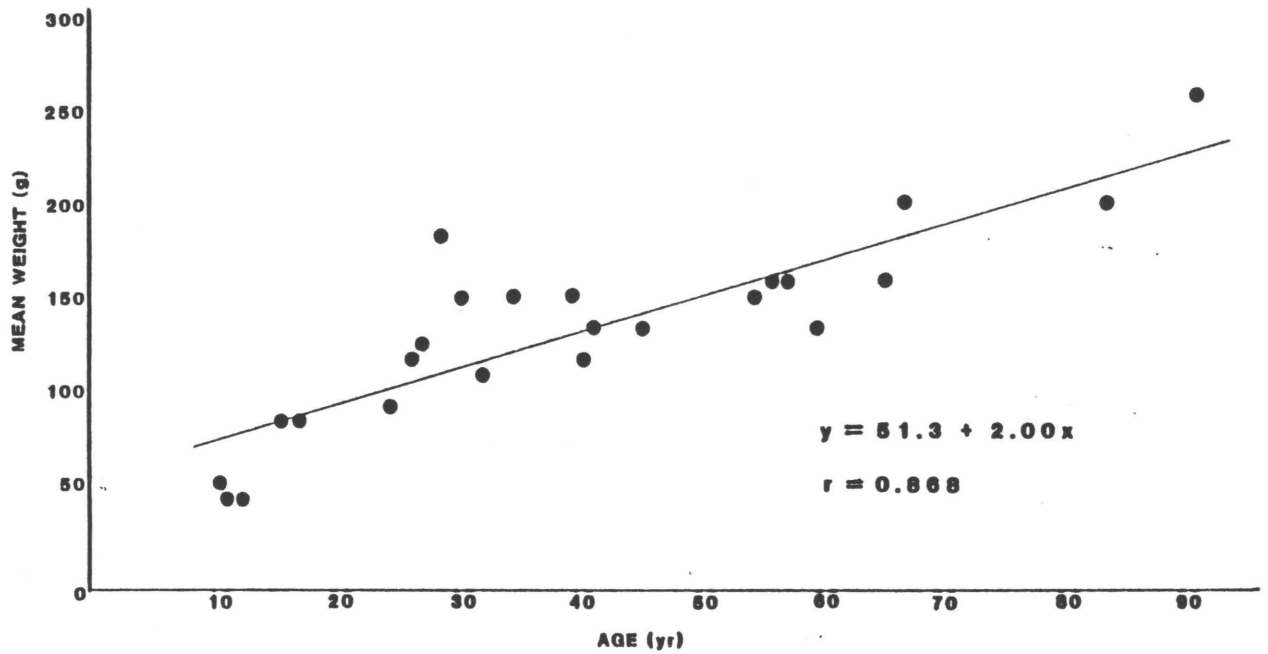


Figure 29. Mean shell weight versus age for Cyclonaias tuberculata collected from site G4 in the Greenbrier River, West Virginia.

of shell dry weight (g/yr) among the four sites based on a Kruskal-Wallis test and an LSD multiple comparison procedure using ranks revealed significant differences among all sites except G2 and G4 (Table 6). Increase in shell weight was greatest at G1 and lowest for sites G2 and G4. No trend of decreasing annual increment of shell weight with increasing distance from Bluestone Dam was observed for the sites in the New River, though the annual increase immediately below the dam was significantly higher than rates at other sites.

The pattern of growth in shell length of Cyclonaias tuberculata at all four sites was distinctly asymptotic (Figures 30 to 33). Growth in all subpopulations was rapid during the first ten years of life and slowed markedly after this time. Asymptotic lengths were approached between the ages of 20 and 25, and growth was extremely slow (<2 mm/yr) beyond the age of 25. Comparisons of the parameters of the von Bertalanffy growth equation among sites produced inconsistent results based on overlap of 95 percent confidence intervals (Table 7). The estimate of L_∞ for mussels from G1 was significantly greater than estimates for the other three sites. G2 had the lowest asymptotic length estimate, but it was not significantly different from sites G3 and G4. Estimates of **w** were significantly different among subpopulations at G1 and G3 only; however, estimates of **w** for subpopulations in the New River did show a decreasing trend with increasing distance from Bluestone Dam. No significant differences in the estimates of **k** were found among subpopulations at the four sites, and no trends in the estimates were apparent.

Table 6. Mean annual increment of shell weight (g/yr) for site G1 to G4 in the New and Greenbrier Rivers, West Virginia.

Site	Annual Increment
G1	7.75
G2	3.86 [a]
G3	5.21
G4	3.87 [a]

a - Sites with the same letter are not significantly different ($p=0.369$). All other comparisons were significantly different ($p<0.001$).

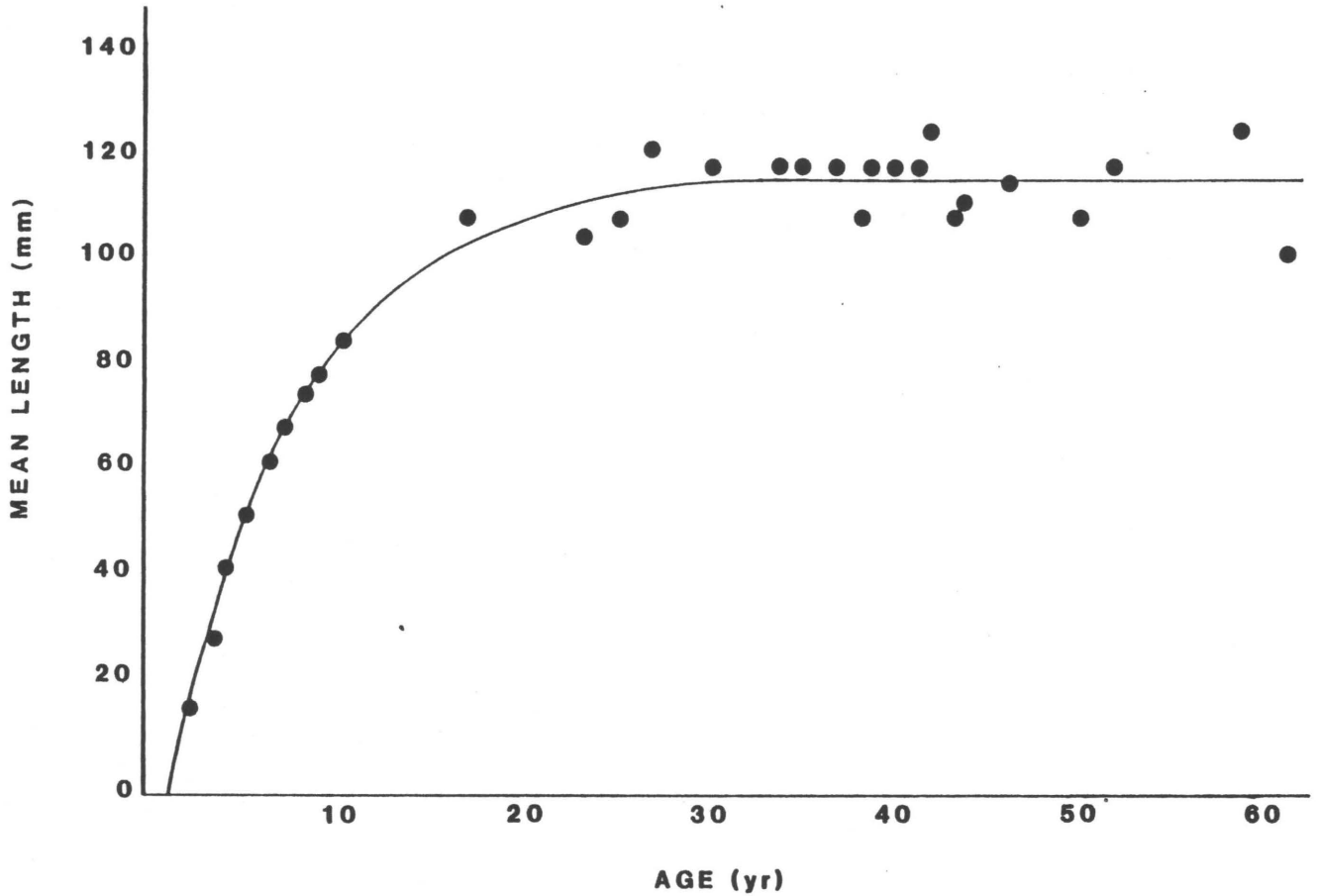


Figure 30. Growth in length of Cyclonaias tuberculata at site G1 as predicted by the von Bertalanffy growth equation. ● - observed mean length (mean lengths for ages 2 to 10 are derived from back measurements).

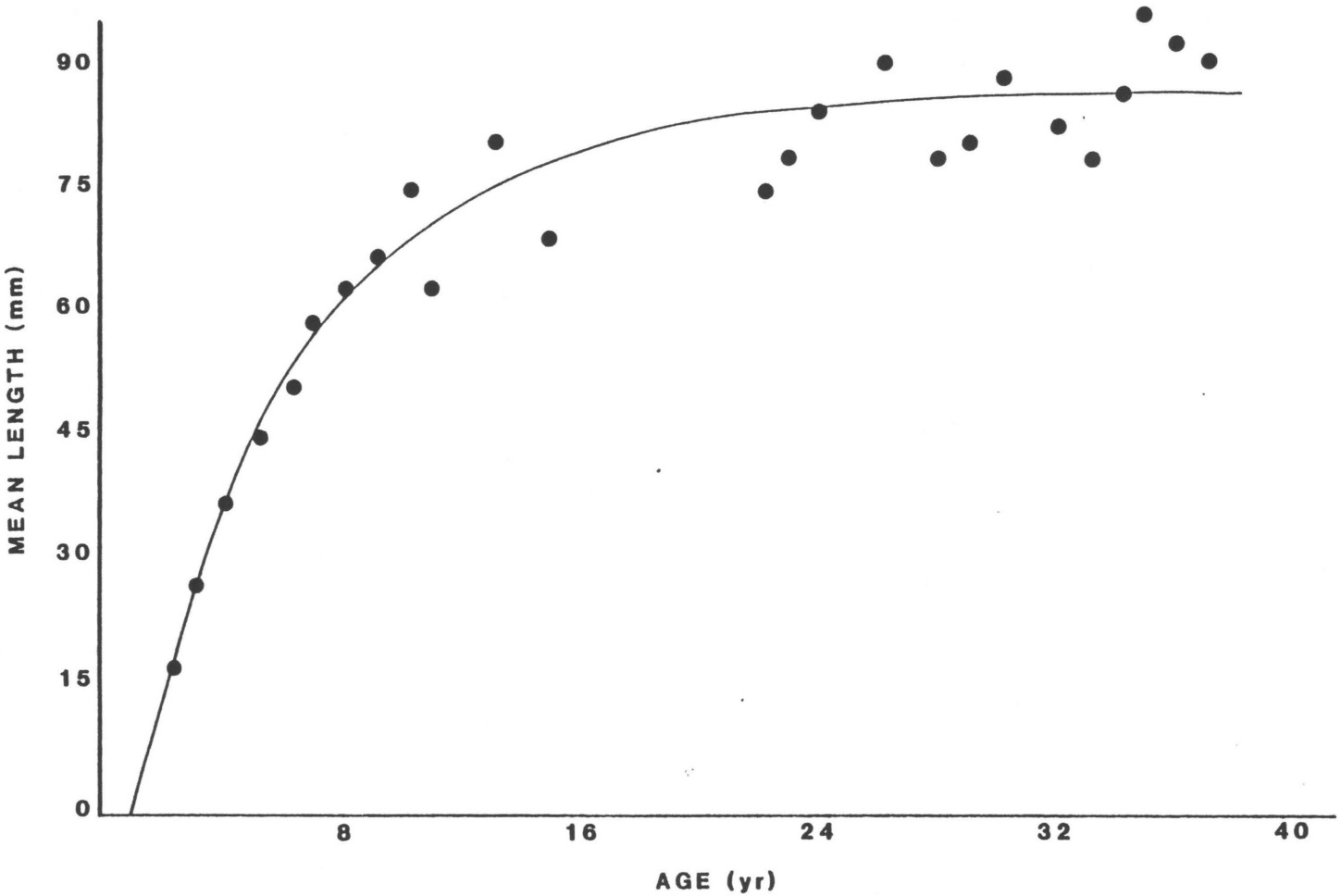


Figure 31. Growth in length of Cyclonaias tuberculata at site G2 as predicted by the von Bertalanffy growth equation. ● - observed mean length (mean lengths for ages 2 to 10 are derived from back measurements).

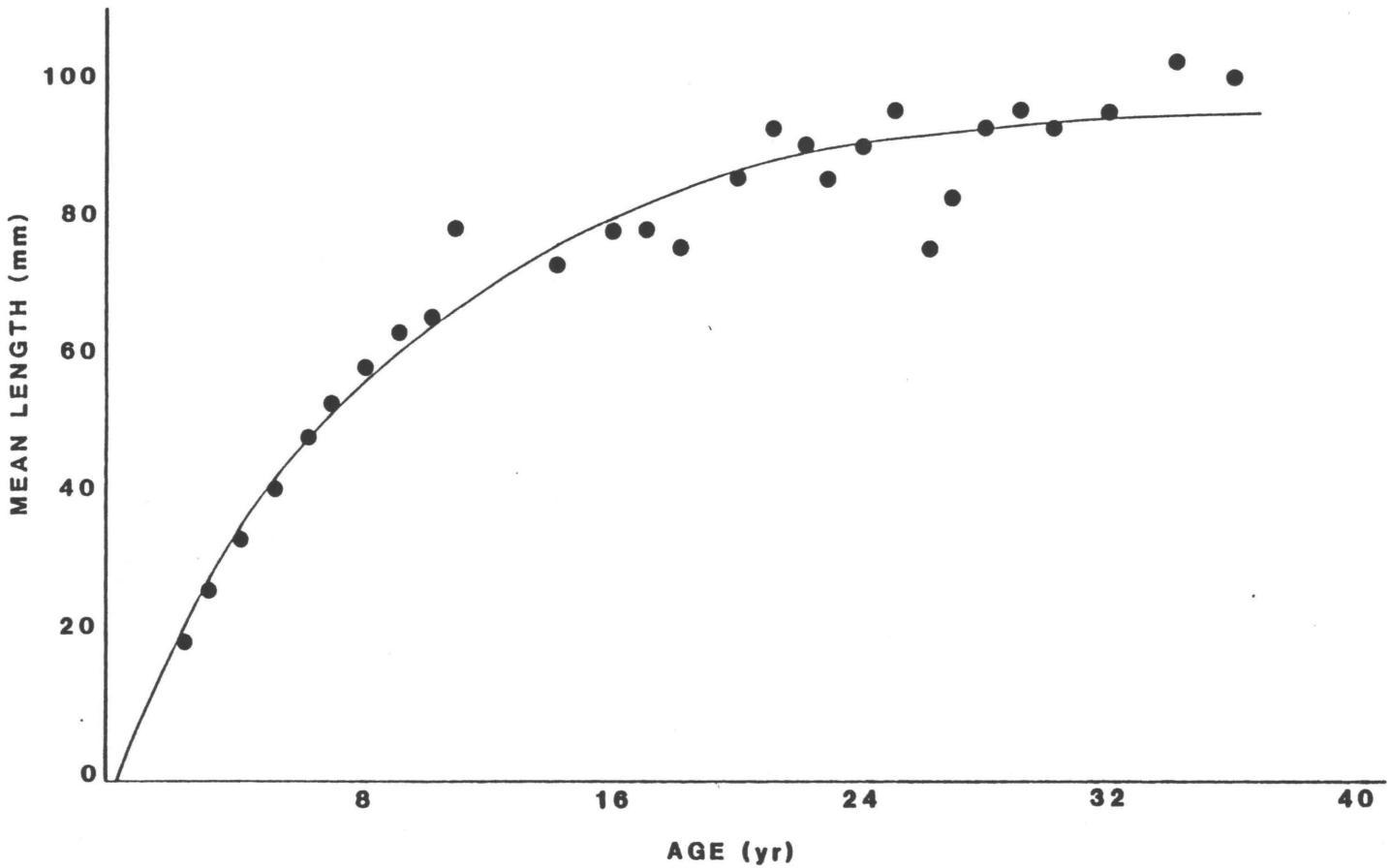


Figure 32. Growth in length of Cyclonaias tuberculata at site G3 as predicted by the von Bertalanffy growth equation. ● - observed mean length (mean lengths for ages 2 to 10 are derived from back measurements).

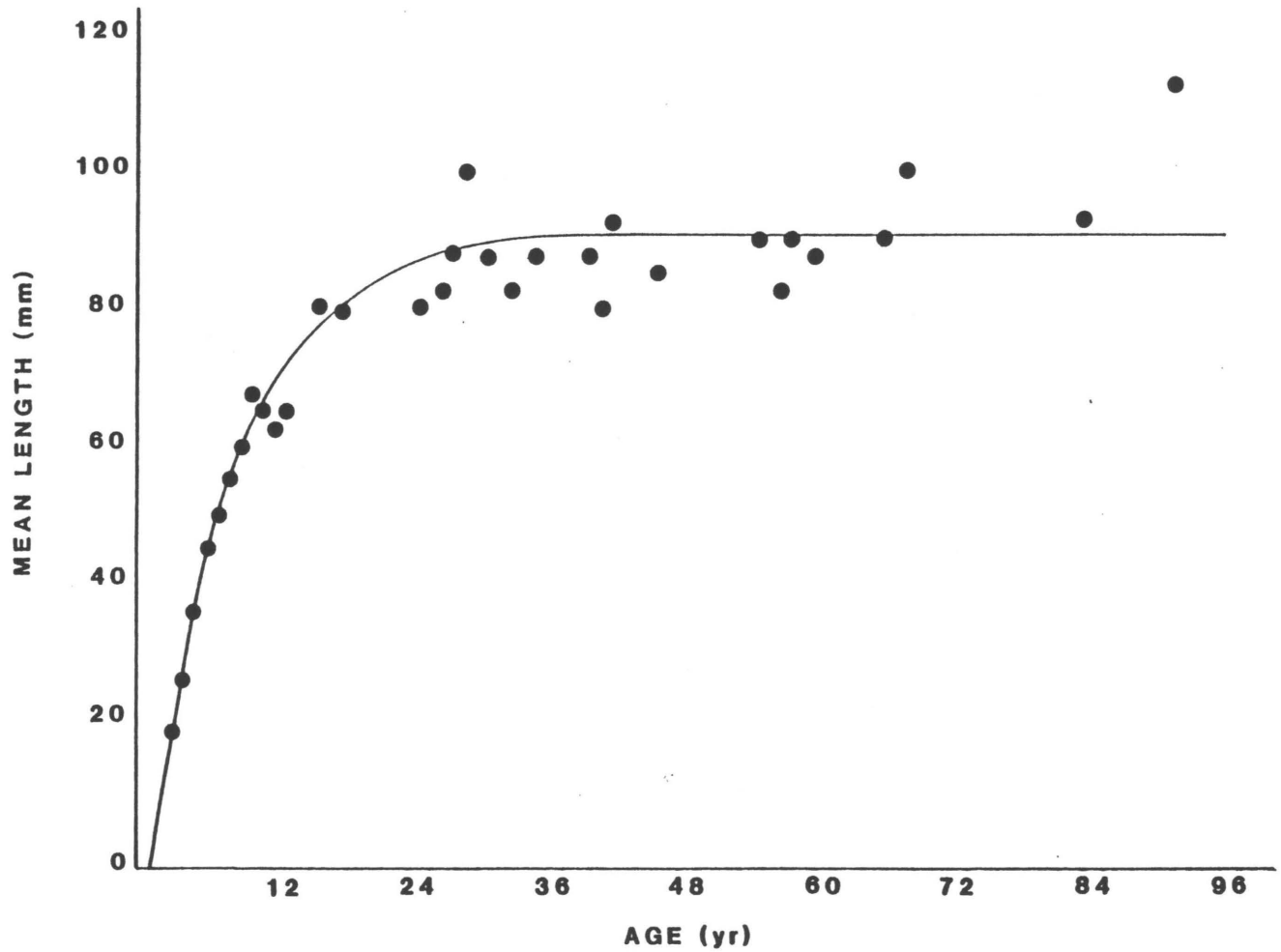


Figure 33. Growth in length of Cyclonaias tuberculata at site G4 as predicted by the von Bertalanffy growth equation. ● - observed mean length (mean lengths for ages 2 to 10 are derived from back measurements).

Table 7. Von Bertalanffy parameters describing growth of *Cyclonaias tuberculata* at sites 1 to 4 in the New and Greenbrier Rivers, West Virginia. Ninety-five percent confidence intervals are given in parentheses.

	Parameters			
Site	w (mm/yr)	k (yr^{-1})	L_∞ (mm)	t_o (yr)
1	17.15 [a]	0.151 [c]	113.9	1.14 [e]
	(14.35-19.95)	(0.125-0.177)	(111.3-116.5)	(0.52-1.76)
2	14.04 [ab]	0.164 [c]	87.0 [d]	0.60 [e]
	(10.51-17.56)	(0.119-0.209)	(83.1-90.9)	(-0.45-1.65)
3	10.56 [b]	0.110 [c]	96.4 [d]	0.00 [e]
	(8.09-13.03)	(0.078-0.141)	(90.4-102.3)	(-1.24-1.25)
4	11.60 [ab]	0.094 [c]	90.6 [d]	0.10 [e]
	(8.75-14.45)	(0.094-0.162)	(87.2-93.9)	(-1.21-1.42)

a,b,c,d,e - estimates with the same letter were not significantly different ($p>.05$).

Quantity and quality of seston below Bluestone Dam decreased with increased distance from the dam (Tables 8, 9). Zooplankton constituted a substantial portion of the seston immediately below Bluestone Dam, but few zooplankton were present in the drift at the other sites. Algae and organic detritus made up the bulk of the seston at all sites. The decrease in quantity and quality of seston with increasing distance from Bluestone Dam parallels the trend exhibited by the parameter w, suggesting that these factors may be related.

Table 8. Concentrations of organic seston (mg AFDW/L) near sites G1 to G4 in the New and Greenbrier Rivers, West Virginia (Voshell 1985a).

	Site			
Date	G1	G2	G3	G4
6/13/84	2.19	1.98	1.66	1.57
7/11/84	3.06	2.51	2.27	1.03
8/7/84	0.78	0.78	0.55	0.71
9/4/84	1.60	0.63	0.61	1.09
10/4/84	1.03	0.64	0.47	0.57
11/1/84	0.75	0.72	0.81	1.28
12/4/84	1.09	0.71	0.50	0.64

Table 9. Mean composition of organic seston (% volume) near sites G1 to G4 in the New and Greenbrier Rivers, West Virginia, from July to December 1984. ZPL=zooplankton; OAN= other animals; ALG= algae; VPL= vascular plant detritus; DET= amorphous detritus.

	Category				
Site	ZPL	OAN	ALG	VPL	DET
G1	3.7	0.6	25.2	1.1	69.3
G2	0.4	6.9	14.3	1.0	77.2
G3	0.1	2.0	17.8	0.4	79.7
G4	<0.1	1.4	11.0	0.2	87.5

DISCUSSION

Reproductive Biology

Actinonaias carinata in the New River is a long-term (bradytictic) breeder, spawning in mid-summer, brooding glochidia throughout winter, and releasing them the following spring. These findings are in agreement with those of Lefevre and Curtis (1912), who found A. carinata from the upper Mississippi River drainage to be long-term breeders, with embryos present from August to late September, and glochidia from late September to July. Spawning was from mid-July to mid-August in their populations as well, and they too reported that usually only the posterior ends of the outer gills served as marsupia. Ortmann (1919) found gravid A. carinata in streams in Pennsylvania from August to May, and Coker (1919) reported glochidia of this species were released primarily in the spring and early summer, though a few may be liberated in the fall. Lefevre and Curtis (1912) reported overlap of annual reproductive cycles for A. carinata from the Mississippi River. Though sex products were found in both sexes throughout the year, no evidence of overlap of annual reproductive cycles was found in this species in the New River. Spawning did not occur until well after the release of the previous year's glochidia.

Elliptio dilatata, Cyclonaias tuberculata, and Tritogonia verrucosa in the New River are short-term (tachytictic) breeders, spawning in the spring and early summer, and releasing glochidia immediately upon maturation. Glochidial release periods for C. tuberculata and T. verrucosa

are mainly based on collections of gravid females containing mature glochidia. Failure to collect glochidia of these two species in all but one drift sample suggests that releases were occurring at times other than when drift samples were collected, either early morning, late afternoon, or night. Spawning in E. dilatata, C. tuberculata, and T verrucosa extended over a three to four month period, unlike the relatively short spawning season observed for A. carinata and reported for several other lampsiline species (Zale and Neves 1982a). Similar spawning and glochidial release periods were reported for populations of E. dilatata, C. tuberculata, and T. verrucosa in Pennsylvania and the upper Mississippi Valley (Lefevre and Curtis 1912; Ortmann 1919). Utterback (1915) documented similar findings for E. dilatata in Missouri, and reported gravid C. tuberculata as late as mid-August.

Gametogenesis in T. verrucosa, as well as E. dilatata and C. tuberculata, was evident and reached advanced stages during the fall and winter in this study. The majority of investigations into gametogenic activity of tachytictic species have shown that the later stages of gametogenesis usually do not occur until late winter or early spring, and fall and early winter are characterized by minimal development of gonadal material (Heard 1969; Yokley 1972). Utterback (1915) noted that T. verrucosa in Missouri lacked developing gametes during the fall and winter, contrary to what was observed for this species in the New River. However, Matteson (1948) found viable sperm throughout the year in males of Elliptio complanata, and females of this species contained numerous mature ova in the fall, although spawning did not occur until the following spring. Matteson (1948) concluded that mature gametes present in

the fall were held within the acini throughout the winter and released in the spring when environmental conditions warranted. Observations for E. dilatata, C. tuberculata, and T. verrucosa closely paralleled those reported for Elliptio complanata. The possibility of biannual gametogenesis (spring and fall), as discussed by Smith (1978) for Margaritifera margaritifera, occurring in these three species is unlikely, since no gravid specimens were collected during the winter months.

Incomplete release of mature ova into the suprabranchial chambers of females was common for the examined species. Apparently, many females produced an over-abundance of ova, and once a portion of these ova were fertilized, release of unfertilized eggs ceased. There was no evidence to suggest that unreleased eggs were spawned at some later date, but were likely resorbed within the gonadal tissue.

Actinonaias carinata, Elliptio dilatata, Cyclonaias tuberculata, and Tritogonia verrucosa of both sexes probably reach sexual maturity between the ages of 4 and 6, depending upon the species. Van der Schalie and van der Schalie (1963) reported that Actinonaias ellipsiformis requires three years to mature. Coker et al. (1921) found that fast growing, relatively short-lived species, such as Proptera laevissima and Anodonta imbecilis, may reach sexual maturity by age 2, but slow growing, longer-lived species may take upwards of eight years to mature. Zale and Neves (1982a) found that four lampsiline species from Big Moccasin Creek, Virginia, matured by age 3. Mussels from headwater streams may have shorter life spans than mussels from large riverine systems, so early maturity in these species is not surprising. A. carinata, E. dilatata, C. tuberculata, and T.

verrucosa in the New River are long-lived, thus achieving sexual maturity between the ages of 4 and 6 is not unexpected for these species.

Trematode infestations were common in Actinonaias carinata and occasional in Elliptio dilatata. In most cases, reproductive abilities of infested individuals appeared severely limited. Infestations were associated only with older, though not senile, specimens collected at R1 in West Virginia, suggesting that infestations may be due to local environmental conditions promoting the existence of these parasites. Van der Schalie and van der Schalie (1963) reported similar infestations in Actinonaias ellipsiformis in Michigan. As was the case in this study, they found parasitism at only one site of many sampled. Why no trematodes were found in specimens of T. verrucosa and C. tuberculata is unknown, but Zale (1980) reported a similar situation existed in Big Moccasin Creek, Virginia, where numerous specimens of Villosa vanuxemi, Villosa nebulosa, and Medionidus conradicus were found with heavy trematode infestations, yet specimens of Lampsilis fasciola were free of parasites.

Though most of the species of unionids are dioecious, sporadic hermaphroditism is observed on occasion in some of these species (van der Schalie 1970). This was the case with the hermaphroditic specimen of Elliptio dilatata examined. This specimen was predominantly male with nonfunctioning female structures. This species previously had been found to be occasionally hermaphroditic, as was Tritogonia verrucosa (van der Schalie 1970). Hermaphroditism in these species is obviously rare, and sporadic.

Growth Comparisons

Ages for some specimens of Cyclonaias tuberculata collected from the New and Greenbrier Rivers were among the oldest yet reported for freshwater mussels. Hendelberg (1960) aged one specimen of Margaritifera margaritifera from Sweden at 116 years and another at 105. Several other specimens were found to exceed 70 years of age. Stober (1972) observed an age range of 10 to 67 years for specimens of this same species collected from the Madison River, Montana. Margaritifera falcata from the Snake River, Montana, have been aged to 40 years (Vannote and Minshall 1982). Some of the oldest reported ages for unionids were 56 years for Pleurobema oviforme and 35 years for Fusconaia cuneolus from Virginia (Moyer 1984). Stansbery (1960, 1970) reported Pleurobema cordatum and Amblema plicata from Lake Erie reaching ages of 40 and 32 years, respectively, and Lefevre and Curtis (1912) made reference to mussels from the Mississippi River reaching 50 years of age, though no species were mentioned specifically. Several studies of the growth and longevity of species in the subfamily Anodontinae show these species to be relatively short-lived (10-15 years) compared to mussels from other subfamilies (Crowley 1957; Negus 1966; Haukioja nad Hakala 1978). Anodontines are typically thin-shelled and fast growing, unlike C. tuberculata and most other species belonging to other taxa. The collection of several specimens of C. tuberculata in excess of 50 years of age from the Greenbrier River probably is reflective of the stability and relatively unaltered condition of this river. The abundance of old (>35 years) individuals

collected at G1 below Bluestone Dam indicates that conditions below the dam also are conducive to long-term survival of mussels.

Shell weight-age relationships for Cyclonaias tuberculata were linear over the range of ages sampled for all sites except G1. Similar relationships have been reported for other bivalves. Sheldon (1967) found shell weight to be linearly related to age for the cockle, Cardium edule, the hard clam, Mercenaria mercenaria, and two freshwater mussels, Anodonta anatina and Unio pictorum. Shell weight increases per year were found to be nearly constant after age 4 for Elliptio complanata from Mirror Lake, New Hampshire (Strayer et al. 1981). Similarly, Coon et al. (1977) reported that Amblema peruviana exhibited constant annual increases in shell weight, but only after age 20; prior to this, annual increments in shell weight increased over time. The weight - age relationship for C. tuberculata from site G1 was highly variable, due primarily to the collection of three individuals that were overly massive for their age, and one specimen, the oldest collected at this site, that was extremely thin-shelled and relatively small. Occurrence of such individuals in a population suggests that environmental influences may act differentially on individuals, or genetic factors are responsible for this anomalous growth.

The relationship between shell dry weight and body tissue weight in bivalves has received little study. Comparisons of shell weight and visceral mass weights (wet and dry) of the asiatic clam, Corbicula manilensis (=C. fluminea), indicate that these variables are linearly related (Joy and McCoy 1975); however, the range of shell weights (0-6 g) studied was extremely small compared to those typical of most unionid

populations. C. fluminea are relatively short-lived, hence it is unknown if long-lived bivalves exhibit the same relationship between shell weight and body size. Negus (1966) found that shell weight and wet body weight exhibited similar rates of increase in Anodonta anatina, Unio tumidus, and Unio pictorum in the Thames River, England. However, these species are relatively thin-shelled and short-lived. The only other investigation of the shell weight - body tissue weight relationship was conducted by Coon et al. (1977) for Amblema peruviana in the upper Mississippi River. They too found corresponding increases in body tissue weight with increases in shell weight; however, this species exhibited extremely rapid growth over the first 20 years of life, and no specimens over age 23 were used in developing this relationship. It is unknown if body tissue weight continues to increase in the same fashion as shell weight once mussels reach the advanced ages attained by C. tuberculata collected in this study. Increases in shell weight at older ages may or may not accurately reflect body growth of C. tuberculata in the New River.

Mean increase in shell weight per year was greatest at site G1, followed by site G3. Sites G2 and G4 showed the smallest increases in weight per year and were not significantly different from one another. Similarity in shell growth at these two stations was not unexpected since G2 was located approximately 2 km below the mouth of the Greenbrier River, along the same side on which this river enters the New. Thus, a significant portion of the water flowing through site G2 is from the Greenbrier River.

Unlike the relationship observed for shell weight and age among sites, estimates of the von Bertalanffy growth equation parameter w indicated

that significant differences in rate of shell growth in length existed only between sites G1 and G3, and there was a trend of decreasing growth rate with increasing distance from Bluestone Dam. Since increases in shell length should be more reflective of increases in the amount of body tissue than are increases in shell weight, growth in shell weight per year for these subpopulations may not be indicative of annual increases in body size. Increases in shell weight may occur through thickening of the shell without the animal itself increasing in size. Other studies of mussel growth patterns have shown that shell length is a reliable and consistent indicator of organism growth and may be a more appropriate measure than shell weight (Negus 1966; McCuaig and Green 1983; Moyer 1984). Differences in shell weight growth among sites may be attributable to genetic differences among subpopulations and/or different phenotypic expressions resulting from varying environmental influences among the sites. This would explain the similarities observed for sites G2 and G4, which are subject to similar environmental conditions present in the Greenbrier River.

Asymptotic lengths were significantly different among site G1 and all other sites, but estimates of **k** did not differ significantly among sites. These results illustrate the problems that may arise when these two parameters alone are used to test for differences in growth among populations. These problems are due to the inverse relationship of **k** and L_∞ (Gallucci and Quinn 1979). Because **k** and L_∞ are usually highly negatively correlated, different combinations of values of the two parameters may describe similar curves for a given data set. This, along with the lack of statistical robustness of estimates of L_∞ and **k**, makes the use of these

parameters undesirable for comparing growth among different populations (Gallucci and Quinn 1979). The parameter **w** takes into account the inverse relationship between **k** and L_∞ and, in effect, examines how long it takes to reach L_∞, the L_∞ value, as well as the rate of increase in length near t_o. Thus, **w** is the most suitable parameter for comparing growth among the subpopulations of C. tuberculata studied here, and the conflicting results observed with analysis of the L_∞ and **k** parameters are avoided.

The trend observed for **w**, a measure of growth rate near t_o with respect to length, describes decreasing growth with increased distance from Bluestone Dam. It is unlikely that this trend is a result of water temperature differences among sites since temperatures immediately below Bluestone Dam varied little from those recorded approximately 12 km downstream of the dam (M. Roell, V.P.I. & S.U., unpublished data). The most probable cause of the observed trend is the quantity and quality of food for mussels at the various sites. Water released from the dam generally contains abundant organic detritus and plankton (Voshell 1985a). Zooplankton in particular are relatively abundant in the water released from Bluestone Dam. This seston provides a rich food source for filter feeders below the dam, as evidenced by the extremely high annual production (0.428 kg AFDW/m^2) of benthic invertebrates immediately below the dam (Voshell 1985b). In addition to the seston from the reservoir, Voshell (1985b) has shown that the extremely dense population of black flies (Simulium jenningsi) immediately below the dam converts a considerable amount of organic detritus to pseudofeces that becomes available to other detritivores. This pseudofeces is nutritionally among the highest quality components of stream detritus (Shepard and Minshall

1981), and growth of detritivores has been shown to be significantly greater when fecal material is a large component of the diet (Ward and Cummins 1979; Voshell 1985b).

Cyclonaias tuberculata at site G1, because of their proximity to Bluestone Dam and the inordinately high densities of black flies in the immediate area, have an extremely abundant, high quality food base. Concentrations of seston become progressively lower downstream as a result of dilution by the Greenbrier, sedimentation, and consumption (Voshell 1983). Black flies, though still relatively abundant, decline in density in the New River downstream, resulting in a decrease in availability of their nutritious feces (Amrine 1982). Mussels at site G2 exhibited slower though not significantly different growth than mussels at G1 due to a decrease in the quantity and quality of food available. Apparently the effects of Bluestone Dam on the food base of filter feeders are still manifested in the river at site G2 despite the effects of the Greenbrier River; hence, the lack of significant differences in growth between sites G1 and G2. Mussels at site G3 grew at a significantly slower rate than mussels at site G1, suggesting that the influences of Bluestone Dam on mussel growth have diminished considerably at this point in the river.

The comparatively slow growth rate of mussels at site G4 is further evidence that the increased availability of high quality food resulting from releases from Bluestone Reservoir is responsible for observed differences in growth rates among subpopulations. Seston in the Greenbrier River at site G4 is less abundant and lower in quality than that found in the New River for the first several kilometers below Bluestone Dam

(Voshell 1985a). Infusion of water from the Greenbrier into the New River results in a reduction in seston concentrations. This dilution serves to reduce the positive effects on the food base resulting from reservoir releases and high invertebrate productivity below the dam.

Bluestone Dam has a localized positive effect on the growth of Cyclonaias tuberculata downstream. Growth in subpopulations located within a few kilometers of the dam is enhanced through improvement of the food base both in quantity and quality. Results of this study may not be applicable to all dams and all species of mussels found below dams. The water released from Bluestone Dam is epilimnial and is characteristically high in organic seston. Because of this, the tailwaters immediately below the dam support one of the most productive invertebrate communities yet documented. Similar conditions do not exist for many tailwaters, and mussel growth responses associated with other dams need to be studied to determine impacts of different dam operations on downstream mussel populations. Any changes in operations at Bluestone Dam would also be expected to alter the effects of the dam on the growth of Cyclonaias tuberculata downstream.

SUMMARY

1. The mucket Actinonaias carinata from the New River is bradytictic, spawning in July and August once water temperatures reached 22°C. Glochidia were brooded throughout the fall and winter and released from March through May when water temperatures reached 9° C. Gametogenesis began in October, ceased during the winter, and continued following release of the previous year's glochidia in the spring.

2. Elliptio dilatata, Cyclonaias tuberculata, and Tritogonia verrucosa from the New River are tachytictic. Spawning in all three species began in mid-March when water temperatures reached 9° C, and continued into May for T. verrucosa, into June for C. tuberculata, and into July for E. dilatata. Glochidia were released upon maturation, beginning in mid-April and continuing through June for T. verrucosa, and into August for E. dilatata. C. tuberculata released glochidia from March through June. Gametogenesis in these three species began in late summer and reached advanced stages by late fall. Mature gametes overwintered in the gonads and were released the following March.

3. Sexual maturity was reached by both sexes of Actinonaias carinata by age 4. Elliptio dilatata females were reproductively active by age 4, and it was assumed that the same is true for males of this species. Both sexes of Tritogonia verrucosa were sexually mature by age 6.

Females of Cyclonaias tuberculata were reproductively active at age 6 or younger, and males of this species matured at least by age 10.

4. Cyclonaias tuberculata in the New and Greenbrier Rivers were extremely long-lived, with one specimen from the Greenbrier exceeding 90 years in age, and one from the New River in excess of 60 years. Growth in shell length in the four subpopulations of C. tuberculata was asymptotic. Growth rate, as described by the parameter w from the von Bertalanffy growth equation, declined significantly with increasing distance from Bluestone Dam.

5. The relationship between shell weight and age was approximately linear for Cyclonaias tuberculata collected from two sites in the New River and one site in the Greenbrier River. The relationship at a fourth site (G1) immediately below Bluestone Dam revealed no distinct pattern for these two parameters. It was concluded that increases in shell weight may not accurately reflect increases in growth of soft parts, and thus were not used for detecting differences in growth among the four subpopulations.

6. Observed differences in growth among the four subpopulations of Cyclonaias tuberculata were attributed to the high quality and quantity of food released through Bluestone Dam. The quality of the food base below the dam was further enhanced by the production of highly nutritious feces by invertebrates, particularly black flies, feeding on seston from the reservoir. Concentrations of seston declined

markedly downstream through dilution by the Greenbrier River, sedimentation, and consumption by macroinvertebrates, resulting in corresponding declines in mussel growth.

7. Changes in the operations of Bluestone Dam can be expected to alter the relationship between mussel growth and proximity to the dam. Any activities that would lead to decreases in the quantity or quality of the seston released from Bluestone Reservoir, or alter the species composition of invertebrates immediately below the dam, would likely negatively impact mussel growth downstream of Bluestone Dam. Observed effects of Bluestone Dam on growth rates in downstream subpopulations of Cyclonaias tuberculata may not apply to other dams or all mussel species. Additional research needs to be done below other dams to assess impacts of different reservoir release patterns on downstream mussel populations.

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APPENDIX A

Collection dates, numbers, and species of fish collected from the New River, West Virginia, for examination for glochidial infestations.

Date	Species	No.
7/12/84	Nocomis platyrhynchus	2
	Campostoma anomalum	4
	Notropis volucellus	8
	Notropis spilopterus	1
8/1/84	Percina roanoka	2
	Notropis albeolus	3
	Notropis sp.	2
8/29/84	Etheostoma caeruleum	3
	Perecina roanoka	6
	Nocomis platyrhynchus	1
	Lepomis auritus	2
	Notropis albeolus	5
9/17/84	Notropis rubellus	18
	Notropis telescopus	11
	Notropis photogenis	2
	Notropis spilopterus	2
	Notropis albeolus	6
5/8/85	Micropterus dolomieui	11
	Ambloplites rupestris	6
	Etheostoma caeruleum	4
	Etheostoma blennioides	6
	Percina oxyrhyncha	2
	Notropis spp.	27
6/27/85	Micropterus dolomieui	12
	Ambloplites rupestris	15
	Nocomis platyrhynchus	21
	Etheostoma blennioides	1
Total		183

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