DISTRIBUTIONAL ANALYSIS OF THE FRESHWATER MUSSEL FAUNA OF THE TENNESSEE RIVER SYSTEM, WITH SPECIAL REFERENCE TO POSSIBLE LIMITING EFFECTS OF SILTATION

by

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(ABSTRACT)

Mussel studies in the Tennessee River drainage (1973 - 1982) examined ecology and distribution and investigated factors limiting to distribution. This river system presently supports 71 freshwater mussel species, 25% of which are endemic to the Cumberlandian Region. Species have been extirpated from this drainage within the past 60 years, however the number of extant species remains high. The major impact of man's activities has been reduction of available habitat

Past and present distribution records indicate that mussel species assemblages are determined by geologic history and stream size. Although some overlap of species exists among stream size categories, there is no longer a continuous gradation from one category to the next; mussels exist in isolated communities separated by nonproductive river reaches. Productive reaches supporting more than 60 mussel species once existed in habitats spanning the transition from medium to large rivers; reaches now altered by impoundment. The maximum number of species reported in recent collections from any one site in the Tennessee drainage is less than 40, which seems to be the maximum number of

species niches available.

Quantitative sampling reveals characteristic patterns of species dominance. Changes in species dominance and age class structure provide a better basis for evaluating changes over time than do species composition or diversity alone. Mussel density was found to be more variable than species composition, and was unrelated to species abundance.

Experiments on effects of siltation indicated that silt can be a significant limiting factor to mussel distribution. Transplant studies showed that mussels transplanted into heavily silted areas exhibited poor survival over a one year period compared to mussels moved to unsilted habitats. Results indicate that siltation may interfere with reproductive activity. Laboratory experiments testing the effect of suspended silt on the uptake of C-14 tagged algae by freshwater mussels showed that suspended silt can interfere with feeding. Food uptake was reduced to approximately 50% (of control) at silt levels of 211 to 820 mg/l, and to 80% at silt levels over 1000 mg/l. It was concluded that the limiting mechanism is one of dilution of food rather than direct interference with filtration or respiration.

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PREFACE

This dissertation is based on three separate but closely related studies of the freshwater mussel fauna of the Tennessee River system. The studies were designed and executed independently; however, each successive work was an outgrowth of the previous one.

I began work on the freshwater mussels of the Tennessee River System in 1972 as a consultant to TVA, continued this work as a TVA biologist from 1973 through 1978, as a Virginia Tech research assistant and student from 1978 to 1980, and as a consultant to the State of Tennessee from 1980-1984.

Early work emphasized species distribution of the upper Tennessee region with the aim of managing the fauna as a resource and for the purpose of endangered species preservation. During the course of these surveys, the absence of basic biological and ecological information necessary to manage the resource became apparant.

Comparison of recent and historical distributional data showed that there had been drastic reductions in the range of freshwater mussels in the Tennessee River system resulting in productive "pockets" between large reaches of unproductive habitat. While some areas (ie. Kyles Ford, Tennessee) had apparently changed little in terms of numbers of species, there was no way of knowing if there had been changes in community structure or mussel densities over time, since there was little quantitative data available for comparison.

While employed by TVA, I began quantitative mussel sampling of two areas of the Clinch River in Tennessee and Virginia to examine community structure. The objective of this sampling was to characterize fauna of the upper Tennessee River system, by comparing two shoal communities, and to provide a baseline for evaluating future changes in the fauna which might not be noticeable based on species composition alone.

In 1978, I began graduate work at Virginia Tech on the endangered molluscs of Virginia, concentrating on distributional work and quantitative sampling of freshwater mussel communities. I was interested in identifying factors which influence mussel distribution such as geologic history, stream size, and habitat type. My doctoral research was to include an analysis of distribution and community structure of the mussel fauna of the upper Tennessee River system, with an emphasis on habitat characterization.

After leaving TVA, I had the opportunity to expand my work to look at possible limiting factors to distribution of freshwater mussels in the Tennessee River Drainage Observations made during previous years sampling in this drainage led to the conclusion that siltation was a major factor in the decline in the mussel fauna.

Heavy siltation was observed in the upper Clinch River, from land scarified by development, and in the Duck River, from gravel dredging. The most drastic evidence of pollution from siltation, however was in the upper Powell River, where heavy deposition of silt from abandoned strip mines resulted in obliteration of all benthic organisms in the uppermost reaches of the river (above Big Stone Gap, Virginia). Although siltation seemed the obvious cause of depauperate molluscan fauna in reaches of all of these streams, there were no data to support this contention. There was some indication in the literature (Ellis, 1931) that silt was detremental to mussels. However, little had been postulated as to the mechanisms by which silt might be limiting short of smothering mussels by excessive deposition.

I designed a two part study involving field and laboratory experiments to test the hypothesis that suspended silt can be limiting to freshwater mussels by interfering with uptake of food.

The Powell River provided an excellent opportunity to observe effects of siltation, since the major input was localized in the headwaters. Moving downstream, the diversity and abundance of benthic organisms increased as the degree of siltation became less, until, at the lowermost reaches, a rich and diverse benthic fauna including freshwater mussels was observed. I undertook mussel transplants to selected reaches of this river to observe field effects of siltation. Later laboratory tests looked at the effects of suspended silt on food uptake.

The result of the above mentioned studies is the present work on distribution of mussels within the Tennessee River System with a special emphasis on siltation as a potential limiting factor. The work is presented in three chapters, each of which is meant to stand alone. Each chapter contains its own introduction and conclusions. A general summary and conclusions follow the chapters. A single list of references serves all chapters.

Chapter 1 treats the freshwater mussel fauna of the Tennessee River system noting factors which influence natural distribution patterns, such as geological history and stream size, and defining faunal associations. This chapter includes discussions of the history of the Tennessee River, the distribution of species throughout the drainage and problems involving systematics and nomenclature of the group. Distributional data, recent and historical, are presented, and the 70 species comprising the Tennessee River fauna are discussed in terms of ecological associations.

Chapter 2 deals with mussel community structure. Data resulting from quantitative sampling are presented and discussed in terms of species composition, density, diversity and age class distribution.

Chapter 3 examines siltation as a potential limiting factor to mussel distribution. Results of field and laboratory experiments on effects of siltation are presented, including mussel transplants, habitat characterization and feeding experiments.

CHAPTER 1

MUSSEL DISTRIBUTION AND FAUNAL ASSOCIATIONS

INTRODUCTION

The Tennessee River Drainage (Figure 1) extends from its headwaters in the Appalachian Mountains of Virginia and North Carolina, through Tennessee and the northern edge of Alabama into Kentucky where it merges with the Ohio River. This large river system has long supported a rich and diverse molluscan fauna, including many endemic forms.

Since establishment of the Tennessee Valley Authority in 1933, impoundment of the Tennessee River and its tributaries, and the subsequent industrialization of the Tennessee Valley has led to a great reduction in the molluscan fauna. In some rivers, such as the French Broad, the mussel fauna of the entire river has been extirpated by pollution. In large rivers, such as the Cumberland and Tennessee, mussel species requiring riverine conditions are limited to river reaches below navigation dams. A few headwater streams, such as the Clinch and Powell Rivers, maintain productive reaches which approximate the original fauna, while their extreme headwaters have been decimated by pollution and siltation from development and strip mining.

Enactment of the Endangered Species Act in 1973, and the subsequent listing of a number of freshwater mussels on the Federal List of Endangered and Threatened Wildlife has renewed interest in this fauna.

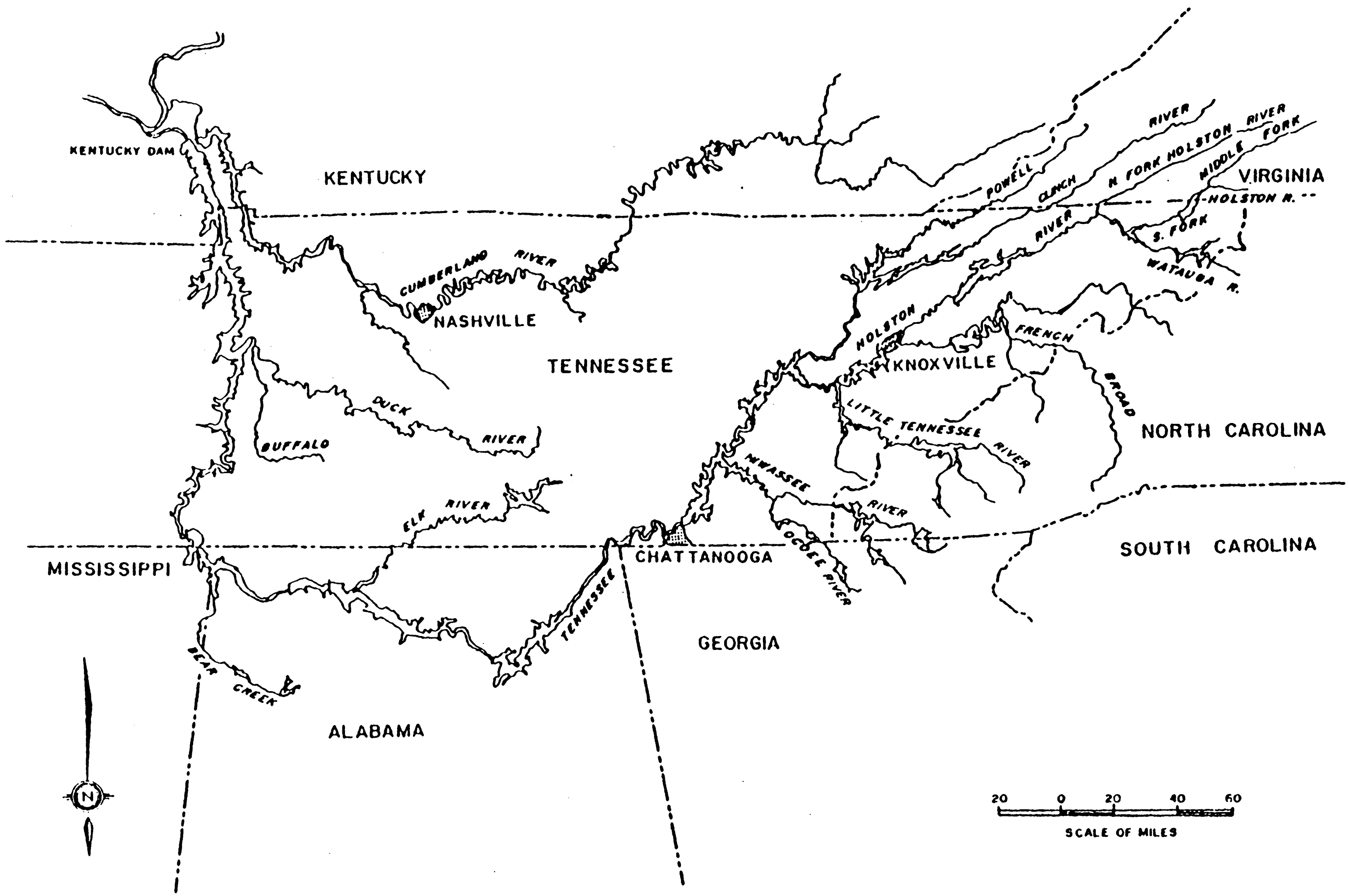


FIGURE I-1. PRINCIPAL RIVERS OF THE TENNESSEE VALLEY REGION

Attempts to predict the impacts of human activities on the continued well being of endangered molluscan species has been hindered by a lack of basic knowledge of the life history and ecological requirements of freshwater mussels.

Factors known to influence the distribution of freshwater mussels include geographic history, physical-chemical characteristics of the habitat, and distribution of host fish species.

Since mussel-host fish species relationships are largely unknown at this time, fish distribution will not be considered in the present study. It is assumed that the same environmental factors operate on mussel and fish species, influencing their distribution patterns in a similar manner.

The physical-chemical characteristics of a stream are largely determined by its geologic history. Historic records of mussel distribution throughout the Tennessee Valley attest to the physical-chemical suitability of this drainage for supporting a diverse molluscan fauna. Within this drainage, patterns of species distribution can be related to stream size and habitat type, including water depth, flow, and substrate type.

Recent changes in physical-chemical conditions of the rivers have resulted mainly in a reduction in the numbers and ranges of mussel species. While these changes have not always been defined, or documented, the faunal record stands as an index of this change.

The objective of the present study is to define the freshwater mussel fauna of the Tennessee River Drainage in terms of distribution and habitat preference. Based on recent and historic collection data, faunal assemblages are characterized on the basis of stream size and habitat type.

BACKGROUND

The Tennessee River

The headwaters of the Tennessee River drain the Ridge and Valley provinces of the Appalachian mountain range in western North Carolina, southwest Virginia and northeast Tennessee. The Tennessee River proper begins at the confluence of the Holston and French Broad Rivers at Knoxville, Tennessee. The river flows in a southwesterly direction through a wide valley to Chattanooga, Tennessee, where it takes a sharp westward turn through a steep gorge cut through Walden Ridge. Below the gorge, the river again assumes a southwesterly direction until it reaches Guntersville, Alabama, where it turns abruptly to the northwest; the lower river, below Muscle Shoals, Alabama, flows directly north to the Ohio River (Figure 1).

The unusual course of this river has prompted much speculation as to its history. Of particular interest is the reach of river which flows through Walden Gorge. Two hypotheses have been presented for the historical course of the Tennessee River, that of Hayes and Campbell (1894) and that of Johnson (1905a).

In a study of the geology of the Appalachian Region, Hayes and Campbell (1894) concluded that the headwaters of the Tennessee River once flowed south via an ancient (pre-Tertiary) Appalachian River which connected with what is now the Coosa River and flowed into the Gulf of

Mexico via the Alabama River. The section of the Tennessee River below Walden Gorge was part of the Sequatchie River Drainage which connected with what is now the Black Warrior River, tributary to the Tombigbee River (see Figure 2).

Hayes and Campbell proposed that a series of uplifts during the Tertiary set the stage for the capture of the upper Appalachian River by the Sequatchie River through Walden Ridge. Hayes (1899) further detailed a complex series of captures which he believed resulted in the river's present winding course through Walden Gorge. A subsequent capture resulted in diversion of the Sequatchie into the westward flowing Tennessee River, and a final capture of the lower Tennessee by the Ohio River resulted in its present northward course. Johnson (1905a), in disagreement with Hayes and Campbell, presents evidence that the Tennessee River has occupied its present course through Walden Gorge since the Cretaceous Period, with no historic connections to the Alabama River System. While Johnson's (1905a) criticism of Hayes and Campbell's conclusions are well presented and sound convincing, a number of biologists have pointed out that the faunal evidence does not support his contention. Simpson (1900b) observed similarities in mussel species assemblages in the Alabama and Tennessee River systems, noting, particularly, that members of the genus Pleurobema, abundant in the Tennessee and Alabama River drainages, were almost absent in the lower Mississippi River Drainage. He concluded, based solely on the distribution of mussel species assemblages, that a connection once

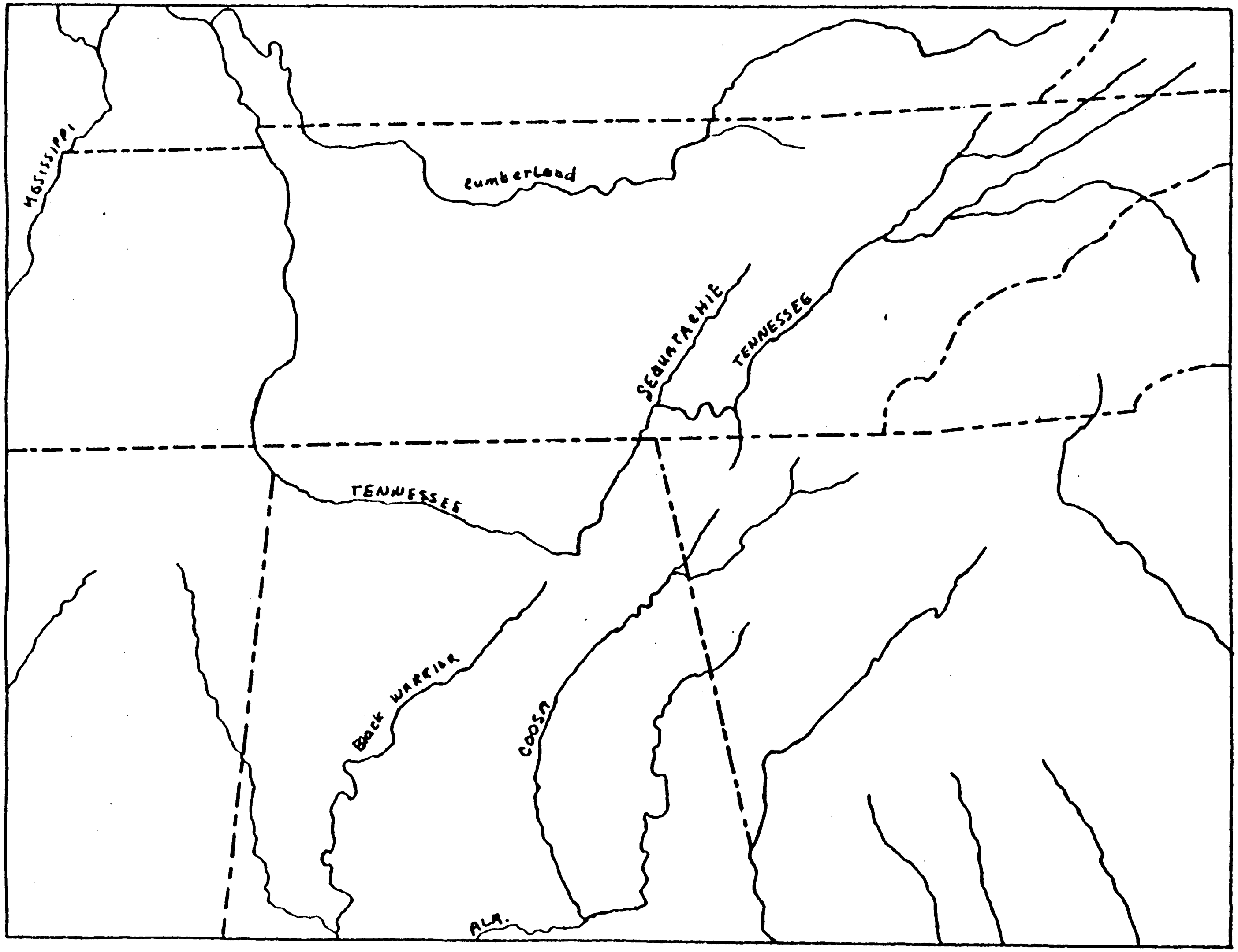


FIGURE I-2 LOCATION MAP after Johnson (1905) existed between the Tennessee and Alabama rivers, probably via the Coosa River, where the genus Pleurobema showed its greatest diversity. In defense of his conclusions, he stated (Simpson, 1900b, p.135):

> I could account for the distribution of these forms of life in no other way, because they cannot travel overland from river to river, but must have water communication in order to pass from one stream to another.

Johnson (1905b) attempted to discredit Simpson's argument by citing instances in which mussels were observed attached to the feet of birds and suggested that water connections were not necessary for the dispersal of mussels.

In a treatment of mussel distribution related to geomorphology, van der Schalie (1939a) presented a convincing argument against the distribution of mussels by birds, stating (van der Schalie, 1939a, p. 252):

> Considering all such specific [life history] requirements in combination with the absence of substantial proof that mussels have ever been transported successfully from one drainage to another by means of aquatic birds, I believe that we can dismiss such contentions until a time when someone can more carefully substantiate them.

In a comprehensive work on the Alleghenian divide and its influence on the freshwater fauna, Ortmann (1913) examined the distribution of freshwater mussels, snails and crayfish related to the geologic history of the Appalachian Mountains and concluded (p.381):

> I think that the present studies have demonstrated the fundamental fact, that certain freshwater animals are apt to furnish important evidence for past conditions of drainage by their present distribution, while others are not. The most important of the former are the Najades [naiades]

Ortmann (1913) also made reference to the "Tennessee-Coosa problem" pointing out in a detailed footnote (p.289) that while he considered Johnson's (1905a) physiographical evidence to be sound, he believed that Johnson was wrong in dismissing the faunal evidence which supported a connection between these two drainages. Ortmann further stated that the distribution of freshwater mussels indicated stream capture of tributaries of the Tennessee River by the Coosa River.

In a study of the freshwater mussels of the Cahaba River in northern Alabama, van der Schalie (1938a) presented evidence, based on faunal assemblages, for two geologic connections between the Tennessee and Alabama River systems. He proposed that a connection between larger streams of the two drainages allowed seven species to enter the Alabama system from the Tennessee, while a later connection between tributary streams allowed three creek species to enter the headwaters of the Alabama drainage.

Stream capture, as discussed by van der Schalie (1939a, 1945) and Ortmann (1913), is indicated as a mechanism which allows the migration of aquatic species across divides. This mechanism can account for patterns of distribution which can not be explained by random transport of individual mussels from one drainage to another by birds.

There have been no recent publications regarding the historical course of the Tennessee River which could resolve these conflicts. Ross (1971) gives an up to date account of the problem, concluding that the geological and biological arguments in favor of major drainage exchanges between the Tennessee and Gulf drainages are much stronger than the arguments against such an exchange. The exact location and direction of the exchange(s) are not known, however. Ross (1971) also presents evidence for a number of small stream captures within the upper Tennessee drainage.

The Mussel Fauna

North American Faunal Assemblages:

Several early workers (Simpson, 1896; Walker, 1918; Ortmann, 1924b) recognized patterns of molluscan distribution related to geomorphology. This concept was expanded by van der Schalie and van der Schalie (1950) who recognized six major faunal regions having distinct mussel species assemblages. These regions are: Atlantic, Pacific, Mississippian, Appalachicholan, Ozarkian, and Cumberlandian.

Two of these regions, the Atlantic and Pacific, support relatively few species. The Mississippian (Interior Basin) Region is the largest and supports the greatest mussel diversity. The Appalachicolan (West Floridian) region consists of elements of the Mississippian and southern Atlantic faunas as well as endemic species. The Ozarkian and Cumberlandian regions can be regarded as "pockets" of endemism within the Mississippian Region. These areas support endemic faunal assemblages and many species common to the Interior basin resulting in high species diversity.

Fauna of the Tennessee River:

The Tennessee River system supports both Cumberlandian and Ohioan faunal assemblages; the headwater reaches are primarily Cumberlandian, while the lower reaches of the Tennessee, Cumberland and Duck Rivers are almost entirely Ohioan.

The Cumberlandian mussel fauna has been defined and discussed in detail by A. E. Ortmann (1918, 1924b). His 1918 work on the mussel fauna of the upper Tennessee River drainage provides site specific collection records as well as ecological and taxonomic information on the fauna of the Tennessee River headwaters, above Knoxville, Tennessee.

In a detailed discussion of the mussel fauna of the Duck River in Tennessee, Ortmann (1924b) defined the Cumberlandian region geographically and faunally. Geographically, he included in the Interior Basin the Ohio, Cumberland and Tennessee River systems, with the Cumberlandian region (sub-basin) limited to the Cumberland River above Clarksville, Tennessee, and the Tennessee River above Muscle Shoals, Alabama; below these reaches, Cumberlandian species were not recorded. Ortmann further divided the Tennessee River into two faunal areas: that reach above Walden Gorge, supporting a primarily Cumberlandian fauna; and that below Walden Gorge, which was primarily Ohioan.

Ortmann (1924b) pointed out that the Duck River was Cumberlandian in its upper reaches and Ohioan in the lower portion. He further defined the fauna of this river in terms of its suspected origin. He listed endemic species which originated in and were confined to the Cumberlandian region and those species known to have originated in the Ohioan region and migrated into the Cumberland region. Additionally, many widespread species occurring throughout the Mississippi-Ohio basins, including the Cumberland Region, were listed as having unknown origin. These designations are indicated on Table I-19 (p. 62)

There are few early works documenting the fauna of the main stem Tennessee River, particularly the lower reaches. The fauna of the Tennessee River below Walden Gorge was treated by Ortmann (1925) in a work based in part on museum records, and in part on his own collections from 4 stations. At this time, there were no collection records from the Tennessee River below Ortmann's lowermost site at Dixie, Tennessee, now inundated by Kentucky Reservoir near New Johnsonville, Tennessee. In his 1925 work, Ortmann documented the change from Cumberlandian to Ohioan fauna in the Tennessee River below Muscle Shoals, Alabama, and speculated on species which might inhabit the lower river.

H. van der Schalie (1939b) reporting on collections made by Ellis in 1931, expanded on Ortmann's (1925) work, adding species records from the lower Tennessee River in Tennessee and Kentucky. Bates (1962) first documented the decline of riverine species and the colonization of overbank areas resulting from impoundment of the Tennessee River by Kentucky Dam. Additional reports on the fauna of the Tennessee River are included in Scruggs (1960), Isom (1965, 1969), Bates (1967, 1975), Stansbery (1972), Yokley (1972) Bates and Dennis (1981) and Sickle and Chandler (1981).

Historical records for the Cumberlandian fauna are provided by Cahn (1936) and Hickman (1936) who examined the mussel fauna of reaches of the Clinch and Powell Rivers prior to their impoundment by Norris Dam. The fauna of the Duck River, Tennessee, was described by Ortmann (1924b) and van der Schalie (1973), reporting on collections made in 1939. More recent records include those of Isom and Yokley (1968b) and Ahlstedt (1981a). The fauna of the Cumberland River was treated by Wilson and Clark (1914) and Neel and Allen (1964).

A number of more recent works provide distribution records for headwater rivers including the Clinch (Stansbery, 1973; Bates and Dennis, 1978), Powell (Ahlstedt and Brown 1980; Dennis, 1981), North Fork Holston (Stansbery and Clench, 1974; Ahlstedt, 1980b), and the South Fork Holston (Stansbery and Clench, 1978). Neves et al. (1980) reported on the fauna of the upper Tennessee River in Virginia. Records for tributary streams include those for Copper Creek (Ahlstedt, 1981b) and Big Moccasin Creek (Neves and Zale, 1982).

Additional mussel distribution records for the Tennessee drainage include those of the Flint and Paint Rock Rivers in Northern Alabama (Isom et al., 1973b), the Elk River in Tennessee and Alabama (Isom et al. 1973a; Ahlstedt, 1982) and the Stones river (Schmidt, 1982).

The references cited here include major distributional works for the Tennessee Basin. However, many additional references on the molluscs of the Tennessee Valley are contained in Shoup's (1974) annotated bibliography of the zoology of the Tennessee Valley Region. An updated bibliography of the mussels in the state of Tennessee was prepared by Bates and Dennis (1981).

Habitat Requirements of Freshwater Mussels

Information on the habitat requirements of freshwater mussels is sparse and widely scattered through the literature. While some ecological information is contained in many of the distributional accounts, there are few works dealing specifically with ecological requirements. Most early accounts of the fauna consisted of lists of species attributed to rivers. Habitat type was only occasionally mentioned in regards to a particular species or collection. Likewise, there was generally no indication as to the number of specimens collected or estimates of relative abundance of species.

Two important works which relate the distribution of mussels to stream size and habitat type are Dawley's (1947) paper on the mussels of the upper Mississippi River, and van der Schalie's (1938b) treatment of the mussel fauna of the Huron River drainage in Michigan. Some information on distribution of Cumberlandian species related to stream size and habitat type can be gleaned from Ortmann's (1918) work on the mussels of the upper Tennessee River, although the emphasis of this work was not placed on habitat characterization.

One paper dealing specifically with habitat is Boycott's (1936) description of the habitats of the freshwater mollusca of Great Britain. While this work is comprehensive in scope, the fauna of Great Britain includes few unionids, and little habitat comparable to that found in the Tennessee River drainage.

There are numerous papers dealing with the mussel fauna of specific geographic regions which contain some information as to the habitats in which various species were found. Such works include: Ortmann (1911) and Dennis (1970) on the mussels of Western Pennsylvania, Isley (1925) on the mussels of Oklahoma, Call (1900) and Goodrich and van der Schalie (1944) on the molluscs of Indiana, Baker (1928a) on the mussels of Wisconsin, Murray and Leonard (1962) on the mussels of Kansas, Parmalee (1967) on the mussels of Illinois, and Clarke (1973) on the mussels of the Canadian Interior Basin. In addition, there are many works on the mussel fauna of specific river systems of North America. A few of the more important for the present purpose include: Danglade (1914), Baker (1922), and Starett (1971), as well as those previously mentioned with regard to the fauna of the Tennessee River system.

Much early work on the biology and ecology of freshwater mussels was done by workers associated with the Bureau of Commercial Fisheries who were interested in sustaining and enhancing a commercial mussel fishery. Some of the more important of these works include: Lefevre and Curtis (1912) and Coker et al. (1921) on natural history and propagation, and Allen (1914, 1921a, 1921b, 1923) on biology of freshwater mussels. Isley (1913) looked at growth and migration of mussels. Ellis (1931) examined factors affecting the replacement of freshwater mussels, attributing the replacement of riverine with lake species following impoundment to the accumulation of erosion silt behind the dams.

The influence of environment on shell morphology was noted by many early workers. Ortmann (1918) recognized differences in shell shape of the same species taken from different habitats and designated forms based on these variations. He expanded on these observations in a paper (Ortmann, 1920) correlating shape with "station" (location) in freshwater mussels. His conclusion, later referred to as "Ortmann's Law" by van der Schalie (1939a), briefly stated is that mussel species are generally more compressed in the headwater reaches of a river and exhibit greater inflation downstream. Additionally, he noted that with the increased compression (decrease in diameter) there was often an increase in the length of the shell. This is particularly true for conservative genera, including *Fusconaia*, *Pleurobema* and *Lexingtonia*, for which Ortmann named forms based on the ratio of diameter to length of the shell.

Grier and Mueller (1926) followed up on Ortmann's work with examples from the Mississippi River, including observations on the shape of shells inhabiting impounded waters. Baker (1928a), working on the mussel fauna of Wisconsin, documented changes in shell shape of species which had adapted from riverine to lake habitats and noted the demise of species which were unable to adapt. Studies of the Lake Erie fauna by Brown, Clark and Gleissner (1938) and van der Schalie (1941) reported stunting in a number of widespread species inhabiting the lake.

Taxonomic Status of Freshwater Mussels

Although the main emphasis of this work is not taxonomic, it is difficult to work in a field in which the nomenclature is so unstable without addressing this problem. This account of the status of nomenclature and systematics in the freshwater mussels, while not definitive, is meant to serve as a brief review of the present problem.

An excellent overview of the situation is given by van der Schalie (1952) in a paper titled "An Old Problem in Naiad Nomenclature". This paper was reprinted 20 years later with a preface by the author stating "The subject was an 'old problem' then and it is somewhat 'older ' now." The problem still exists - older yet, with no solution in sight.

Nomenclature:

The nomenclature of freshwater mussels of North America is unsettled and often the subject of controversy. This lack of stability has led to continuous name changes, often without explanation. The lack of agreement on nomenclatural issues is particularly distressing when species in question appear on endangered species lists or are the subject of environmental litigation. At present, there is no mechanism for resolving taxonomic disputes other than petitioning the International Committee on Zoological Nomenclature for a ruling, a laborious and time consuming procedure. While it is within the scope of this committee to aid in the resolution of otherwise insurmountable nomenclatural problems, it does not seem the function of this group (as some malacologists suggest) to rule upon every generic designation for which more than one name has been proposed. A better resolution would be for workers in the field to submit to arbitration by a jury of peers, as has been the case in some fields (e.g. Icthyology).

While nomenclatural instability is not unique to malacology, it is an important problem in this field, particularly for the non-taxonomist. The problem in a broader context was aptly stated by Elton and Miller (1954):

> There is enormous inconvenience and a good deal of wasted time for ecologists in mere changes of nomenclature unaccompanied by substantive discovery of new genetic groupings. One of the hopes of all ecological surveyors is a stabilized nomenclature.

Since early taxonomy was based solely on shell characters, the animals were generally cooked out and the soft parts discarded by collectors, a practice which greatly facilitated transport and storage of the specimens. Shells were often collected with no notation as to relative abundance, habitat type or condition of the animal.

Some early collections from North America were sent to Lamarck to be named, and the types deposited in European museums. Many more species were named by independent workers with scanty collections and poor locality data. Rafinesque, who traveled the country naming species, created much confusion among those who followed by failing to designate reliable type specimens. His species descriptions, written in French, were often ambiguous and poorly illustrated. Consequently, other workers, particularly Lea, Say, and Barnes, ignored Rafinesque's' work in describing new species. This resulted in a proliferation of names attributable to the same species.

Charles Torrey Simpson attempted to bring some order to the chaos by publishing his Synopsis of the Naiades (1900a), followed by his monumental Descriptive Catalogue of the Naiades (1914). In the introduction to the Catalogue, he summarized the situation as follows:

> The literature is scattered, expensive, largely out of print and in many cases practically unattainable. The necessary consequence has been that the identification of nearly all of the rarer species has been based upon the individual conceptions of the more prominent collectors rather than on a careful study of the original descriptions.

Walker (1918) prepared a synopsis of the classification of all of the freshwater mollusca of North America. Basing his classification of the freshwater mussels on the works of Simpson (1900a, 1914) and Ortmann (1910, 1912) he presented a guide which included keys and illustrations of the shells and soft part anatomy. Still the nomenclature was confused.

In an attempt to clear up the confusion, Ortmann and Walker, with Pilsbry acting as arbiter, began a complete revision of the unionid nomenclature. Frierson was initially involved in the venture, but eventually refused to submit to the system of arbitration the others had established and went his separate way (van der Schalie, 1952). Ortmann and Walker reviewed species descriptions, discarding those for which a type could not be designated with certainty. This resulted in abandonment of many of Rafinesque's species. Frierson (1927) published his own work championing Rafinesque, who he thought was treated unjustly by his co-workers. Although the revision by Ortmann and Walker (1922) was adopted by many malacologists, there remained a school of malacological thought dedicated to the resurrection of Rafinesque's' taxonomy.

For more than a decade, some workers in the field have pleaded for an end to the name changing by proposing adherence to the "50-year rule" of zoological nomenclature, a move that would expedite arrival at a stable system. Recent changes in the International Code of Zoological Nomenclature, however, have resulted in abandonment of this rule in favor of a system based entirely on priority. This has opened the door to a rash of name changes based on reinterpretation of Rafinesque's' species descriptions.

Systematics:

Our knowledge of the systematic relationships of the freshwater mussels has not profited by a pre-occupation with nomenclatural problems. There have been few major works dealing with the systematics of this group. Prior to Simpson's (1900a) Synopsis, taxonomy was based primarily on shell characters. While a few authors had addressed the anatomy of freshwater mussels, information was scattered and incomplete. Based on his review of the literature and personal observation, Simpson devised a system of classification of the freshwater mussels of the world. Using a combination of anatomical and shell characters, he defined 2 families, 2 sub-families, and a number of generic groupings. Simpson used this system as a basis for his Catalogue, which was completed in 1901, although not published until 1914.

In the meantime, Ortmann (1910) defined a system of higher classification based primarily on reproductive anatomy. His revision of the families and genera of freshwater mussels (Ortmann, 1912) gained wide acceptance, and is still widely used.

Modell (1942) devised a taxonomic system based primarily on beak (umbo) sculpture of the shell. This system has not gained wide acceptance since most workers recognize that shell characters alone are not adequate to define higher levels of classification. More recent work by Modell (1964) attempting to incorporate anatomical characters does not depart much from his original system.

Subsequent workers (Morrison, 1955: Hass, 1969) have attempted to reorganize the taxonomic system with little success. More recently, Heard and Guckert (1970) devised a complex system of classification based primarily on reproductive anatomy which combines elements of the previous systems resulting in three North American families with eight sub-families.

There have been a few recent attempts to revise the nomenclature of generic groups of Unionids based on systematic relationships. Johnson

(1978) in attempting to revise the genus Plagiola (=Dysnomia =Epioblasma) has presented a useful treatment of the species, while confounding problems at the generic level. His attempt to substitute Plagiola for the more widely recognized Dysnomia (or the recently resurrected Epioblasma) has not gained wide acceptance.

Clarke (1981) revised the tribe Alasmidontini of the sub-family Anodontinae providing a comprehensive treatment of three genera.

In the absence of additional scholarly revisions of the Unionidae, workers in the field of malacology are left to choose from a variety of names proposed by taxonomists, with no resolution in sight.

In the present work, the system of classification used is that of Ortmann (1912). This classification of the North American fauna is as follows:

- CLASS Lamellebranchia
  - ORDER Eulamellebranchia
    - FAMILY Margaritanidae
    - FAMILY Unionidae
      - SUB-FAMILY Unioninae
      - SUB-FAMILY Anodontinae
      - SUB-FAMILY Lampsilinae

The nomenclature used in this work is based primarily on Ortmann and Walker (1922) and on a number of subsequent works by Ortmann (1924b, 1925) and van der Schalie (1938b, 1973).

METHODS AND MATERIALS

From 1973 to 1981, a comprehensive evaluation of the distribution of fresh water mussels was conducted in the Tennessee River basin. Rivers sampled include the North Fork Holston, South Fork Holston, Middle Fork Holston, Clinch, Powell, and Duck as well as tributary streams including Big Moccasin, Little Moccasin, Brumley and Copper Creeks. Additionally, portions of the main stem Tennessee and Cumberland Rivers were sampled. Observations as to habitat were noted for all collections.

Small to medium sized streams were sampled in as many locations as possible as determined by access. Intensive collecting was concentrated in shallow riffles and shoal areas which are characteristically more productive than the deeper, slow moving pools. Sampling methods used here included primarily hand picking or pollywogging; a fish scope and Needham scraper were used where applicable. In areas too deep to wade, snorkel and SCUBA were used.

In large rivers, selected areas were sampled intensively. A 35 mile reach of the Cumberland River was sampled intensively. The Tennessee River was sampled at a number of sites throughout Kentucky Lake. Where hand picking was not possible, collecting was aided by the use of SCUBA and commercial harvest methods. In the Cumberland River, SCUBA gear was used to sample mussels from beds previously identified by commercial musselers. In Kentucky Lake, commercial musselers also aided in the location of mussel beds and in the collection of samples. In riverine portions of the lake, below Pickwick Dam, brailing was the primary collection method. In backwater and overbank areas, hand picking and diving were employed.

While collection data were recorded on a site specific basis, all sites are not listed here. For the purpose of this study, species records are listed for river reaches rather than individual sites.

RESULTS

Recent and historic mussel records for small streams of the Tennessee system are presented in Tables I-1 through I-6. All streams, except the Middle Fork Holston (Table I-2) show a decrease in the number of species over time. The apparent increase in species reported for the Middle Fork Holston is probably due to a greater sampling effort in recent studies rather than to an actual increase in numbers of species.

Table I-7 summarizes recent species records for small streams and presents, for comparison, historic totals. The streams are listed from left to right in order of increasing size. As indicated by historic totals, the number of mussel species which may be expected to inhabit a stream increases with increasing stream size. Comparison of recent to historical totals gives an indication of the degree to which the stream has been subjected to habitat alteration in recent years. Only two of the five streams listed have maintained a significant mussel fauna. For comparative purposes, Table I-8 summarizes species records from several small streams in the Ohio River drainage in Pennsylvania (Dennis, 1970). With the exception of French Creek, streams listed are comparable in size to Big Moccasin Creek. All streams except for Oil Creek and French Creek, showed evidence of pollution. Historical records are not available for all of these streams.

French Creek is comparable in size and gradient to the Middle Fork

Holston River and supports a comparable number of species. The species composition differs considerably, however, reflecting differences between the Cumberlandian and Ohioan regions. A striking difference is observed in the subfamily Anodontinae, which has few representatives in the upper Tennessee system.

Recent and historical species records for medium sized streams in the Tennessee River drainage are presented in Tables I-9 through I-12 and summarized in Table I-13. Three of the four streams listed show that contemporary species numbers compare favorably to historical totals.

In Tables I-15 and I-16, recent and historical species records are presented for reaches of the Cumberland and Tennessee Rivers. The Cumberland River (Table I-15), sampled between river mile 270 and 305, supports representatives of both the Cumberlandian and Ohioan mussel faunal assemblages, and would, therefore, be comparable to areas of the Tennessee River above Muscle Shoals. The Tennessee River (Table I-16) was sampled in Kentucky Lake, beginning approximately 60 miles below Muscle Shoals. In this reach, the fauna is primarily that of the Ohio Basin, with few records of Cumberlandian elements.

TABLE I-1

MUSSEL SPECIES RECORDS, RECENT AND HISTORIC
BIG MOCCASIN CREEK
Scott Co., VA

Mussel species	Ortmann (1918)	Dennis collections, 1979
Unioninae:		
Fusconaia cuneolus	x	-
F. barnesiana	x	x
Pleurobema oviforme	x	-
Quadrula cylindrica	x	-
Anodontinae:		
Alasmidonta marginata	x	-
A. minor	x	-
Pegias fabula	x	-
Lampsilinae:		
Dysnomia capsaeformis	x	-
Lampsilis fasciolaris	x	-
L. ovata ventricosa	x	x
Medionidus conradicus	x	x
Ptychobranchus subtentum	x	-
Villosa (=Micromya) nebulosa	x	x
V. vanuxemensis	x	x
Totals	14	5

TABLE I-2

MUSSEL SPECIES RECORDS, RECENT AND HISTORIC
MIDDLE FORK HOLSTON RIVER

Mussel species	Ortmann (1918)	Dennis collections, 1979
Unioninae:		
Cyclonaias tuberculata	-	x
Elliptio dilatatus	x	x
F. barnesiana	x	x
Lexingtonia dollabelloides	-	x
Pleurobema oviforme	x	x
Anodontinae:		
Alasmidonta marginata	x	x
A. minor	x	-
Lasmigona costata	x	x
L. holstonia	-	x
Lampsilinae:		
Actinonaias carinata	-	x
A. pectorosa	-	x
Dysnomia florentina walkeri	x	x
Lampsilis fasciolaris	x	x
L. ovata ventricosa	-	x
Medionidus conradicus	x	x
Ptychobranchus fasciolaris	-	x
P. subtentum	x	x
Villosa (=Micromya) nebulosa	x	x
V. vanuxemensis	x	x
Totals	14	5 18

TABLE I-3

MUSSEL SPECIES RECORDS, RECENT AND HISTORIC
SOUTH FORK HOLSTON RIVER

	Ortmann (1918)	Stansbery and Clench (1978)	Dennis 1979
Unioninae:			
Elliptio dilatatus	x	x	-
Pleurobema oviforme	x	x	-
Anodontinae:			
Alasmidonta marginata	x	-	-
A. minor	x	-	-
Lasmigona costata	x	x	-
Pegias fabula	x	x	-
Lampsilinae:			
Actinonaias pectorosa	x	x	-
Dysnomia florentina walkeri	x	-	-
Lampsilis fasciolaris	x	x	-
Medionidus conradicus	x	x	-
Ptychobranchus subtentum	x	-	-
Villosa (=Micromya) nebulosa	x	x	-
V. vanuxemensis	x	x	x -
Totals	12	9	0

TABLE I-4

MUSSEL SPECIES RECORDS, RECENT AND HISTORIC
NORTH FORK HOLSTON RIVER
Headwaters, Smythe Co., Virginia

Mussel species	Ortmann (1918)	Dennis 1978*
Unioninae:		
Fusconaia barnesiana	x	x
F. edgariana	-	x
Lexingtonia dollabelloides	x	x
Pleurobema oviforme	x	x
Anodontinae:		
Alasmidonta marginata	x	-
A. minor	x	x
Lasmigona costata	x	x
Strophitus rugosus	x	-
Lampsilinae:		
Actinonaias pectorosa	x	x
Carunculina moesta	x	-
Lampsilis fasciolaris	x	x
L. ovata ventricosa	x	x
Medionidus conradicus	x	x
Pegias fabula	x	-
Ptychobranchus fasciolaris	-	x
P. subtentum	x	x
Villosa (=Micromya) nebulosa	x	x
V. vanuxemensis	x	x
Totals	14	5
	16	14

* recent collections

TABLE I-5

MUSSEL SPECIES RECORDS, RECENT AND HISTORIC
CLINCH RIVER
Headwaters (CRM 296-340)

Mussel species	Ortmann (1918)	Bates and Dennis (1978)
Unioninae:		
Elliptio dilatatus	x	-
Fusconaia barnesiana	x	x
F. pilaris	x	-
Lexingtonia dollabelloides	x	-
Pleurobema oviforme	x	-
Quadrula cylendrica	x	-
Anodontinae:		
Alasmidonta marginata	x	-
A. minor	x	-
Lasmigona costata	x	-
Strophitus rugosus	x	-
Lampsilinae:		
Dysnomia capsaeformis	x	-
D. haysiana	x	-
Lampsilis fasciolaris	x	x
L. ovata ventricosa	x	-
Medionidus conradicus	x	x
Ptychobranchus fasciolaris	-	x
P. subtentum	x	-
Villosa (=Micromya) nebulosa	x	x
V. perpurpurea	x	-
Totals	19	5

TABLE I-6

MUSSEL SPECIES RECORDS, RECENT AND HISTORIC
POWELL RIVER
Headwaters (PRM 145-180)

Mussel species	Ortmann (1918)	Dennis (1981)
Unioninae:		
Amblema costata	-	x
Elliptio dilatatus	x	x
Fusconaia barnesiana	x	x
F. cuneolus	x	-
F. pilaris	x	-
Lexingtonia dollabelloides	x	-
Pleurobema oviforme	x	-
Quadrula cylindrica	x	-
Anodontinae:		
Alasmidonta marginata	x	-
A. minor	x	-
Lasmigona costata	x	-
Strophitus rugosus	x	-
Lampsilinae:		
Actinonaias carinata	-	x
Carunculina moesta	x	-
Lampsilis fasciolaris	x	-
L. ovata ventricosa	x	x
Medionidus conradicus	x	-
Pegias fabula	x	-
Ptychobranchus subtentum	x	-
Villosa (=Micromya) nebulosa	x	x
V. perpurpurea	x	-
V. vanuxemensis	x	x
Totals	21	6
	20	7

TABLE I-7

COMPARISON OF MUSSEL FAUNA OF SMALL STREAMS
BASED ON RECENT RECORDS

Mussel species	Sites 1	2	3	4	5
Unioninae:					
Amblema costata	-	-	-	-	x
Cyclonaias tuberculata	-	-	x	-	-
Elliptio dilatatus	-	-	x	-	x
Fusconaia barnesiana	x	x	x	x	x
F. edgariana	-	x	-	-	-
Lexingtonia dollabelloides	-	-	x	-	-
Pleurobema oviforme	-	x	x	-	-
Anodontinae:					
Alasmidonta marginata	-	-	x	-	-
Lasmigona costata	-	x	x	-	-
L. holstonia	-	-	x	-	-
Lampsilinae:					
Actinonaias carinata	-	-	x	-	x
A. pectorosa	-	x	x	-	-
Dysnomia florentina walkeri	-	-	x	-	-
Lampsilis fasciolaris	-	x	x	x	-
L. ovata ventricosa	x	x	x	-	x
Medionidus conradicus	x	x	x	x	-
Ptychobranchus fasciolaris	-	-	x	x	-
P. subtentum	-	x	x	-	-
Villosa (=Micromya) nebulosa	x	x	x	x	x
V. vanuxemensis	x	x	x	-	-
Totals	5	11	18	5	6
Historical Totals	14	16	12	19	21

Sites: 1. Big Moccasin Creek; 2. North Fork Holston, headwaters; 3. Middle Fork Holston River; 4. Clinch River, headwaters; 5. Powell River, headwaters.

x= species present
-= species absent

TABLE I-8

COMPARISON OF MUSSEL FAUNA OF SMALL STREAMS IN THE OHIO RIVER DRAINAGE, PENNSYLVANIA

Mussel species	Sites: 1	2	3	4	5	6
Unioninae:						
Amblema costata	-	-	x	-	-	-
Elliptio dilatatus	-	x	-	x	x	x
Fusconaia flava	-	-	-	-	x	-
F. subrotunda	-	x	-	-	-	-
Pleurobema clava	-	-	x	-	x	x
P. cordatum	-	-	x	-	-	x
Quadrula cylindrica	-	-	x	-	-	x
Anodontinae:						
Alasmidonta marginata	-	-	-	x	-	x
Anodonta grandis	-	-	-	x	x	x
A. imbecillis	-	-	-	-	-	x
Anodontoides ferusscianus	-	-	-	-	-	x
Lasmigona compressa	-	-	-	x	x	x
L. costata	-	x	-	x	x	x
L. viridis	-	-	-	-	-	x
Strophitus rugosus	x	x	-	x	x	x
Lampsilinae:						
Actinonaias carinata	-	-	x	x	x	x
Dysnomia perplexa (=rangiana)	-	-	-	-	-	x
D. triquetra	-	-	-	-	-	x
Lampsilis fasciola	-	x	-	x	x	-
L. ovata ventricosa	-	x	-	x	x	x
L. radiata	-	-	-	x	-	x
L. siliquoidea	-	x	x	x	x	x
Ptychobranchus fasciolaris	-	-	-	x	-	x
Villosa (=Micromya) fabalis	-	-	-	x	-	x
Totals	1	7	6	12	12	19
Historical Totals	9	na	na	na	na	21

Sites: 1. Buffalo, 2. Little Mahoning, 3. Muddy, 4. Oil, 5. Sandy, 6. French Creeks.

x= species present -=species absent na= not available

TABLE I-9

MUSSEL SPECIES RECORDS, RECENT AND HISTORIC
CLINCH RIVER, TENNESSEE AND VIRGINIA
Middle Section (CRM 190-280)

Mussel species	Ortmann (1918)	Bates and Dennis (1978)
Margaritiferidae		
Cumberlandiinae:		
Cumberlandia monodonta	x	x
Unionidae		
Unioninae:		
Amblema costata	x	x
Cyclonaias tuberculata	x	x
Elliptio dilatatus	x	x
Fusconaia barnesiana	x	x
F. cuneolus	x	x
F. edgariana	x	x
F. pilaris	x	-
Lastena lata	x	x
Lexingtonia dollabelloides	x	-
Plethobasus cyhyus	x	x
Pleurobema cordatum	x	x
P. oviforme	x	x
Quadrula cylindrica	x	x
Q. pustulosa	-	x
Anodontinae:		
Alasmidonta marginata	x	x
A. minor	x	-
Lasmigona costata	x	x
Strophitus rugosus	x	x
Lampsilinae:		
Actinonaias carinata	x	x
A. pectorosa	x	x
Carunculina moesta	x	-
Conradilla caelata	x	-
Cyprogenia irrorata	-	x
Dromus dromas	-	x

TABLE I-9 (Continued)

Mussel species	Ortmann (1918)	Bates and Dennis (1978)
Lampsilinae (continued):		
Dysnomia capsaeformis	x	x
D. brevidens	x	x
D. torulosa gubernaculum	x	x
D. triquetra	x	x
Lampsilis fasciola	x	x
L. ovata ventricosa	x	x
Leptodea fragilis	-	x
Ligumia recta latissima	x	x
Medionidus conradicus	x	x
Proptera alata	x	x
Ptychobranchus fasciolaris	x	x
P. subtentum	x	x
Truncilla trucata	x	x
Villosa (=Micromya) nebulosa	x	x
V. perpurpurea	x	-
V. vanuxemensis	x	x
Totals	39	36

TABLE I-10

MUSSEL SPECIES RECORDS, RECENT AND HISTORIC
POWELL RIVER, TENNESSEE AND VIRGINIA
Middle Section (PRM 80-141)

Mussel species	Ortmann (1918)	Dennis (1981)
Unioninae:		
Amblema costata	x	x
Cyclonaias tuberculata	-	x
Elliptio crassidens	x	x
E. dilatatus	x	x
Fusconaia barnesiana	x	x
F. cuneolus	x	-
F. edgariana	x	x
Lastena lata	-	x
Lexingtonia dollabelloides	x	-
Plethobasus cyhyus	x	x
Pleurobema oviforme	x	x
Quadrula cylindrica	x	x
Q. intermedia	-	x
Q. pustulosa	-	x
Q. sparsa	-	x
Anodontinae:		
Alasmidonta marginata	x	x
Lasmigona costata	x	x
Strophitus rugosus	-	x
Lampsilinae:		
Actinonaias carinata	x	x
A. pectorosa	x	x
Carunculina moesta	x	-
Conradilla caelata	x	x
Dromus dromas	x	x
Dysnomia brevidens	x	x
D. capsaeformis	x	x
D. haysiana	x	-
D. torulosa gubernaculum	x	-
D. triquetra	x	x
Lampsilis fasciola	x	x
L. ovata ventricosa	-	x
Leptodea fragilis	-	x
Ligumia recta latissima	-	x
Medionidus conradicus	x	x
Proptera alata	-	x
Ptychobranchus fasciolaris	x	x
P. subtentum	x	x
Truncilla trucata	-	x
Villosa (=Micromya) nebulosa	x	x
V. vanuxemensis	-	x
Totals	30	35

TABLE I-11

MUSSEL SPECIES RECORDS, RECENT AND HISTORIC
DUCK RIVER, TENNESSEE
Lower Section (DRM 15-180)

Mussel species	Otrmann (1924) van der Schalie (1931)	Dennis 1972-76*
Unioninae:		
Amblema costata	x	x
Cyclonaias tuberculata	x	x
Elliptio dilatatus	x	x
Fusconaia barnesiana	x	x
Lexingtonia dollabelloides	x	x
Megalonaias gigantea	x	x
Pleurobema cordatum	x	-
P. oviforme	-	x
Quadrula cylindrica	x	x
Q. pustulosa	x	-
Q. quadrula	x	-
Tritogonia verrucosa	x	x
Anodontinae:		
Alasmidonta marginata	x	x
Anodonta grandis	x	-
A. imbecillis	x	-
Lasmigona complanata	x	x
L. costata	x	x
Strophitus rugosus	x	-
Lampsilinae:		
Actinonaias carinata	x	x
A. pectorosa	x	x
Carunculina moesta	x	x
Conradilla caelata	x	x
Dysnomia brevidens	x	x
D. capsaeformis	x	x
D. florentina	x	-
D. triquetra	x	-
Lampsilis anodoontoides	x	-
L. fasciola	x	x
L. ovata ventricosa	x	x
Leptodea fragilis	x	x
Medionidus conradicus	x	x
Obliquaria reflexa	-	x
Obovaria subrotunda	x	x
Proptera alata	x	x
Ptychobranchus fasciolaris	x	-
Villosa (=Micromya) fabalis	x	-
V. vanuxemensis	x	x
Totals	35	27

* Collection records

TABLE I-12

MUSSEL SPECIES RECORDS, RECENT AND HISTORIC
NORTH FORK HOLSTON RIVER
Lower Section, Scott, Hawkins Co.

Mussel species	Ortmann (1918)	Dennis 1978*
Unioninae:		
Amblema costata	x	x
Cyclonaias tuberculata	x	-
Elliptio dilatatus	x	-
Fusconaia barnesiana	x	-
F. cuneolus	x	-
F. edgariana	x	-
F. pilaris	x	-
Lexingtonia dollabelloides	x	-
Pleurobema oviforme	x	-
Quadrula cylindrica	x	-
Anodontinae:		
Alasmidonta marginata	x	-
Lasmigona costata	x	-
Strophitus rugosus	x	-
Lampsilinae:		
Actinonaias carinata	x	-
A. pectorosa	x	x
Carunculina moesta	x	-
Conradilla caelata	x	-
Dysnomia brevidens	x	-
D. capsaeformis	x	x
D. haysiana	x	-
D. lenoir	x	-
D. torulosa gubernaculum	x	-
D. triquetra	x	-
Lampsilis fasciola	x	x
L. ovata ventricosa	-	x
Ligumia recta latissima	-	x
Medionidus conradicus	x	-
Plethobasus cyphyus	x	-
Proptera alata	x	-
Ptychobranchus fasciolaris	x	-
P. subtentum	x	x
Villosa (=Micromya) fabalis	x	-
V. nebulosa	x	x
V. perpurpurea	x	-
V. vanuxemensis	-	x
Totals	35	9

TABLE I-13

COMPARISON OF MUSSEL FAUNA OF MEDIUM SIZED STREAMS
BASED ON RECENT RECORDS

Mussel species	River: North Fork Holston	Duck	Powell	Clinch
Margaritiferidae				
Cumberlandiinae:				
Cumberlandia monodonta	-	-	-	x
Unionidae				
Unioninae:				
Amblema costata	x	x	x	x
Cyclonaias tuberculata	-	x	x	x
Elliptio crassidens	-	-	x	x
E. dilatatus	-	x	x	x
Fusconaia barnesiana	-	x	x	x
F. cuneolus	-	-	-	x
F. edgariana	-	-	x	x
F. pilaris	-	-	x	-
Lastena lata	-	-	x	x
Lexingtonia dollabelloides	-	x	-	-
Megalonaias gigantea	-	x	-	-
Plethobasus cyhyus	-	-	x	x
Pleurobema cordatum	-	-	-	x
P. oviforme	-	x	x	x
Quadrula cylindrica	-	x	x	x
Q. intermedia	-	-	x	-
Q. pustulosa	-	x	x	x
Q. sparsa	-	-	x	-
Tritogonia verrucosa	-	x	-	-
Anodontinae:				
Alasmidonta marginata	-	x	x	x
Lasmigona complanata	-	x	-	-
L. costata	-	x	x	x
Strophitus rugosus	-	-	x	x

TABLE I-13 (continued)

Mussel species	River: North Fork Holston	Duck	Powell	Clinch
Lampsilinae:				
Actinonaias carinata	-	x	x	x
A. pectorosa	x	x	x	x
Carunculina moesta	-	x	-	-
Conradilla caelata	-	x	x	x
Cyprogenia irrorata	-	-	-	x
Dromus dromas	-	-	x	x
Dysnomia brevidens	-	x	x	x
D. capsaeformis	x	x	x	x
D. torulosa gubernaculum	-	-	-	x
D. triquetra	-	-	x	x
Lampsilis fasciola	x	x	x	x
L. ovata ventricosa	x	x	x	x
Leptodea fragilis	-	x	x	x
Ligumia recta latissima	x	-	x	x
Medionidus conradicus	-	x	x	x
Obliquaria reflexa	-	x	-	-
Obovaria subrotunda	-	x	-	-
Proptera alata	-	x	x	x
Ptychobranchus fasciolaris	-	x	x	x
P. subtentum	x	-	x	x
Truncilla truncata	-	-	x	x
Villosa (=Micromya) nebulosa	x	-	x	x
V. vanuxemensis	x	x	x	x
Totals	9	27	35	37
Historical Totals	35	35	30	39

x= species present -= species absent

TABLE I-14

MUSSEL RECORDS, OHIO RIVER DRAINAGE
ALLEGHENY RIVER, PENNSYLVANIA

Mussel species	Ortmann (1919)	Dennis (1970)
Unioninae:		
Amblema costata	x	x
Elliptio crassidens	x	x
E. dilatatus	x	-
Fusconaia flava	x	-
F. subrotunda	x	-
Pleurobema clava	x	-
P. cordatum	x	-
Plethobasus cyphyus	x	-
Quadrula cylindrica	x	-
Q. metanevra	x	-
Q. pustulosa	x	-
Tritognia verrucosa	x	-
Anodontinae:		
Alasmidonta marginata	x	-
Anodonta grandis	-	x
Anodontoides ferusscianus	-	x
Lasmigona compressa	-	x
L. costata	x	x
Strophitus rugosus	x	-
Lampsilinae:		
Actinonaias carinata	x	x
Cyprogenia irrorata	x	-
Dysnomia perplexa (=rangiana)	x	x
D. triquetra	x	-
Lampsilis fasciola	x	x
L. ovata ventricosa	x	x
L. radiata	-	x
L. siliquoidea	x	x
Leptodea fragilis	x	-
Ligumia recta latissima	x	x
Obovaria subrotunda	x	-
Plagiola lieolata	x	-
Proptera alata	x	-
Ptychobranchus fasciolaris	x	-
Totals	28	13

x= species present -=species absent

TABLE I-15

MUSSEL RECORDS, CUMBERLAND RIVER, TENNESSEE

Species	Wilson & Clark (1914)	Recent 1976-83
Cumberlandiinae:		
Cumberlandia monodonta	x	x
Unioninae:		
Amblema costata	x	x
Cyclonaias tuberculata	x	x
Elliptio crassidens	x	x
Elliptio dilatatus	x	x
Fusconaia ebenus	x	x
Fusconaia subrotunda	x	x
Fusconaia undata	x	x
Megalonaias gigantea	x	x
Plethobasus cooperianus	x	-
Plethobasus cyphyus	x	x
Pleurobema cordatum	x	x
Quadrula cylindrica	x	-
Quadrula metanevra	x	x
Quadrula pustulosa	x	x
Quadrula quadrula	x	x
Tritogonia verrucosa	x	x
Anodontinae:		
Alasmidonta marginata	x	-
Lasmigona complanata	-	x
Lasmigona costata	x	x
Strophitus rugosus	x	-
Lampsilinae:		
Actinonaias carinata gibba	x	x
Cyprogenia irrorata	x	x
Dromus dromas	x	x
Dysnomia brevidens	-	x
Dysnomia haysiana	x	x
Dysnomia sulcata	x	x
Dysnomia triquetra	x	x
Lampsilis anodontoides	x	x
Lampsilis orbiculata	x	x
Lampsilis ovata	x	x
Leptodea fragilis	x	x
Ligumia reacta latissima	x	x
Obliquaria reflexa	x	x
Obovaria olivaria	x	-
Obovaria retusa	x	x
Obovaria subrotunda	x	-
Plagiola lineolata	x	x
Proptera alata	x	x
Ptychobranchus fasciolaris	x	x
Truncilla donaciformis	x	-
Truncilla truncata	x	x
Totals:	40	34

TABLE I-16

MUSSEL SPECIES DISTRIBUTION, TENNESSEE RIVER, KENTUCKY LAKE

Mussel Species	Pickwick TW Tailwater				New Johnsonville				Lower River		Kentucky Tailwater			
Reference:	1 1939	2 1960	3 1972	4 1981	5 1925	6 1939	7 1967	8 1972	9 1981	10 1939	11 1981	12 1975	13 1969	14 1939
Cumberlandiinae:														
Cumberlandia monodonta	–	–	x	–	–	–	x	–	–	–	–	–	–	–
Unioninae:														
Amblema costata	–	x	x	x	x	x	x	x	x	–	x	x	x	x
Cyclonaias tuberculata	x	x	x	x	x	x	x	x	x	–	–	x	x	x
Elliptio crassidens	x	x	x	x	x	x	x	x	x	–	–	x	x	x
E. dilatatus	x	x	x	–	x	–	x	–	–	–	–	x	x	x
Fusconaia ebenus	x	x	x	x	x	–	x	x	x	x	x	x	x	x
F. subrotuda	–	–	x	x	x	x	–	–	x	–	–	–	–	x
F. undata	–	–	x	–	–	–	x	x	x	–	x	–	x	x
Lexingtonia dolabelloides	–	–	x	x	–	–	–	–	–	–	–	–	–	–
Megalonaias gigantea	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Plectomerus dombeyanus	–	–	–	–	–	–	–	–	–	–	x	–	–	–
Plethobasus cooperianus	x	x	x	x	x	–	x	–	–	–	–	–	–	x
P. cyphyus	x	x	x	–	x	–	x	–	–	–	–	–	–	–
Pleurobema cordatum	x	x	x	x	x	x	x	x	x	x	–	x	x	x
Quadrula cylindrica	–	–	–	–	–	–	x	–	–	–	–	–	x	–
Q. metanevra	x	x	x	x	x	–	x	–	–	x	–	x	x	x
Q. nodulata	–	–	–	–	–	–	–	x	x	–	–	–	–	x
Q. pustulosa	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Q. quadrula	–	x	x	x	x	x	x	x	x	x	x	x	x	x
Tritogonia verrucosa	–	x	x	x	x	–	x	x	x	–	–	–	x	–

TABLE I-16 (continued)

Reference:	1 1939	2 1960	3 1972	4 1981	5 1925	6 1939	7 1967	8 1972	9 1981	10 1939	11 1981	12 1975	13 1969	14 1939
Lampsilinae:														
Actinonaias carinata	-	x	-	-	-	x	x	-	-	-	-	-	-	-
Carunculina parva	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Cyprogenia irrorata	-	-	x	-	-	-	x	-	-	-	-	-	x	-
Lampsilis anodontoides	-	x	x	x	x	-	x	-	-	-	-	-	x	x
L. orbiculata	-	-	x	x	x	-	-	-	-	x	-	-	-	-
L. ovata ventricosa	-	x	x	x	x	-	x	-	-	-	-	-	-	-
Leptodea fragilis	-	-	x	-	-	-	x	x	x	-	x	-	-	-
L. laevissima	-	-	-	-	-	-	x	x	-	-	-	-	-	-
Ligumia recta latissima	-	x	x	x	x	x	x	-	-	-	-	-	x	-
Obliquaria reflexa	x	x	x	x	x	-	x	x	x	x	x	x	x	x
Obovaria olivaria	x	x	-	-	x	-	-	-	-	-	-	-	-	x
O. retusa	x	-	x	-	x	x	x	-	-	-	-	-	-	-
Plagiola lineolata	-	x	x	x	x	-	x	x	-	-	-	x	x	-
Proptera alata	-	x	x	x	x	x	x	x	x	-	-	x	x	-
Ptychobranchus fasciolaris	-	x	x	-	x	-	x	-	-	-	-	-	-	-
Truncilla donaciformis	x	-	-	-	-	-	x	x	x	x	-	x	x	x
T. truncata	x	-	-	-	-	-	-	-	-	-	-	-	-	x
Anodontinae:														
Anodonta grandis	-	-	x	-	-	-	x	x	x	-	x	-	-	-
A. imbecillis	x	-	-	-	-	-	x	x	-	-	-	-	-	-
A. suborbiculata	-	-	-	-	-	-	x	x	-	-	-	-	-	-
Arcidens confragosus	-	-	x	x	-	-	x	x	x	-	x	-	-	-
Lasmigona complanata	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Totals:	16	22	30	21	24	12	35	21	18	9	11	14	20	19

References:
1, 6, 10, 14. van der Schalie (1939b)
2. Scruggs (1960)
3, 8. Yokley (1972)
4, 9, 11. Bates and Dennis (1981)
5. Ortmann (1925)
7. Bates (1967)
12. Bates (1975)
13. Isom (1969)

DISCUSSION

Stream Classification

Many attempts have been made to classify streams in terms of physical and/or biotic characteristics. Perhaps the best known and most widely used classification based on physical characteristics of river basins is that based on stream order, i.e. the ranking of streams in a hierarchy by number of tributaries.

A system of drainage analysis based on the relationship of stream length to stream order was proposed by Horton (1945) and further developed by Strahler (1954, 1957). Generally defined, a first order stream is one which has no tributaries; two first order streams join to form a second order stream; two second order streams join to form a third order stream, etc.. The confluence of a stream with one of a lower order does not change the order of the stream.

In setting up a scheme based on stream order, the definition of the first order stream is critical. Leopold et al. (1964) suggested that for most purposes, the first order stream could be considered the smallest one marked on a 1:24,000 scale map. Hynes (1970) suggests that for the biologist, nothing smaller than perennial streams, or those which exist long enough to support a biota, should be considered. In this case, a map with a scale of 1:250,000 would suffice for most areas.

While the order system is useful in a general way for comparing streams within or between basins, it is not exact. As pointed out by Hynes (1970), streams with similar drainages may be placed in different orders because of the presence of small tributaries. As noted by Horton (1945), Strahler (1954), Leopold et al. (1964) and Hynes (1970) some clear relationships exist between the numbers, lengths, and drainage areas of streams in each order. For this reason, stream length or drainage area may be used in some applications in place of stream order.

A number of workers have attempted to classify streams in terms of both physical and biotic characteristics. Shelford and Eddy (1929) advocated using methods similar to those used in terrestrial studies for classification of aquatic communities. They suggested a classification based on aggregations of species which are indicative of stream conditions such as current, gradient, age and size. For example, the community associated with rapid water would be a Cladophora-Hydropsyche- Ethiostoma community. Since the dominant reaction in this community is to strong current and rock substrate, the association would be known as "litho-rheotactic" (Shelford and Eddy, 1929). Elton and Miller (1954) emphasized the importance of studying the "species network", the interaction of groups of species, in relation to changes in habitat, and warned against attempts to identify a single species with a given habitat characteristic. To define habitat types, they devised a physical classification of the aquatic environment based on two parameters, stream size and speed of water. Dividing each parameter into five categories would result in a total of 25 possible (if not realistic) combinations, each representing a different habitat. These categories, based on subjective observation of flow and size, were not much more definitive than other subjective classifications based on stream size (i.e. small, medium, large).

Along similar lines, Illies and Botosaneau (1963) attempted to define zones based on a combination of physical and biotic features, identifying points which seem to mark faunal divisions. They developed two large categories, Ritheron and Potamon, for small, fast moving and large, slow moving bodies of water. Each of these was further subdivided based on physical and faunal characteristics. While providing a number of useful descriptive terms, this scheme does not appear significantly different from those proposed by Shelford and Eddy or Elton and Miller.

The observation of zonal distribution of animals in river systems has led to the development of classification systems based on these zones. Most early classifications developed in Western Europe (Huet, 1949, 1954) were based on the zonation of fish, and the zones named for the fish species. Kuehne (1962) listed fish species associated with various stream orders for streams in Kentucky. Burton and Odum (1945) related fish distribution to altitude in tributaries of the New River in Virginia. Similar information is available for many regions. Hynes (1970) pointed out that such schemes based on fish data are only good for limited areas due to the local differences in fauna, altitude and climate which prohibit development of a clear general pattern.

Zonal arrangement of species has also been demonstrated for algae and many invertebrate groups, including mussels. In a study of mussels of the Huron River in Michigan, van der Schalie (1938b) listed mussel species by habitat type, including lakes, river-lakes, and streams of various sizes. Similarly, Dawley (1947) listed the mussel species of Minnesota according to type (lentic or lotic) and size of water body.

The most workable classification for freshwater mussels seems to be one based on stream size, habitat type, and faunal associations. The works of van der Schalie (1938b) and Dawley (1947) provide a basis for the present classification system. Both authors divided the aquatic habitat into categories of lotic and lentic waters, then divided the streams into categories according to size. Van der Schalie established 14 habitat types including seven stream sizes: brooks, small creeks, larger creeks, small rivers, medium sized rivers, and large rivers. Both authors also established a habitat type known as "river-lake" referring to portions of a large river impounded for navigation but still maintaining a constant flow.

While many of the habitat types of these two authors are comparable, the drainages studied were considerably different. Van der Schalie's intensive work in the Huron River Drainage involved an abundance of small productive streams, the largest of which (Huron River) is considerably smaller than the large river (Mississippi) of Dawley. The present study is more comparable to that of Dawley in terms of stream sizes sampled.

For purposes of this study, I have categorized stream reaches as small, medium, or large. The large river category, which includes primarily impounded rivers, has been divided into three sub regions, the tailwater, main channel (river-lake) and overbank areas. In the present study, stream size categories are based in part on stream order (Strahler, 1954) and in part on subjective observation.

While mussel distribution relates well to the generally defined stream sizes, attempts to correlate mussel species composition or diversity directly to stream length were non-productive. Appearance of the river at a given site, diversity of habitat, type of substrate, and abundance of shoal area were of greater significance in determining species abundance and richness than stream length or drainage area.

For example, two of the most productive sites in the Tennessee drainage are the Clinch River at Kyles Ford, Tennessee, with 35 species, and the Powell River at McDowell Ford, Virginia, with 36 species. Both areas include an abundance of riffle, shoal, and pool habitat and both are classified, for present purposes, as medium sized steams. The approximate drainage area of the Powell River site is 685 square miles; the drainage area for the Clinch River site is approximately 1,474 square miles, yet, these sites support mussel assemblages which are similar in species composition and number. The Tennessee River at Savannah, Tennessee, with a drainage area of 33,140 square miles supports 35 species.

The stream reaches sampled during this study are listed in Table I-17 according to their size classification. Size categories used in this analysis are defined below:

Small Streams

This category includes second to forth order streams (Strahler, 1954), generally designated creeks, and the extreme headwater reaches of some medium sized streams. These streams are generally 1 to 4 meters across, with water depths of 10 to 40 centimeters during periods of low flow. While there may be some deeper pool areas, the stream is always wadeable except during periods of high runoff. The gradient here is moderate to low and streams may exhibit considerable meandering. Substrate is generally a mixture of fine gravel and mud. Mussels are found most often in gravel shoals, but may also inhabit muddy areas along banks or slightly silted backwater areas. Mussels are generally not found in unstable substrate, such as sand bars, or in areas that are separated from the main channel during low flow. High gradient mountain streams having rock and boulder substrate do not characteristically support mussels, nor do intermittent streams.

Small streams found to support freshwater mussels are listed in Table I-17. Other small streams which were sampled but produced no living records of mussels include: Little Moccasin Creek, Brumley Creek, and South Fork Holston River, in Virginia. The headwater reaches of the Duck River, Tennessee, produced only relic shells.

TABLE I-17

Size Classification of River Reaches Sampled

Stream Reach:	Size Classification: Small	Medium	Large
Big Moccasin Cr.	Entire		
Copper Cr.	Entire		
North Fork Holston R.	Headwaters Smythe Co.	Lower River Scott, Hawkins Co.	
South Fork Holston R.	Entire		
Clinch R.	RM 296-320	RM 190-290	
Powell R.	RM 145-180	RM 80-141	
Duck R.		RM 15-180	
Cumberland R.			RM 270-305
Tennessee R.			Kentucky Lake

Medium Sized Streams

This category includes fifth to seventh order streams generally designated as small to medium sized rivers. They are characterized by high gradient riffle areas having depths of 20 to 40 centimeters during low flow, separated by low gradient pool areas which may have depths of two to three meters. The term "riffle" is used here to designate an area of breaking water, while "shoal" refers to a shallow river reach exhibiting a uniform flow of unbroken water.

The substrate of medium sized streams varies from bedrock and boulders in some riffle areas to rock and gravel in the shoal areas, and muddy gravel in backwater areas. Although mussels may be found anywhere in these streams, the species composition and density varies with habitat. The most productive areas are shoals having stable substrates consisting of mixtures of fine particulates, gravel, and rocks. A few species may be found wedged between rocks and boulders in riffle areas; however, their occurrence here may be accidental, a result of young mussels washing in from upstream. The muddier pool areas exhibit lower diversity than the shoals, and support a different species assemblage. Shifting sand and gravel bars are generally unproductive.

Medium sized streams sampled during this study include lower portions of the North Fork Holston and Duck River and middle sections of the Clinch and Powell Rivers in Tennessee. The main Holston River is largely impounded and generally unproductive, as are the lower portions of the Clinch and Powell Rivers.

Large Rivers

This includes rivers of eighth order or larger which are generally navigable waterways. The Tennessee and Cumberland Rivers, which once consisted of riffles, shoals, and pools, have been impounded by a series of navigation dams, completely eliminating the riffles and shoals. Present habitat includes three intergrading regions: the tailwater, main channel, and overbank.

The tailwater reaches, extending for several miles below a dam, are subject to extreme variations in flow due to the operation of the dam for water storage or hydro-electric generating purposes. The substrate here is generally rock and coarse gravel kept free of silt by releases from the dam. Because of the availability of clean gravel in these areas, they are often exploited by commercial graveling companies. The tailwater reach of a river is often productive, supporting mussel assemblages characteristic of the river before its impoundment.

The river below the tailwater area gradually changes from a riverine to a lake environment as it approaches the next dam. The original river channel becomes deeper and the water slower moving, resulting in the loss of riverine mussel species. The shallow overbank areas become more extensive downstream supporting mussel species which are adapted to lake conditions. The substrate of the overbanks is primarily sand and soft mud.

Large rivers sampled during this survey include a portion of the Cumberland River, from river mile 270 to 205, and the Kentucky Lake portion of the Tennessee River from Pickwick Dam to Kentucky Dam.

Mussel Fauna Related to Stream Size

There are few papers which specifically address the relationship between the numbers and kinds of species and stream size. The association is apparent, however, upon examination of distribution records where site specific data are available.

In comparing species lists of various authors, it is important to consider differences in the number of taxa resulting from the recognition of sub-specific designations by some authors, and not others. By listing forms of species as separate taxa, or in some cases, as separate species, a species list may be lengthened considerably.

In listing species records, I have recognized only those which I consider to be good species. I have generally lumped forms into one species complex. For example, I include the forms of *Pleurobema cordatum* (*pyramidatum*, *catillus*, *coccineum*, and *plenum*) in the *Pleurobema cordatum* complex which counts as one taxon. Other authors may list these forms as five separate species. In making comparisons, I have lumped these taxa consistently for all authors. In some cases, a sub-specific designation has been retained for purposes of clarity as in the case of Ligumia recta latissima. Here, the sub-specific latissima is used to designate the riverine form of L. recta, which was named from Lake Erie.

Tennessee Drainage

The trend toward increased mussel species numbers with increased stream size was noted by Baker (1922), van der Schalie (1938b) and Dawley (1947). This trend is most apparent in small to medium sized streams. In figures I-3 and I-4 the number of species is plotted against river mile for three small stream reaches: the North Fork Holston (headwaters), the Middle Fork Holston River, and Copper Creek. River miles are measured beginning with "0" at the mouth, and increasing upstream, as presented on U.S. Geological Survey Topographic Maps. Figures I-3, A and B, show a similar pattern in species distribution for stream reaches which are similar in size, gradient, and habitat type. In both streams, the gradient was relatively high and there was an increasing occurrence of pool areas downstream.

Figure I-4 shows similar distribution data (from Ahlstedt, 1981b) for Copper Creek. This stream is somewhat smaller and lower in gradient than those plotted in Figure I-3 and exhibits a meandering course. The uniformity of habitat is evidenced by the general uniformity in species numbers in all but the lower reaches of the stream.

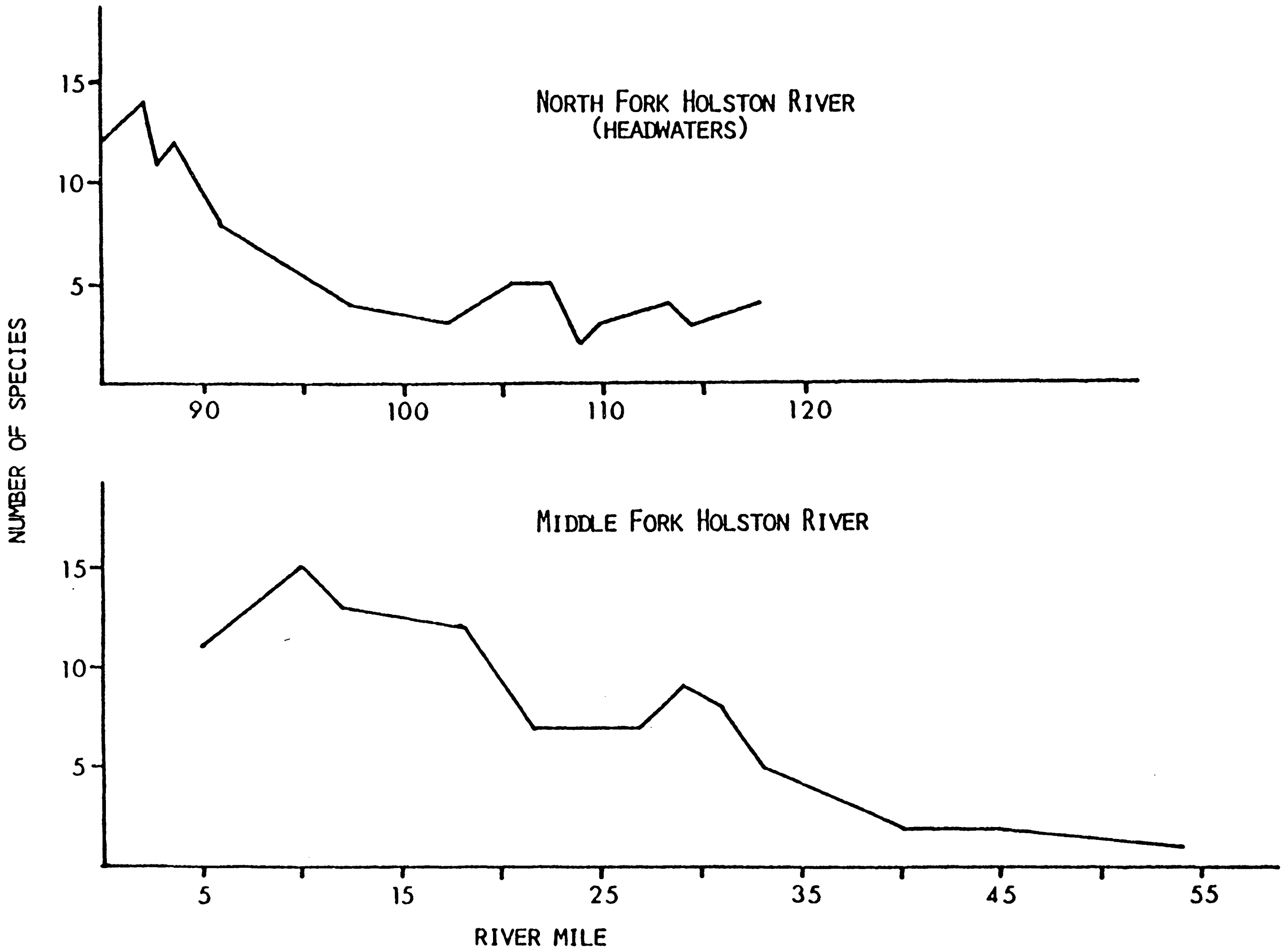


FIGURE I-3. NUMBER OF MUSSEL SPECIES VERSUS RIVER MILE FOR THE NORTH FORK HOLSTON (A) AND MIDDLE FORK HOLSTON (B) RIVERS

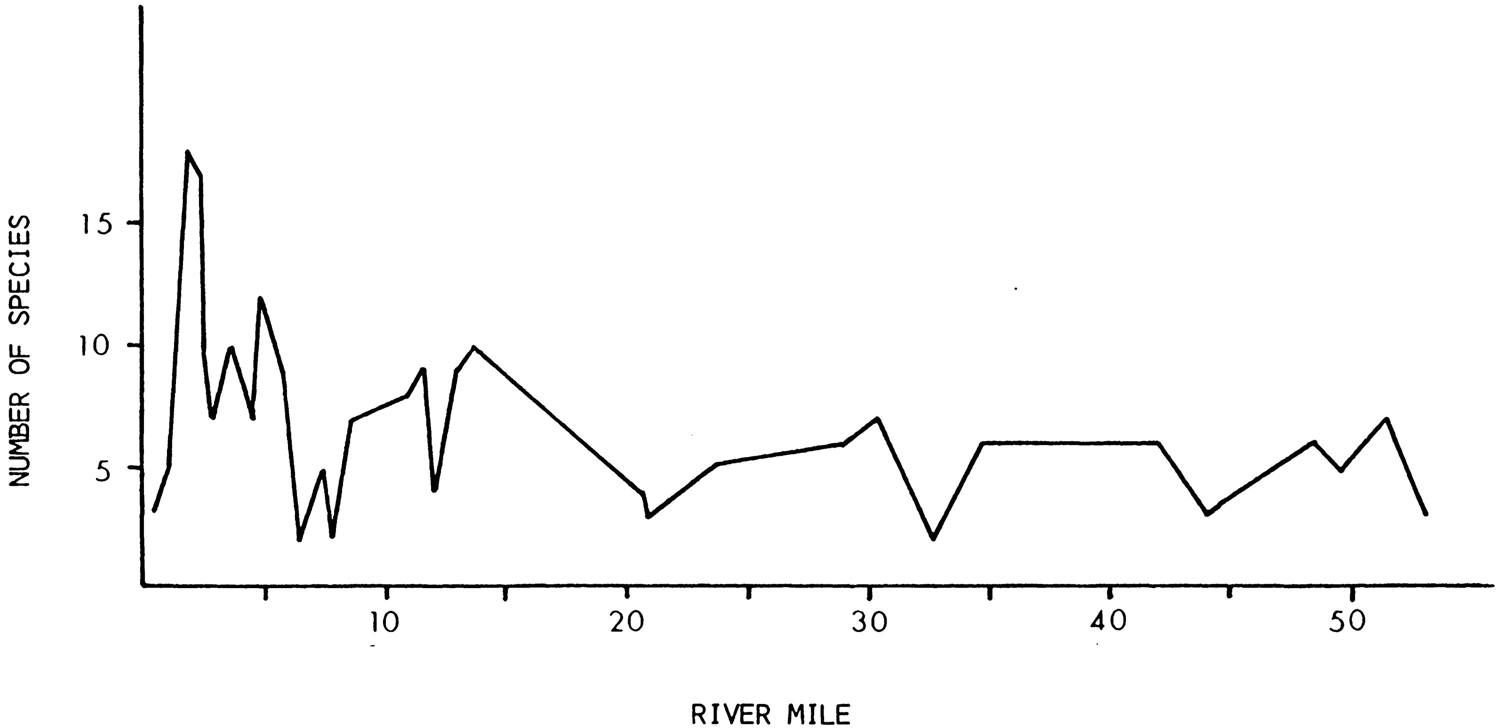


FIGURE I-4. NUMBER OF MUSSEL SPECIES VERSUS RIVER MILE FOR COPPER CREEK

In Figure I-5, the number of species is plotted against river mile for a medium sized stream (Powell River). While the tendency towards greater diversity downstream is still apparent, the variation from site to site is great in the lower river reaches. Below river mile 100, the effects of impoundment from Norris Dam become pronounced and the number of species tapers off rapidly.

The wide variation observed between consecutive sites makes correlation of species numbers with single physical features such as drainage area or stream order difficult. Specific differences are undoubtedly due to a wide variety of factors which may involve behavior patterns of host fish.

Patrick (1961) in comparing the numbers and kinds of aquatic organisms in streams of similar size and hardness found the number of taxa to be similar for similar streams even though the species composition may differ considerably. She attributed this consistency to the "finite and similar number of habitats or niches for species occupancy" (p. 230). This concept seems to hold true for freshwater mussels; as the habitat becomes more diverse, the number of species increases to a point of maximum diversity. While species composition may differ, the number of species is similar for similar streams.

Hynes (1970) defines the region of highest diversity for stream organisms as somewhere between the small and large river, presumably the rithron-potamon boundary. This definition is consistent with observations as to freshwater mussel diversity. The maximum number of

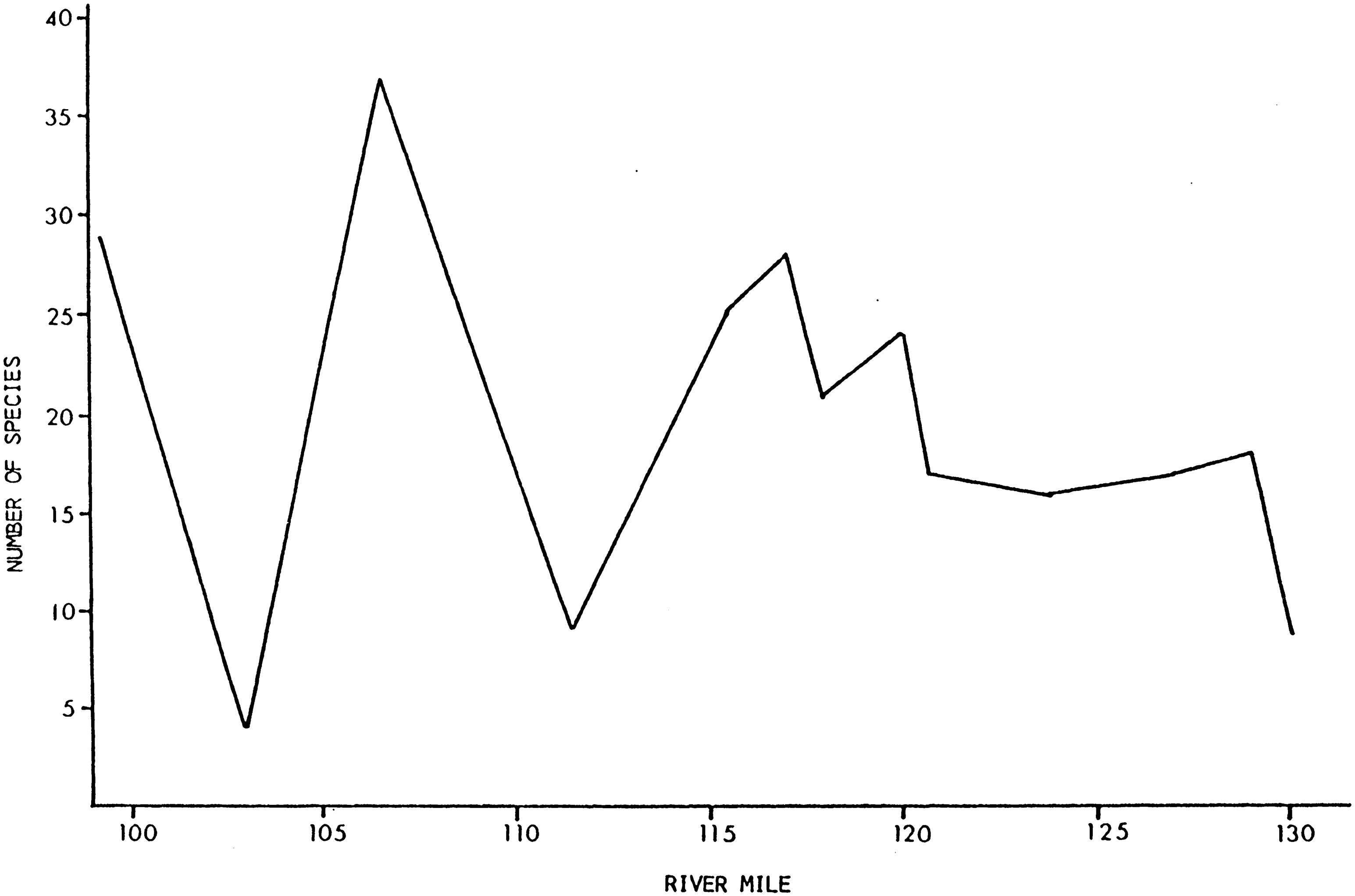


FIGURE I-5. NUMBER OF MUSSEL SPECIES VERSUS RIVER MILE FOR POWELL RIVER mussel species is reached in medium to large streams. In the Tennessee River system, the maximum number of mussel species presently found to occupy one site is 36-40, depending on taxonomic breakdown. This number is found in the middle sections of the Clinch and Powell Rivers in Tennessee. The habitat in these productive reaches is a riffle-pool-shoal environment containing a variety of substrate types from clean gravel to mud. These river reaches generally include grassy islands which may be be submerged part of the year.

The river reaches which span the border between medium and large river (lower Clinch and Holston, and upper Tennessee Rivers) have been subjected to such habitat modification that the mussel fauna is now depauperate, and not comparable to that of undisturbed reaches. Although historical collections from this region are few, available records indicate that this transition region supported a greater diversity than presently exists in the Tennessee drainage.

Ortmann (1918) reported a total of 50 species from the lower 50 miles of the Clinch River, with a maximum of 38 species present at one site (Clinton, Tennessee). The area of maximum species diversity in the upper Tennessee drainage was the lower Holston - upper Tennessee River boundary near Knoxville, Tennessee. Ortmann, pooling all available records for this reach, listed 56 species (64 species and forms prior to synonymization). The maximum number of species reported from one site within this reach was 42 at Mascot, Tennessee.

The only mussel records from the Tennessee River prior to its impoundment by the TVA are those of Ortmann (1925) who reported records from four sites, and van der Schalie (1939b) who reported on Ellis's collections from 15 sites. There are no records from the reach between Knoxville and Chattanooga. Based on available records from below Walden Gorge, it appears that species decreased in the mainstem Tennessee River from the maximum of 42 species reported from the lower Holston River to approximately 30 species. An exception to this is the unusually diverse river reach known as Muscle Shoals, which is described in detail below.

Muscle (Mussel) Shoals, a unique area

There has been considerable controversy over the spelling "Muscle" vs. "Mussel" Shoals, Alabama. Arguments in favor of using "Mussel" are presented by Ortmann (1925) and Dexter (1961, 1967). The reach of the Tennessee River known as Muscle (or Mussel) Shoals once supported a unique mussel fauna. The richness of this area was first reported by Conrad (1834), who described the river here as a reach of grassy shoals and islands. Ortmann (1924a) described the Mussel Shoals as the richest area in the world in mussel species, attributing this richness to the mixing of two faunas, the Ohioan and the Cumberlandian. Van der Schalie (1939b) pointed out that the diversity of this area was also due to stream rejuvenation from tributary streams entering the large shoal areas which provided habitat for riffle species. In this river reach there was a mix of species which characteristically inhabit large, medium, and small streams.

Although records from Muscle Shoals are often reported as if the reach were one site, Isom (1969) pointed out that the area known as Muscle Shoals was actually a series of large shoals extending for 53 miles (TRM 234.6 to 287.7). Early records of mussels reported from the Shoals may have come from any one of the four shoals known as Colbert Shoals, Little Muscle Shoals, Big Muscle Shoals, and Elk River Shoals.

The fauna of this region prior to completion of Wilson Dam was described by Ortmann (1924a). Van der Schalie (1939b) reported results of collections made by Ellis in 1931, six years after completion of the dam. A comparison of these records (presented in Table I-18) demonstrates the effect of impoundment on this fauna.

Even though the 62 species reported by Ortmann (synonymized from 69 original records) may have come from more than one site within the Muscle Shoals area, this still represents an unusually high number of species from one such reach. In comparing Ortmann's records to those of Ellis (van der Schalie, 1939b), it is apparent that the impact of Wilson Dam was to destroy the unique quality of the Muscle shoals habitat. The post impoundment fauna of 36 species reported by van der Schalie more closely matches that expected from one site in the Tennessee River system.

The first taxa to disappear following impoundment were those associated with small streams (Micromya) and those associated with riffle areas (Dysnomia). The effect of impoundment was to change the

Shoals from an area where small, medium and large river habitat existed together to a typical large river habitat.

In recent years, the fauna of this area has continued to decline. Isom (1969), reporting on collections made by Stansbery in 1964, listed 31 species from below Wilson Dam. Many of these, however, may represent relic populations.

TABLE I-18

MUSSEL SPECIES REPORTED FROM MUSCLE SHOALS, ALABAMA
BASED ON HISTORICAL RECORDS

Species	Origin**	Ortmann (1925)	van der Schalie (1939b)***
Margaritiferidae:			
Cumberlandiinae:			
Cumberlandia monodonta	U	X	X
Unionidae:			
Unioninae:			
Amblema costata	U	X	X
Cyclonaias tuberculata*	U	X	X
Elliptio crassidens	U	X	X
Elliptio dilatatus	U	X	X
Fusconaia barnesiana*	C	X	-
Fusconaia cuneolus*	C	X	-
Fusconaia edgariana	C	X	-
Fusconaia ebenus	O	X	X
Fusconaia subrotunda	U	X	X
Lastena lata	U	X	-
Lexingtonia dollabelloides*	C	X	X
Megalonaias gigantea	O	X	X
Plethobasus cyphyus	U	X	X
Pleurobema cordatum*	U	X	X
Pleurobema clava	O	X	-
Pleurobema oviforme	C	X	-
Quadrula cylindrica	U	X	X
Quadrula intermedia	C	X	-
Quadrula metanevra	O	X	X
Quadrula quadrula*	O	X	X
Tritogonia verrucosa	O	X	X
Anodontinae:			
Lasmigona costata	U	X	-
Strophitus rugosus	U	X	X
Lampsilinae:			
Actinonaias carinata gibba	C	X	X
Actinonaias pectorosa	C	X	X
Conradilla caelata	C	X	X
Cyprogenia irrorata	U	X	X

TABLE I-18 (continued)

Species	Origin**	Ortmann (1925)	van der Schalie (1939b)***
Dromus dromas	C	X	X
Dysnomia biemarginata	C	X	-
Dysnomia brevidens	C	X	-
Dysnomia capsaeformis	C	X	-
Dysnomia florentina	C	X	-
Dysnomia haysiana	C	X	-
Dysnomia personata	O	X	-
Dysnomia sulcata	O	X	-
Dysnomia torulosa*	O	X	X
Dysnomia triquetra	U	X	X
Dysnomia turgidula	C	X	-
Lampsilis fasciola	U	X	X
Lampsilis orbiculata	O	X	X
Lampsilis ovata	U	X	X
Lampsilis viriscens	C	X	-
Leptodea fragilis	U	X	X
Leptodea leptodon	U	X	-
Ligumia recta latissima	U	X	X
Medionidus conradicus	C	X	-
Obliquaria reflexa	U	X	X
Obovaria olivaria	O	X	X
Obovaria retusa	O	X	X
Plagiola lineolata	O	X	X
Proptera alata	U	X	X
Ptychobranchus fasciolaris	U	X	X
Ptychobranchus subtentum	C	X	-
Truncilla donaciformis	O	X	X
Truncilla truncata	O	X	X
Villosa nebulosa	C	X	-
Villosa taeniata	C	X	-
Villosa trabilis	C	X	-
	Totals:	62	35

* includes forms
** from Ortmann (1924): U= unknown, O= Ohioan, C= Cumberladian
*** reporting on collections of Ellis, 1931.

Faunal Associations

Most mussel species are associated with a particular stream size and habitat type. The 72 species recorded from the Tennessee River drainage are listed in Table I-19 according to the size of stream with which they are associated. These size categories are: 1. small, 2. small to medium, 3. medium, 4. medium to large, 5. large, and 6. all sizes.

Only six species were common to all stream sizes. The greatest number of species were found in the medium to large category; the medium and large groups together accounted for almost 70% of the species.

In the following discussion, species are grouped within the six stream categories listed in Table I-19. Within these sections, individual species are discussed as to habitat preference and taxonomic status, where clarification is needed. Mussel species have been categorized based on recent records from the Tennessee River drainage; where this designation differs from historical or other records, it will be noted in the discussion of the species.

I. Mussel species associated with small streams

Only two species (*Lasmigona holstonia* and *Dysnomia walkeri*) were restricted to small streams, and both are recently known only from the Middle Fork Holston River in Virginia. *Lasmigona holstonia* was found

TABLE I-19

MUSSEL SPECIES OF THE TENNESSEE RIVER SYSTEM LISTED BY STREAM SIZE CATEGORY

I. Small streams:
   Lasmigona holstonia (Lea, 1838)
   Dysnomia walkeri (Wilson and Clark, 1914)

II. Small to medium sized streams:
   Elliptio dilatatus (Raf.,1820)
   Fusconaia barnesiana (Lea, 1838)
   Fusconaia edgariana (Lea, 1840)
   Fusconaia pilaris (Lea, 1840)
   Pleurobema oviforme (Conrad, 1834)
   Alasmidonta minor (Lea, 1845)
   Alismidonta marginata (Say, 1819)
   Lasmigona costata (Raf., 1820)
   Actinonaias pectorosa (Conrad, 1834)
   Lampsilis fasciola (Raf., 1820)
   Medionidus conradicus (Lea, 1834)
   Ptychobranchus subtentum (Say, 1825)
   Villosa vanuxemensis (Lea, 1838)
   Villosa nebulosa (Conrad, 1834)

III. Medium sized streams:
   Cumberlandia monodonta (Say, 1829)
   Fusconaia cuneolus (Lea, 1840)
   Quadrula intermedia (Conrad, 1836)
   Quadrula sparsa (Lea, 1841)
   Lastena lata (Raf., 1820)j
   Strophitus rugosus (Swainson, 1822)
   Carunculina moesta (Lea, 1841)
   Conradilla caelata (Conrad, 1834)
   Dysnomia brevidens (Lea, 1831)
   Dysnomia capsaeformis (Lea, 1834)
   Dysnomia torulosa (Reeves, 1865)
   Dysnomia triquetra (Raf., 1820)
   Obovaria subrotuda (Raf., 1820)

TABLE I-19 (contiued)

IV. Medium to large sized streams:
Megalonaias gigantea (Barnes, 1823)
Plethobasus cyphyus (Raf., 1820)
Pleurobema cordatum (Raf., 1820)
Quadrula cylindrica (Say, 1817)
Quadrula pustulosa (Lea, 1831)
Quadrula quadrula (Raf., 1820)
Tritogonia verrucosa (Raf., 1820)
Anodonta grandis (Say, 1824)
Anodonta imbecillis (Say, 1829)
Lasmigona complanata (Barnes, 1823)
Cyprogenia irrorrata (Lea, 1828)
Dromus dromas (Lea, 1828)
Lampsilis anodotoides (Lea, 1828)
Leptodea fragilis (Raf., 1820)
Leptodea laevissima (Lea, 1829)
Ligumia recta latissima (Raf., 1820)
Obliquaria reflexa (Raf., 1820)
Proptera alata (Say, 1817)

V. Large rivers:
Elliptio crassidens (Lam., 1819)
Fusconaia ebenus (Lea, 1831)
Fusconaia surotunda (Lea, 1831)
Fusconaia undata (Barnes, 1823)
Plethobasus cooperianus (Lea, 1834)
Plethobasus cicatricosus (Say, 1834)
Quadrula metanevra (Raf., 1820)
Quadrula nodulata (Say, 1834)
Plectomerus dombeyanus (Val., 1833)
Anodonta suborbiculata (Say, 1831)
Arcidens confragosus (Say, 1829)
Carunculina parva (Barnes, 1823)
Dysnomia sulcata (Lea, 1829)
Lampsilis orbiculata Hildreth, 1828)
Obovaria olivaria (Raf., 1820)
Obovaria retusa (Lam., 1819)
Plagiola lineolata (Raf., 1820)
Truncilla donaciformis (Lea, 1829)

VI. All sizes of streams:
Amblema costata (Raf., 1820)
Cycloaias tuberculata (Raf., 1820)
Lexigtonia dolabelloides (Lea, 1840)
Actinonaias carinata gibba (Simpson, 1900)
Lampsilis ovata (Say, 1817)
Ptychobranchus fasciolaris (Raf., 18210)

during the present study in the extreme headwaters of this stream where it was the only species present. *Dysnomia walkeri* was found farther downstream, in the most productive reach of the river, along with 17 other species. Both were found in habitats characteristic of their genus: *Lasmigona* in slow moving water with mud substrate, *Dysnomia* in swift water with gravel substrate.

Dysnomia walkeri belongs to the species complex of *D. florentina* and was believed by Ortmann (1918) to be the headwater form of that species. While often given species status, it should more appropriately be designated *D. florentina walkeri*. Most members of this genus, commonly known as riffle shells, are threatened, endangered, or extinct. *D. walkeri* is listed as endangered (Federal Register, 1976). The taxonomic problems associated with the genus *Dysnomia* are addressed in more detail in section III.

II. Mussel species associated with small to medium sized streams

The 14 species in this category are listed in Table I-20. Only four of these, *Elliptio dilatatus*, *Lampsilis fasciola*, *Lasmigona costata*, and *Alasmidonta marginata*, occur throughout the Ohio drainage; the rest are Cumberlandian in origin.

Elliptio dilatatus, *Lampsilis fasciola* and *Lasmigona costata* are common inhabitants of small to medium sized streams; *E. dilatatus* and *L. costata* occur rarely in large rivers. They commonly inhabit muddy gravel substrates in areas of moderate to slow current, and will tolerate some silt deposition during periods of low flow. These species were reported by Ortmann (1918) and van der Schalie (1939b) in collections from small to large streams, but were more common in the former. H. van der Schalie (1939b) noted in all cases, a preference for sand and gravel substrates and flowing water. Dawley (1947) did not report L. fasciola in the upper Mississippi drainage, but reported E. dilatatus and L. costata from medium and large rivers.

The genus Alasmidonta is generally associated with small steams, except for A. marginata, which is the only member of this genus commonly found in medium sized steams in rock and gravel substrate (Clarke, 1981). A. minor is rarely found in medium sized streams, more commonly inhabiting gravel substrate of creeks and small streams where it is seldom abundant. Alasmidonta minor is the upper Tennessee representative of the more common A. calceolus of the Interior Basin. Both A. minor and A. calceolus were synonymized with A. viridis by Clark (1981) in his revision of this group.

The genus Fusconaia, generally more common in small to medium sized streams, has attained a high degree of morphological diversity in the Cumberlandian region. Ortmann (1918) listed small, medium and large river forms of the three species reported here (F. barnesiana, F. edgariana, and F. pilaris); however, the large river forms are apparently no longer extant.

Ortmann's forms were designated on the basis of the ratio of the diameter to the length of the shell, in accord with his observations that headwater forms are more compressed. I have not attempted to separate these forms in this work. *Fusconaia barnesiana* is unique to the Tennessee River system, having no apparent analog in the Mississippi fauna. It is widespread throughout the Cumberlandian region, where it is common in gravel shoals. This species was most often found in shady areas adjacent to the bank, seldom in the swifter riffle areas. *Fusconaia pilaris* is the upper Tennessee representative of *F. subrotunda* of the Mississippian fauna and is replaced by that species in the Cumberland and Tennessee Rivers. Ortmann (1925) reported that he could see no difference in these taxa to warrant their designation as separate species. I have found *F. pilaris* only in the Powell River, where it is a common inhabitant of gravel shoals.

Fusconaia edgariana (=*F. cor*) is closely related to *F. cuneolus*; the species are distinguished only by the texture and ray pattern of the periostracum (Ortmann, 1918). While the taxonomic relationship between these species is unclear, they are undoubtedly upper Tennessee representatives of the Mississippian *F. flava*. Bates and Dennis (1978) did not recognize *F. cuneolus* as distinct from *F. edgariana*. Further work on their systematic relationship is needed.

Although *F. edgariana* is more abundant in small streams, replacing *F. cuneolus* in the extreme headwaters, they are found together in some reaches of the Clinch River. Both taxa, presently listed as endangered species (Federal Register 1976), are found in swift water on gravel shoals. Ortmann (1918) listed these species (barnesiana, cuneolus, edgariana, and pilaris) as widespread throughout the upper Tennessee drainage. Only barnesiana and edgariana, however, have maintained their original distribution.

The genus Pleurobema, is represented in small to medium sized streams of the upper Tennessee drainage by P. oviforme, the Cumberlandian analog of P. clava from the Mississippi drainage. In headwater regions, P. oviforme is often confused with Fusconaia barnesiana and Lexingtonia dollabelloides. While these species can be separated on the basis of female reproductive anatomy (Ortmann, 1912), the shells are almost indistinguishable. P. oviforme is widespread in headwater streams where it inhabits gravel shoals. Actinonaias pectorosa and Ptychobranchus subtentum are Cumberlandian species, widespread and locally abundant in medium sized streams, less abundant in small streams. They are found in gravel substrate of riffles and shoals, and in the gravel-mud substrate of quieter water.

Medionidus conradicus is a small endemic species, widespread and locally abundant in small to medium sized streams of the Tennessee drainage. Medionidus is uncommon, and there is no analog in the Mississippian fauna. A common inhabitant of gravel shoals, this species was the most abundant taken in quantitative samples from the Clinch River at Kyles Ford, Tennessee, during 1973 and 1974. In small streams, Medionidus is often only partly buried in the substrate, as evidenced by the presence of filamentous algae and caddis fly cases (Neophylax) on the posterior slope of the shells.

Three members of the genus *Villosa* (=*Micromya*) are reported from the Tennessee River Drainage. *Villosa nebulosa* and *V. vanuxemensis* are widespread and common in small streams throughout the drainage, occurring in lesser abundance in medium sized streams. The two species share the same habitat and are often found together in gravel shoals, particularly in areas of quiet water adjacent to the bank.

Villosa nebulosa is an extremely variable species (or species complex) which appears to be the upper Tennessee analog of the Mississippian *V. iris*. Ortmann (1918) indicated that he tried, unsuccessfully, to separate this species into racial groups. *Villosa taineata* was found only in the Duck River Tennessee, where it inhabited gravel shoals adjacent to small islands where it occurred with *V. vanuxemensis*.

III. Species associated with medium sized streams

The thirteen species in this category are listed in Table I-19. *Cumberlandia monodonta* has a wider distribution than the name implies, occurring in the Mississippi as well as the Tennessee drainage. While it has been reported historically (Ortmann, 1918) from medium and large rivers within the Tennessee drainage, it has been found recently only in the Clinch River, where it occurs in fair abundance. This long, cylindrical mussel, commonly called the Spectacle case, burrows deeply in the gravel among boulders in the swift current of riffle areas. While live specimens are often difficult to find, I have taken 20 living specimens in one square meter quadrat at Kyles Ford, TN, indicating the highly clumped distribution characteristic of this species.

Fusconaia cuneolus, which was found only in the Clinch River during this study, has been discussed with other members of this genus in the preceding section.

Two Cumberlandian representatives of the genus Quadrula (sparsa and intermedia) were once widespread in the headwaters of the Tennessee River (Ortmann, 1918), but are now restricted to a portion of the Powell River. Although there have been occasional records of Q. intermedia from the Duck River (Tennessee Valley Authority, 1979) and a dead specimen of Q. sparsa recorded from the Cumberland River (Tennessee Valley Authority, 1976) the viability of these species in rivers other than the Powell is questionable. Both species inhabit gravel shoals with a swift current.

I believe Quadrula sparsa to be the Cumberlandian representative of the Ohioan Q. quadrula which inhabits the lower Tennessee River. Likewise, the Cumberlandian Q. intermedia appears to be the headwater expression of Q. metanevra which occurs in the Tennessee and Cumberland Rivers (Bates and Dennis, 1978). Both species are listed as Endangered (Federal Register, 1976).

Lastena lata is a rare species reported historically (Ortmann, 1918) from the Tennessee and Holston Rivers, although Ortmann reported finding it only in the Clinch River. This species was found only in the Clinch River, where it inhabited deeper (2-3 ft) reaches of riffles and shoals in very swift current. It could only be collected by hand picking during periods of extreme low flow. This mussel is generally buried deeply in the substrate, securely anchored by a remarkably long foot.

Strophitus rugosus, widespread throughout the Interior Basin, was reported by Ortmann (1918) as abundant in large and small streams of the Tennessee drainage. This species was rare in recent collections; only a few live specimens were observed in the Clinch and Powell Rivers where they were found in fine gravel and mud substrate of shoal areas.

While uncommon in the Tennessee River system, S. rugosus was found in relative abundance in small streams of Western Pennsylvania (Dennis, 1970), where it was common in mud and sand substrates. This was the only mussel species found in a number of streams of the Allegheny River drainage in Pennsylvania.

Carunculina moesta was reported by Ortmann and Walker (1922) as the upper Tennessee form of the widespread C. glans, closely related to and possibly synonymous with C. cylindrella. C. moesta was rare in recent collections, reported only from the Duck River where it was found living in a mixture of gravel and mud in moderate current.

Carunculina moesta was listed as Toxolasma lividum (Rafinesque) by Ortmann (1918); however, Ortmann and Walker (1922) rejected the genus Toxolasma when they determined that Rafinesque's type was unrecognizable. The genus Carunculina was widely accepted at that time and has been in common use until recently, when the genus name Toxolasma has reappeared, without explanation, in the literature (Buchanan, 1980).

Conradilla caelata, presently listed as endangered (Federal Register, 1976), belongs to a monotypic genus known only from the Tennessee River system. An earlier taxonomic designation of Lemoix rimosus (Rafinesque) was discarded by Ortmann and Walker (1922) as being unidentifiable. This species was reported by Ortmann (1918) as widespread, but nowhere abundant, in medium to large sized rivers of the upper Tennessee River. During the present studies, it was found to be very rare in the Clinch and Powell Rivers, while locally abundant in the Duck River at Lillard's Mill, Tennessee, where it is threatened with extirpation by the closing of a TVA dam at Columbia, Tennessee. Reasons for the unusual abundance of C. caelata in one reach of the Duck River are unknown, but undoubtedly related to the habits of its fish host (also unknown). This species prefers gravel and mud substrate in areas of swift current. In the Duck River, it is abundant in gravel shoals adjacent to small islands.

The genus Dysnomia is represented in medium sized streams by four species, brevidens, capsaeformis, torulosa gubernaculum, and triquetra. Dysnomia brevidens, D. triquetra, and D. capsaeformis were widespread throughout the Tennessee drainage. While triquetra and brevidens were not found in abundance, capsaeformis was common in the Clinch River at Kyles Ford, where it comprised nearly 20% of mussels sampled in 1973-

1975. This species appears to be declining in its range and should be considered for threatened or endangered status.

A rare sub-species, D. torulosa gubernaculum is represented in recent collections (Bates and Dennis, 1978) only by one freshly dead shell taken from the Clinch River. Ortmann (1918) recognized torulosa gubernaculum as the headwater form of D. torulosa more often found in large rivers. He noted the taxonomic affinities of these species to the D. perplexa - rangiana complex of the Ohio drainage.

All members of the genus Dysnomia are found in swift water shoals and riffles. Their apparent inability to adapt to habitat alteration has resulted in the extirpation of many species, particularly those which inhabited large river shoals. Ortmann (1918) reported eight species now believed to be extinct from the Tennessee River system.

The name Epioblasma (Rafinesque) has recently come into use for this genus. As pointed out by Ortmann and Walker (1922), van der Schalie (1973), and Bates and Dennis (1978), the type of the genus Epioblasma is unrecognizable and therefore should be discarded in favor of Dysnomia.

Obovaria subrotunda is not known from the upper Tennessee drainage, although Ortmann (1918) reported a small stream form O. subrotunda levigata from tributaries of the lower Tennessee River. Obovaria subrotunda is known from recent records from the Duck River, where it was found in gravel shoals in swift water, and from the Cumberland River.

IV. Species associated with medium to large streams

There are 18 species in this category, listed in Table I-19. With the exception of the Cumberlandian *Dromus dromas*, all of these are common throughout the Interior Basin.

Many medium and large rivers in the Interior Basin have been subjected to commercial mussel harvest. Consequently, the majority of mussel species inhabiting these rivers have been given common names (usually colorful and occasionally unprintable) by commercial musselers. Some of the more widely used of these have been included here. A more complete list is presented by Coker (1915). While regional differences are common, most of the names used here are recognizable throughout the Tennessee and Ohio drainages. Problems associated with the use of common names of freshwater mussels are discussed by Bates and Dennis (1983).

Approximately half of the species listed in this category require riverine conditions for their survival, while the other half have adapted to some degree to conditions of impoundment. The nine species requiring riverine conditions will be addressed first. Although habitat requirements for members of this group are not well defined, these species are generally found together in gravel substrate.

The only endemic species in this assemblage is *Dromus dromas* (Dromedary Mussel) now listed as endangered (Federal Register, 1976). Once widespread in the Tennessee River, *D. dromas* is now limited to a few areas in the Clinch and Powell Rivers (Bates and Dennis, 1978; Dennis, 1981). It is included in this section because of the discovery of living specimens in the Cumberland River (Tennessee Valley Authority, 1976), although, the age and eroded condition of those specimens casts doubt on the continued viability of D. dromas in that river. Like most Cumberlandian mussel species, D. dromas has been reduced in range to the upper Tennessee River where the headwater form continues to exist, while the large river form is extinct.

The group of Pleurobema cordatum (Pig Toe) consists of a number of forms which are often listed as separate species. Ortmann (1918) listed the main species as P. obliquum, recognizing forms cordatum (including plenum), catillus, coccineum, and rubrum (including pyrimidatum). In describing this complex in the upper Tennessee River, he stated (Ortmann, 1918, p.547):

> ...they all intergrade with each other, and there is very little indication of their separation into geological or ecological races. Mostly, the various forms are found associated, so that they are hardly more than individual variation.

Ortmann and Walker (1922) revised the taxonomic status of this group, recognizing P. cordatum as the main species and discarding P. obliquum. I use the designation P. cordatum to indicate a complex including the forms previously mentioned for P. obliquum.

Members of this complex found in the Clinch River were most often the pyrimidatum form, while those collected in the Tennessee River were most often representative of the typical P. cordatum. This species has long been sought by commercial musselers because of the thickness and clarity of the shell material. Once abundant in the Tennessee River (Bates, 1962), it is now restricted to tailwater areas which maintain riverine conditions (Bates and Dennis, 1981). The form plenum is listed as endangered (Federal Register, 1976).

Quadrula cylindrica (Rabbits Foot) is rare in the main Tennessee River, but the headwater form Q. cylindrica strigillata (Wright 1898), continues to exist in the Clinch and Powell Rivers. This species was found most often inhabiting muddy areas close to banks, and, unlike most riverine species, was seldom buried in the substrate. Quadrula pustulosa (White Warty Back) and Obliquaria reflexa (Three Horn) are most abundant in large rivers, occurring only occasionally in medium sized streams. Both are common in riverine portions of the Tennessee and Cumberland Rivers.

Tritogonia verrucosa (Pistol Grip) was reported by Ortmann (1918) from the Tennessee River below Walden Gorge. It is reported more recently from the Duck (Ahlstedt, 1981a), Cumberland (Tennessee Valley Authority, 1976), and Tennessee (Bates and Dennis, 1981) Rivers, where it inhabits swift water.

Lampsilis anodontoides (Yellow Sand Shell) and Ligumia recta latissima (Black Sand Shell) are able to inhabit sand bars, a habitat generally unfavorable to mussels. Lampsilis anadontoides is very mobile and may be located by following the tracks it leaves in the sand. This mobility is probably what allows this species to survive in a constantly shifting substrate. Ligumia recta latissima is the riverine form of L. recta, described by Lamarck in 1819 from Lake Erie. It is more versatile in its habitat selection than L. anodontoides, occurring in a variety of substrate types.

Cyprogenia irrorata (Fan Shell) is locally abundant in some areas of the Interior Basin, but generally rare in the Tennessee River system. Ortmann (1925) reported it from museum collections, but did not collect it himself in the lower Tennessee River; nor did van der Schalie (1939b). It was reported from the Tennessee River below Pickwick dam by Yokley (1972) and from the New Johnsonville area by Bates (1967). More recently, it was reported as rare in the Cumberland (Tennessee Valley Authority, 1976) and Clinch (Bates and Dennis, 1978) Rivers.

Quadrula quadrula (Maple Leaf) and Megalonaias gigantea (Washboard) are common riverine species which have apparently adapted to conditions of impoundment and are colonizing overbank areas of Kentucky Lake. M. gigantea, a large mussel of some commercial importance, was found in the Duck, Cumberland, and Tennessee Rivers. It was reported by Ortmann (1925) as abundant in the lower Tennessee River (before impoundment) and remains locally abundant in this river.

Quadrula quadrula, an important commercial species, is one of the most successful colonizers of Tennessee River overbanks. Ortmann (1925) recognized two forms of this species, the typical Q. quadrula, and the more elongate Q. quadrula fragosa. While he reported finding both forms together, he noted that Q. quadrula seemed to prefer quiet waters and muddy bottoms, while fragosa was most often found in gravel. Recent collections from Kentucky Lake are primarily Q. quadrula, although fragosa appears occasionally in collections from riverine habitats. Quadrula quadrula is the dominant species in the sand and mud substrate of backwater areas where it is heavily harvested by musselers. Neel (1941) discussed the wide variation in forms described for this species complex.

The remaining species in this section belong to a number of thin shelled genera (Anodonta, Lasmigona, Proptera, and Leptodea) which are of no commercial importance. They characteristically inhabit slow moving water with soft substrate. Of these species, only Proptera alata (Pink Heelsplitter) and Leptodea fragilis (Papershell) are known historically from the Tennessee River drainage (Ortmann, 1925). They remain widespread throughout this drainage, inhabiting gravel and mud substrate outside of the main river flow.

The remaining species in this category have invaded the Tennessee drainage from the Ohio River system (Ortmann, 1925). Impoundment of the Tennessee and Cumberland Rivers has provided ideal habitat for these species which require soft substrates with a little current. Leptodea laevissima (Paper Heelsplitter) is similar in shell character to both L. fragilis and P. alata and is often called Proptera laevissima. While the systematic status of this species is not resolved, I will, for the present, leave it with the genus Leptodea. Ortmann (1925) noted that L. laevissima, unlike its two close relatives, was rare in the Cumberland

and had never been reported from the Tennessee River. Recent records (Bates and Dennis, 1981) indicate that this species is now common in the lower Tennessee River.

Lasmigona complanata (White Heelsplitter) is not common in the Tennessee drainage. Ortmann (1925) reported it only from the lower Duck and Cumberland Rivers, but suspected its occurrence in the lower Tennessee as well. Its presence there, however was not confirmed by van der Schalie (1939b). Recent records show it present, but not abundant, in the Cumberland, Duck, and Tennessee Rivers. Its habitat requirements are similar to those for Proptera alata with which it is often associated.

Anodonta imbecillis, rare in the Tennessee River drainage, is widespread throughout the Interior Basin. It was reported by van der Schalie (1938b) from small to large streams in a mud-sand or gravel-sand substrate, by Baker (1928a) from quiet water in ponds, and by Isely (1925) from gravel bottomed streams. Ortmann (1925) noted this species from scattered localities in the Cumberland and lower Tennessee River drainages, and reported it as rare in the upper Tennessee drainage (Ortmann, 1918). Present records indicate that it is extant, but rare in streams throughout the Tennessee drainage including the Clinch, Powell, Duck, and Tennessee Rivers where it inhabits gravel and mud substrate in flowing water. Since this is a small species of rare occurrence, it may have a wider distribution in the Tennessee drainage than indicated by recent collections.

Another member of the genus Anodonta (A. grandis, the Floater) is a more recent invader of the Tennessee River drainage. This species, common in lakes and ponds throughout the Interior Basin, has the ability to rapidly colonize newly impounded water bodies, including rivers, lakes, ponds and even fish hatcheries. Ortmann (1925) reported scattered records of A. grandis from creeks and ponds in the Tennessee and Cumberland basins. Present records indicate that it is common in the lower Tennessee River, in the soft mud of backwater areas and adjacent ponds. An inflated form of this species, designated A. grandis corpulenta, is often listed as A. corpulenta, but should not be given species status.

V. Species associated with large rivers

All 18 of the species listed in this category (Table I-19) are members of the Interior Basin fauna, some only recent invaders of the Tennessee River drainage. Eleven species are generally associated with swift current and gravel substrate. Ten of these were reported from the lower Tennessee River by Ortmann (1925), while one species, Dysnomia sulcata, was believed until recently, to be extinct (Isom, Gooch and Dennis, 1979).

Elliptio crassidens (Elephant Ear) was once common in the lower Tennessee River (Ortmann, 1925) but is now limited to riverine portions of the river. Due to its abundance and lack of commercial value, this species was often thrown on the river bank by commercial musselers attempting to eradicate it.

Two valuable commercial species, Fusconaia ebenus (Niggerhead) and F. subrotunda, have declined in abundance since impoundment of the Tennessee River. They are presently limited to riverine portions of the Tennessee and Cumberland Rivers where they continue to be harvested. Neither of these species has been reported from the upper Tennessee drainage, although F. subrotunda has a Cumberlandian analog, F. pilaris, which extends into the headwaters (Ortmann, 1925).

Plethobasus cooperianus is a rare species of no commercial value. It has not been given a common name by musselers since it is easily mistaken for other more common species (Quadrula pustulosa, Cyclonaias tuberculata). The common name "orange footed pimple-back pearly mussel" was given to this species by U.S. Fish and Wildlife Service personnel when it was listed as endangered (Federal Register, 1976), and, while descriptive, would not be recognized by commercial fishermen. Ortmann (1925) reported P. cooperianus as rare in the Tennessee River, but not uncommon in the Cumberland River. Present records indicate that it survives below Pickwick Dam in the Tennessee River, but I have no records of it from the Cumberland.

Quadrula metanevra (Monkey Face) and Plagiola lineolata (Butterfly) were once abundant in the lower Tennessee and Cumberland Rivers (Ortmann, 1925) but are now restricted to riverine portions of these rivers where both are harvested by commercial musselers.

Lampsilis orbiculata (Pink Mucket), which is listed as endangered (Federal Register, 1976) closely resembles the more common "Mucket", Actinonaias carinata gibba. Male specimens of these species are almost indistinguishable except for nacre color. Lampsilis orbiculata is widespread and locally abundant in riverine portions of the Tennessee and Cumberland Rivers.

Obovaria olivaria (Eggshell) and O. retusa (Sheepsnose), once common in the Tennessee River are now very rare and possibly extinct. While O. olivaria occurs elsewhere in the Interior Basin, I have never collected a living specimen of O. retusa. Although shells of this species occasionally turn up in commercial musselers' shell piles (Parmalee, 1981), the exact locality and date of collection is generally undeterminable.

Dysnomia sulcata (Cats Paw) is a rare species believed to be extinct until recently discovered in the Cumberland River (Isom, Gooch, and Dennis, 1979). This population, inhabiting a reach of swift water below a dam, is the only one remaining of this endangered species.

Truncilla donaciformis (Deer Toe) is listed as a large river species since it was only reported in the present studies from the Tennessee River. It is, however, more versatile over its entire range. Ortmann (1925) noted that it was generally found with T. truncata, but was missing in the upper Tennessee R. where T. truncata was found. Baker (1928a) described its distribution in Wisconsin as "erratic", noting its occurrence in both large and small rivers. This small species has no commercial value but is often taken on brails by musselers.

Two commercial species, Fusconaia undata (Ohio Pigtoe) and Quadrula nodulata (Pimpleback) were not reported by Ortmann (1925) from the Tennessee River, but were reported by van der Schalie (1939b) from the lower river in Kentucky (below Ortmann's lowermost site). Both species have subsequently colonized overbank areas of Kentucky Lake, where they inhabit mud and sand substrate. Fusconaia undata has become very abundant, rivaling Q. quadrula in commercial importance.

The remaining three species in this category, Plectomerus dombeyanus (Bank Climber), Arcidens confragosus (Squawfoot) and Anodonta suborbiculata, were not reported by Ortmann (1925) or van der Schalie (1939b) from any portion of the Tennessee River. Arcidens confragosus and Anodonta suborbiculata were, first reported from Kentucky Lake by Bates (1967). A. suborbiculata has successfully invaded the shallow backwater areas of Kentucky Lake, where it is easily collected by hand picking when water levels are low. A. confragosus continues to live in deeper water in gravel and mud substrate.

Plectomerus dombeyanus was only recently discovered in the lower Tennessee River in Kentucky (Sickle et al., 1981). The two young specimens found living on a muddy overbank may indicate that this species is moving into the Tennessee from the Mississippi drainage. This species is common in medium to large streams of the Mississippi River drainage in West Tennessee and Arkansas, where it inhabits muddy substrate along the banks.

VI. Mussel species occurring in all sized streams

Of the six species which were not restricted in distribution by stream size (Table I-20), only Lexington dollabelloides is of Cumberlandian origin. It is most common in tributary streams, where the compressed headwater form, L. dollabelloides conradi (Vanatta) continues to exist. Rare in the Tennessee River, it was not reported from below Muscle Shoals by Ortmann (1925) or van der Schalie (1939b). Recent living specimens taken from below Pickwick Dam (Bates and Dennis, 1981; Yokley, 1972) exhibited badly eroded shells, indicating that this species may be represented here by a relic population, in which no recruitment is occurring.

Amblema costata (Three Ridge, Bluepoint) is one of the most widespread and common species in the Interior Basin. It lives in streams of all sizes, as well as in lakes. Variation in shell morphology in populations from different habitats has led to a variety of sub-specific designations for this species.

The name A. costata has been used to refer to the riverine form of this species, while A. plicata, the type of the genus, was named from Lake Erie. In keeping with strict laws of zoological nomenclature, the riverine form should more properly be called A. plicata costata, just as Ligumia recta latissima is used to refer to the riverine form of L. recta, which was also named from Lake Erie. The use of A. plicata alone, however, to refer to this species, is misleading.

occurring in small to large rivers, but not lakes (van der Schalie, 1938b). They prefer a swift current and gravel substrate, but, in smaller streams may inhabit mud and gravel, seldom sand. Both show differences in shell shape in different environments, generally following Ortmann's Law in that the headwater forms are more compressed.

Actinonaias carinata gibba (Mucket, Fat Mucket) is the Cumberlandian form of A. carinata, which is widespread throughout the Interior Basin. A. carinata gibba is abundant in the Clinch and Cumberland Rivers, indicating a medium to large stream preference, but may be found in lesser abundance in smaller steams, and in the Tennessee River.

Lampsilis ovata and L. ventricosa (Pocket Book, Grandma) are two widespread taxa which are separated rather arbitrarily, on the basis of the outline and degree of obesity of the shell. These forms appear to be intergrading, L. ventricosa having a somewhat more northerly distribution within the Interior Basin. Cvancara (1963) reported on the clinal distribution of this species complex. Ortmann (1918) reports L. ovata ventricosa as the headwater variety of L. ovata within the Tennessee River system. Lampsilis ventricosa was reported by van der Schalie (1938b) primarily from small streams in Michigan, while Dawley (1947) reported it from small, medium and large streams in Minnesota. Members of the L. ovata ventricosa complex were found recently in all stream sizes, inhabiting a variety of substrates. It generally avoids the swiftness of riffle areas in favor of quieter shoals having a gravel and mud or sand substrate.

Truncilla truncata (Elk Toe) is a widespread species inhabiting a variety of habitats from small creeks to lakes, throughout the Interior Basin. Ortmann (1925) reported it locally abundant in the lower Tennessee drainage in large and small rivers, noting that it was rare in the upper Tennessee. Recent collections indicate a similar distribution. It is often found in medium to large streams, but not in abundance.

CONCLUSIONS

The Tennessee River drainage presently supports 71 freshwater mussel species, approximately 25% of which are endemic to the Cumberlandian region. While a number of species, primarily members of the genus *Dysnomia*, have been extirpated from this drainage within the past 60 years, the number of extant species remains high. The major impact of man's activities over the past half century has been the reduction of available habitat for mussel species.

The mussel fauna remaining in the Tennessee drainage can be divided into species assemblages based on stream size. While some overlap of species exists among stream size categories, there is no longer a continuous gradation from one category to the next. Rather, mussel assemblages exist in isolated communities separated by river reaches which no longer support mussels.

Mussel assemblages associated with small streams exist in tributaries to the Clinch and North Fork Holston Rivers and in extreme headwaters of the North Fork Holston. Headwater reaches and tributaries to the Powell River have been decimated by strip mine activities, headwater reaches of the Clinch River by siltation from development. The upper Duck and Elk Rivers have been impounded.

Mussel assemblages associated with medium sized streams remain viable in mid-reaches of the Clinch and Powell Rivers, and in isolated reaches of the Duck River. Large portions of the Duck River are affected by siltation from gravel dredging operations, and accumulation of silt behind small mill dams. Lower reaches of the Clinch, Powell and Holston Rivers are impounded.

Large River assemblages presently exist in limited river reaches below mainstream impoundments of the Tennessee and Cumberland Rivers. New faunal assemblages (primarily Ohioan species) are colonizing overbank areas of large impoundments on these Rivers.

The maximum number of species reported in recent collections from any one site in the Tennessee River system is less than 40. This seems to be the maximum number of species niches available for colonization. Historic records indicate that areas once existed which supported more than 60 species. These reaches (Tennessee River at Muscle Shoals, and lower Holston River) represented areas of transition between medium and large stream faunas. The area at Muscle Shoals additionally marked a transition from Cumberlandian to Ohioan species assemblages. These areas of maximum species diversity have been eliminated by impoundment of the Tennessee River.

CHAPTER 2

ANALYSIS OF MUSSEL COMMUNITY STRUCTURE AT TWO SITES IN THE CLINCH RIVER, TENNESSEE AND VIRGINIA

INTRODUCTION

Community structure has long been recognized as important in the assessment of biological systems. Early work on population ecology by Lotka (1925), Volterra (1926) and Elton (1927) provided a basis for the more theoretical works of Gause (1934), Alee et al. (1949), Andrewartha and Birch (1954), Cole (1954) and MacArthur (1958).

Patrick (1949) was among the first to propose using community structure data as a monitoring tool by pointing out that changes in species dominance in diatom communities may reflect environmental changes before serious damage is done to the fauna or flora. Subsequently, a number of workers including Gaufin and Tarzwell (1952), Wurtz (1955), and Cairns et al. (1973) have studied community structure in groups of aquatic organisms. As Gaufin (1973, p.112) pointed out, "Community composition is now recognized as being much more reliable than particular indicator organisms for evaluating environmental conditions." Little work of this kind, however, has been done with molluscan communities.

The terms "community" and "community structure" are subject to various interpretations, and numerous definitions are available in the literature. Pielou (1975) described a community as "all organisms in a chosen area that belong to the taxonomic group being studied." In keeping with this definition, I use the term "community" to refer to the fresh water mussels, more specifically, members of the molluscan family Unionidae (and one member of the Margaritiferidae) which occur in the study area. The fresh water mussel community is composed of populations of all species found in the area.

As noted by Pianka (1975) communities have structure and properties which transcend those of component populations just as populations have properties which transcend individuals. Community structure involves the ways in which members relate to one another, and includes properties such as trophic structure, rate of energy fixation, stability, diversity, distribution of species and successional stages.

Cody and Diamond (1975) stated that community structure is defined by patterns of allocation of resources among species, and the patterns of their spatial and temporal abundance. The interspecific interactions, competition and predation, tend to compress the species' niches and control population growth.

For mussel communities, most of these properties have not been studied: questions of energy flow have not been addressed; neither inter- nor intraspecific competition has been documented; and predation is not well understood. The study of mussel communities is still at the descriptive stage. The autecology of a single mussel species is as yet, unknown. While some synecological data are available, functional aspects of molluscan ecology have not been explored.

Analysis of changes in mussel species composition and distribution over time have often provided a basis for assessing faunal changes resulting from such environmental perturbations as impoundment and severe pollution. Such drastic environmental effects have generally resulted in elimination of species or entire communities. More subtle changes in mussel densities or species dominance are not reflected in distributional data alone.

Mussel species distribution within the Tennessee River system is well documented (see Chapt. 1). A review of available literature, however, reveals little historical data which would allow for interpretation of community structure. Since sampling freshwater mussels has been primarily aimed at documenting species distributions, available data on this fauna is of limited value in predicting effects of environmental alterations.

Freshwater mussels are a unique component of the benthic invertebrate fauna of the Tennessee River system, differing from the rest of the invertebrates in a number of important respects. Most significant among these are their large size, long life span, sedentary habit, and parasitic life history. A large heavy-shelled mussel species, such as *Actinonaias carinata*, may weigh 600 grams at maturity and live to be more than 30 years of age. Freshwater mussels of the genus *Margaratifera* have been estimated to live as long as 80 years

(Hendelberg, 1960). Thus, one riverine mussel population may outlive many generations of freshwater insects or other invertebrates.

Due to the longevity of most riverine mussel species, freshwater mussel communities are slow to respond to slight environmental changes and do not show dramatic shifts in species composition from year to year unless catastrophic events occur. This constancy in species composition can be seen when present distribution records for reaches of the Clinch and Powell Rivers are compared to those of Ortmann (1918). Where mussels remain abundant, species composition has changed little in 50 years (Bates and Dennis, 1978; Dennis, 1981). The fact that species composition has remained constant in some areas, however, does not mean that changes have not occurred. Changes in species dominance and age class structure are not reflected in species lists alone. In order to evaluate temporal changes, information as to community structure is needed.

One factor which has contributed to the absence of community structure data in mussel studies is the difficulty of sampling this fauna quantitatively. It was, therefore, necessary to develop a sampling method prior to initiation of the studies. The present study was designed to provide a profile of mussel communities representative of the Upper Tennessee Drainage. This study is, necessarily, limited to the spatial aspects of community structure, with the intent of providing a baseline for future temporal evaluations.

A quantitative sampling program was undertaken at two sites in the

Clinch River. These sites, Kyles Ford, Tennessee, and Speers Ferry, Virginia, were determined, based on previous surveys (Bates and Dennis, 1978) to be the most productive of those sampled. The object of the sampling was to compare these sites as to species composition, age class structure and abundance.

METHODS AND MATERIALS

In a preliminary mussel survey of the Clinch River during 1972 (Bates and Dennis, 1978), I established distribution patterns and located areas of high diversity and density. Two of the 33 sites sampled during this survey, Speers Ferry, Virginia (Mile 211.2) and Kyles Ford, Tennessee (Mile 189.6) were found to support the greatest diversity of mussels (see Figure II-1). Intensive qualitative sampling was subsequently carried out at these sites to establish species composition and location of mussels. At both sites, mussels were concentrated in shoal areas extending from the north bank to just over half the width of the river, an area of approximately 35 by 150 meters. Water depth in these areas ranged from 10 to 100 centimeters when sampled during low flow (August through November). The substrate was primarily gravel interspersed with boulders and bedrock.

Quantitative sampling was begun at these sites in 1973, and continued through 1975. Approximately ten 1 m^2 samples were taken each year from the shoal habitat at each site. Five 1 m^2 meter samples were collected from a pool area at Kyles Ford for comparison to the shoal samples. Also, for comparative purposes, limited quantitative sampling was conducted at selected sites throughout the upper Tennessee River drainage including the Powell, North Fork Holston, and Middle Fork Holston Rivers.

In most reaches of the upper Tennessee River system, mussels were sampled by hand picking. The square foot Surber sampler commonly used

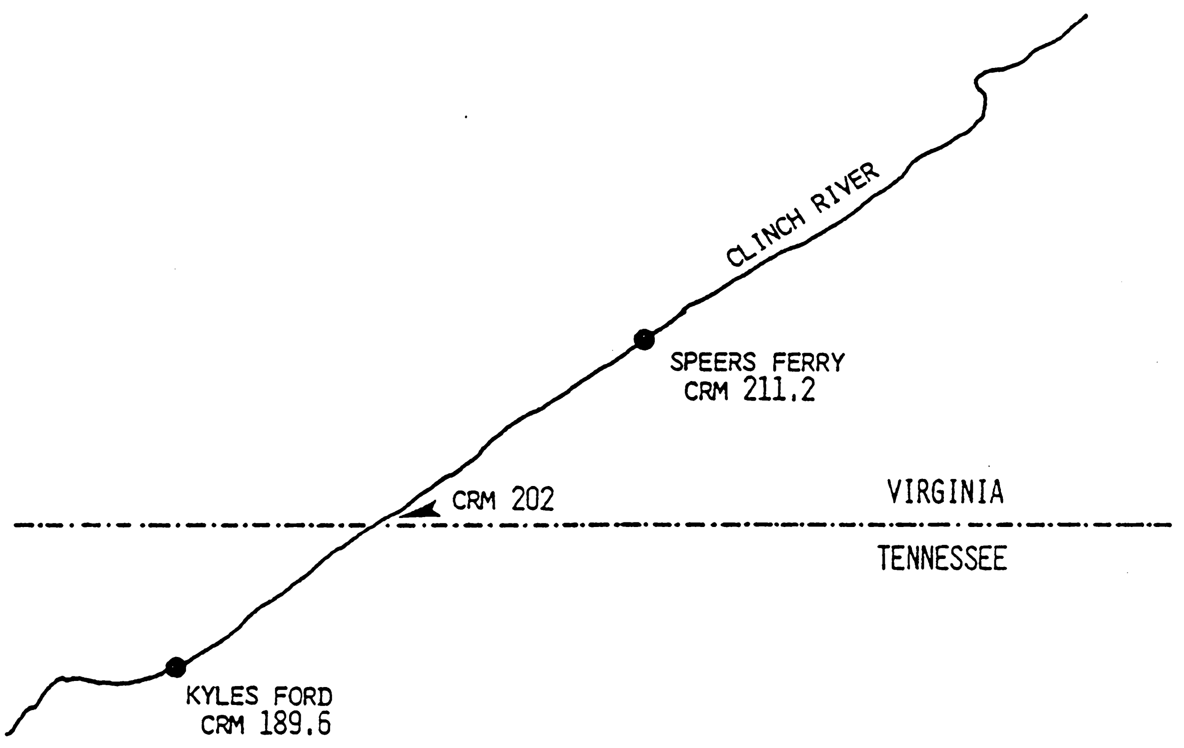


FIGURE II-1. LOCATION OF QUADRAT SAMPLING SITES, CLINCH RIVER (NOT TO SCALE) in macroinvertebrate studies is adequate for sampling small mollusks such as snails, Sphaeriids, and *Corbicula*, but was too small to adequately sample the larger unionid mussels. A sampling device was therefore constructed, patterned after the Surber sampler, but larger and heavier to withstand the swift currents of shoal areas of medium sized streams such as the Clinch and Powell Rivers.

The sampler consisted of a frame made of 1/8 inch flat iron, 40 inches (approximately 1 meter) on each side enclosing an area of approximately 1 square meter. A spike welded to each corner aided in securing the frame to the substrate, and a screened basket 12 inches (30.5 cm) high and deep attached to one side aided in recovery of small specimens (Figure II-2).

Collections from shoal areas were made by securing the sampler to the substrate with the basket end downstream and hand picking through the gravel enclosed by the frame. In order to find young specimens, all gravel was removed and carefully examined before being discarded outside of the quadrat. Each quadrat was worked by two or three people simultaneously. An average of five man-hours of time was required to complete each sample. In the pool area, SCUBA equipment was used to aid in collecting mussels from the quadrat which was located in water 1.5 to 2 meters deep.

All mussels collected were identified, measured, aged, and weighed in the field. Length was measured at the longest axis with a caliper and recorded to the nearest 0.01 mm. Age was estimated by counting

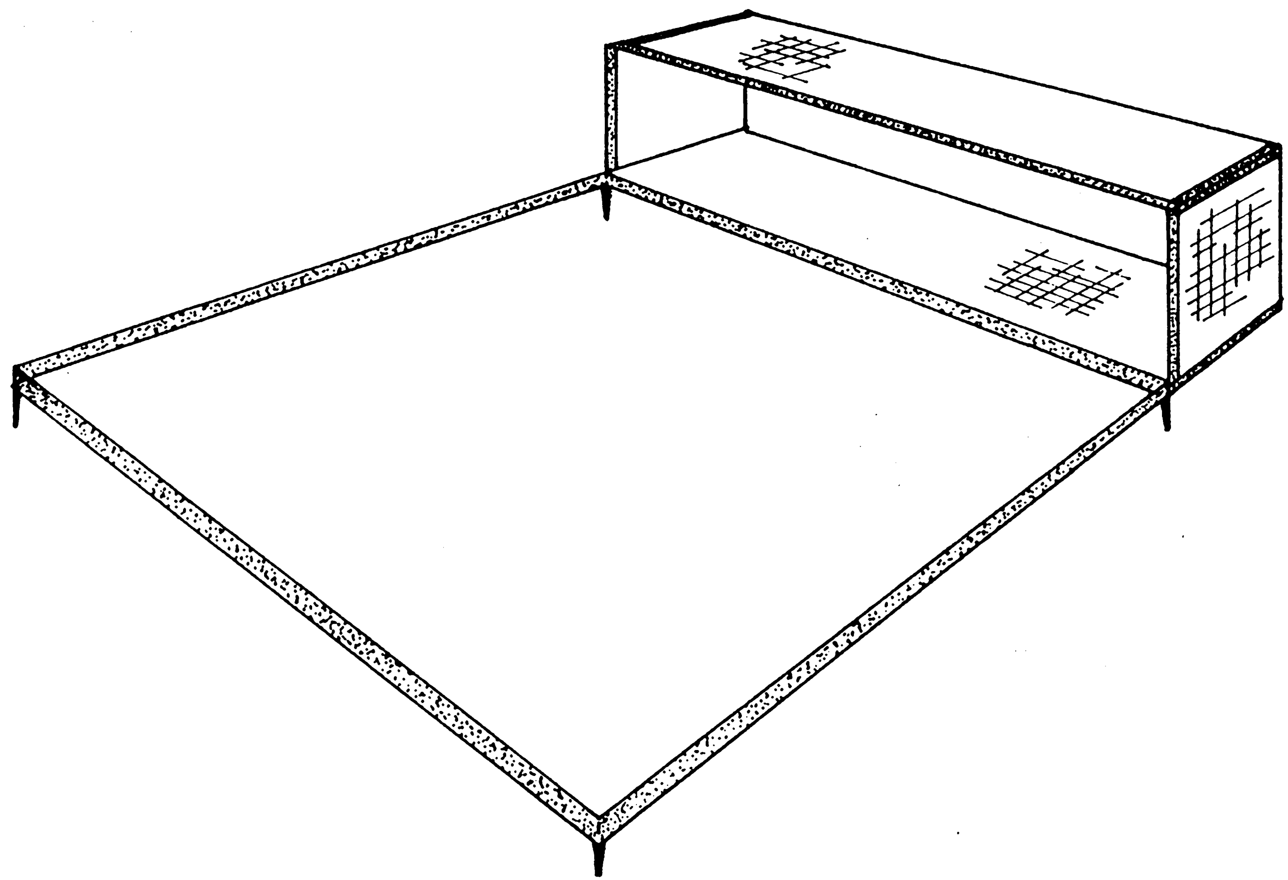


FIGURE II-2. SKETCH OF QUADRAT SAMPLER (NOT TO SCALE) growth arrests as discussed by Chamberlain (1931). Weights were measured with an Ohaus triple-beam balance and recorded to the nearest 0.1 gram.

A representative sample of species was preserved for reference; the remainder of specimens were returned to the river alive. Dead shells found within the quadrat were discarded, as their site of origin could not be determined.

RESULTS AND DISCUSSION

Quantitative Sampling of Fresh Water Mussels

Analysis of community structure requires enumeration of individuals which occupy a given area so that spatial and numerical relationships among component species populations can be seen. Until the present studies, there was little mussel data which could be called truly quantitative. While there have been a number of studies in which numerical data are reported, most of these data do not allow for analysis of community structure.

In an extensive mussel survey of the Mississippi River during 1930-31, Ellis (van der Schalie and van der Schalie, 1950) used a grab sampler which collected six sq. feet of substrate to collect samples at 254 stations over 700 miles of river. Van der Schalie and van der Schalie (1950) summarized these collection records, reporting numbers of species and individuals for river zones. While community structure was not addressed in this work, the large size and number of samples taken during this survey might allow for future analysis of community structure.

In a number of resource management studies (Scruggs, 1960; Bates, 1967, 1970; Isom, 1969; Thiel, 1981; Bates and Dennis, 1982) a variety of collecting techniques including brails, dredges and SCUBA have been used to assess standing crop of mussels. Since the objective of these studies was to evaluate the status of commercial mussel populations over large areas, little intensive quantitative sampling was done in any one area.

Scruggs (1960) was first to combine quadrat sampling (using SCUBA) and brail sampling to determine efficiency of the brail as a collecting device. Using a frame measuring one square yard, he collected a total of 96 square yard samples from 48 stations in the Tennessee River. His results were reported as yield per effort based on brail samples taken.

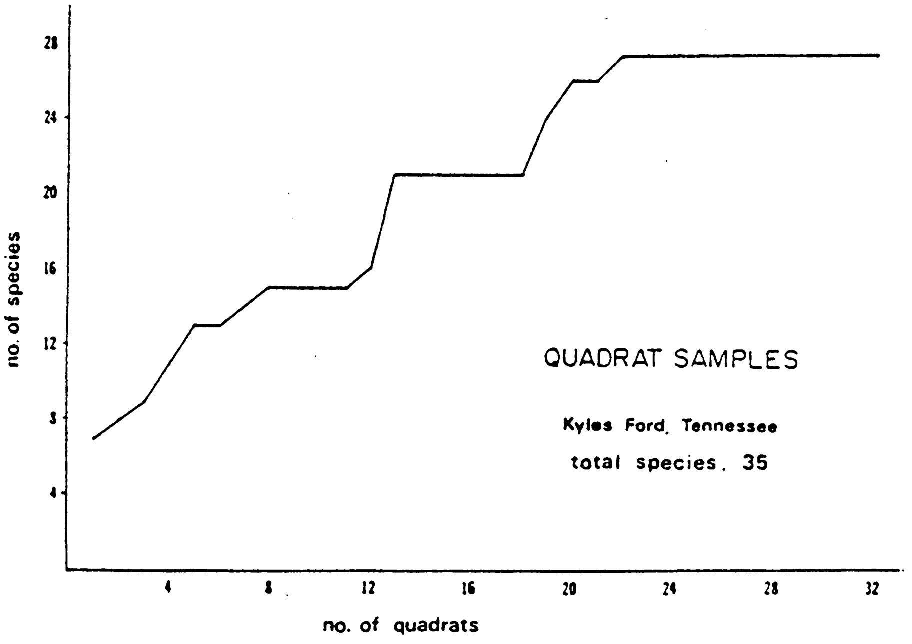
Bates (1970) sampled 80 miles of the Muskingum River in Ohio with commercial gear, supplementing brail samples with quadrat sampling in selected areas to calculate standing crop. Isom (1969) sampled the Tennessee River with a modified Peterson type grab sampler which collected approximately 1/3 square yard of river bottom. He took 3,000 samples over 500 river miles using a stratified random sampling technique on mussel beds to estimate standing crop of commercial species. Thiel (1981) also used quadrat sampling in conjunction with brail sampling to establish brail efficiencies, relying primarily on the brail data to assess mussel resources in the upper Mississippi River.

Some reports and publications (e.g. Grace and Buchanan, 1981; Coon et al., 1977) mention quantitative sampling techniques even though data reported are not quantitative. In other cases (e.g. Buchanan, 1980) relative abundance is reported based on qualitative sampling and treated as quantitative information. One unusual example of a "quantitative" mussel study was reported by Hendelberg (1960), who sampled a small

Swedish stream using a "water-glass" to count mussels in situ within a measured area of bottom. This approach, while apparently successful given the uni-species fauna of that stream, would not be effective in our gravel bottomed streams which support a diverse mussel fauna.

Since completion of the present sampling in 1975, similar quadrat techniques have been employed by TVA in conjunction with endangered species programs. In the Cumberland River, TVA (Tenessee Valley Authority, 1976) used SCUBA to collect samples from quadrats of various types including a meter square frame, a hoop, and a m^2 area marked with rope. In similar studies in the Tennessee River, Gooch et al.(1978) reported quadrat data from m^2 samples but did not describe the sampling method. Few endangered species, however, were reported from these samples. Similarly, TVA (Tenessee Valley Authority 1979) reported results of quadrat sampling in the Clinch and Powell rivers. From a total of 248 samples (.25 m^2) averaging 4 to 10 samples per site, only seven individuals of endangered species were reported.

The relationship between number of quadrats collected and number of species reported at Kyles Ford and Speers Ferry during the present studies is represented in Figure II-3, A and B respectively. In both cases, the number of species sampled in 32 m^2 fell short of the total number recorded from the site. Most species were sampled in the first 20 quadrats; an additional 12 quadrats resulted in addition of only one or two species. Most rare species were not collected at all in the quantitative samples.



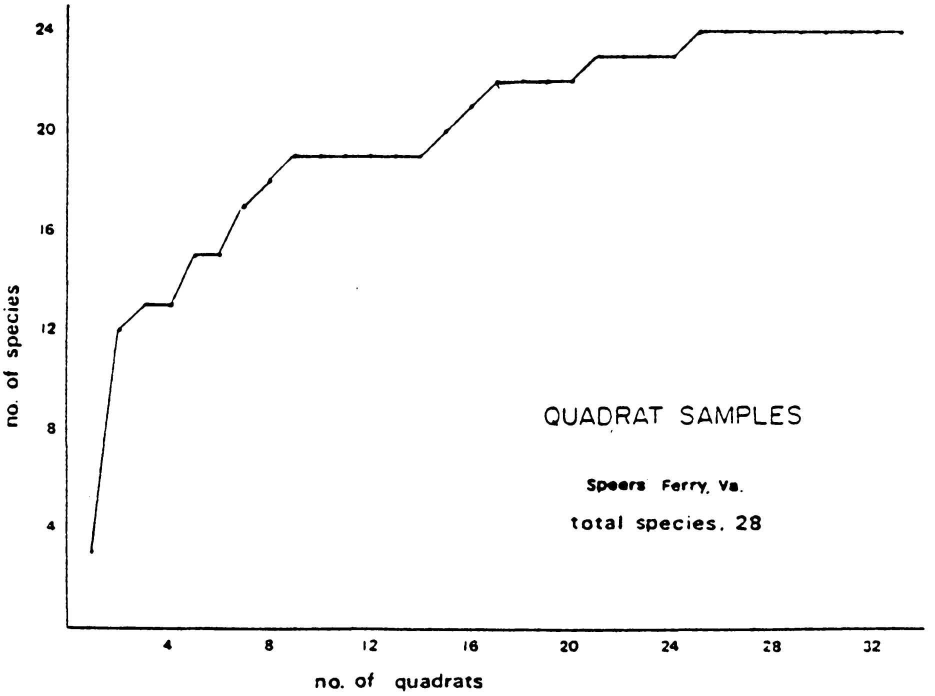


FIGURE II-3, NUMBER OF SPECIES COLLECTED VERSUS NUMBER OF QUADRAT SAMPLES TAKEN AT (A) KYLES FORD AND (B) SPEERS FERRY, CLINCH RIVER

While the use of quantitative methods for evaluating populations of rare species is limited, there is clearly a need for quantitative mussel data in assessing mussel community structure. One important community characteristic is the presence of dominant species. The relative abundance, density and age class distribution of dominant populations can be used to establish baseline community structure. Since most species occur in low numbers, the age class structure of the community as a whole can be useful in comparing communities spatially and temporally.

Analysis of Species Composition

Analysis of community structure is based on the study of species inter-relationships. Important in this regard are the numbers of species and their relative abundance. As pointed out in Chapter 1, mussel species composition is related to stream size and habitat type. While individual species within a community may vary regionally, basic community structure seems to be similar for similar habitat types.

To determine if there is predictable structure in freshwater mussel communities, it is necessary to study selected areas in detail. Three years of sampling mussels at two similar sites in the Clinch River provide a basis for characterization of mussel communities of medium to large rivers.

Tables II-1 and II-2 list mussel species in order of abundance in quadrat samples taken at Kyles Ford and Speers Ferry, respectively. The total number of specimens of each species collected is given along with frequency of occurrence (the number of quadrats in which each species occurred). Species for which "0" is given as the total number are those which were reported in qualitative sampling but which were not collected in quadrat samples.

Of the 35 species recorded from Kyles Ford, five were abundant, averaging three to six per m^2 sampled, and widely distributed over the quadrat sample sites. For most species, however, density averaged less than one per m^2 sampled; over half averaged less than one

TABLE II-1

Mussel species reported from the Clinch River at Kyles Ford, Tennessee, listed in order of abundance in quadrat samples. Number of Individuals=number collected in 32 m^2 quadrats during 1973-75. Frequency of occurance= number of quadrats in which species was found.

	Species	Number of Individuals	Frequency of occurance
1.	Medionidus conradicus	197	21
2.	Dysnomia capsaeformis	168	26
3.	Actinonaias pectorosa	162	20
4.	Ptychobranchus subtentum	130	18
5.	Actinonaias carinata	106	21
6.	Fusconaia barnesiana (complex)*	35	16
7.	Cumberlandia monodonta	26	4
8.	Fusconaia edgariana	25	3
9.	Elliptio dilitatus	23	10
10.	Lasmigona costata	19	9
11.	Alasmidonta marginata	11	10
12.	Truncilla truncata	9	7
13.	Cyclonaias tuberculata	7	6
14.	Ptychobranchus fasciolaris	6	5
15.	Lampsilis fasciola	5	5
16.	Lampsilis ovata	4	3
17.	Cyprogenia irrorata	3	3
18.	Dromus dromas	3	3
19.	Dysnomia brevidens	3	3
20.	Dysnomia triquetra	3	3
21.	Quadrula cylindrica	3	3
22.	Villosa nebulosa	2	2
23.	Lastena lata	1	1
24.	Ligumia recta latissima	1	1
25.	Plethobasus cyphyus	1	1
26.	Proptera alata	1	1
27.	Strophitus rugosus	1	1
The following species were found in qualitative samples only:			
28.	Amblema costata	0	0
29.	Conradilla caelata	0	0
30.	Dysnomia torulosa gubernaculum	0	0
31.	Elliptio crassidens	0	0
32.	Leptodea fragilis	0	0
33.	Pleurobema cordatum (complex)	0	0
34.	Quadrula pustulosa	0	0
35.	Villosa vanuxemensis	0	0

* includes: Fusconaia cuneolus

TABLE II-2

Mussel species reported from the Clinch River at Speers Ferry, Virginia, listed in order of abundance in quadrat samples. Number of Individuals=number collected in 33 m^2 quadrats during 1973-75. Frequency of occurance=number of quadrats in which species was found.

	Species	Number of Individuals	Frequency of occurance
1.	Dysnomia capsaeformis	89	25
2.	Actinonaias carinata	43	22
3.	Medionidus conradicus	24	14
4.	Ptychobranchus subtentum	14	11
5.	Actinonaias pectorosa	13	8
6.	Dysnomia brevidens	12	11
7.	Fusconaia barnesiana (complex)*	8	7
8.	Cyclonaias tuberculata	7	6
9.	Lampsilis ovata	5	4
10.	Lasmigona costata	5	4
11.	Quadrula cylindrica	5	5
12.	Elliptio dilatatus	4	4
13.	Ptychobranchus fasciolaris	4	4
14.	Dysnomia triquetra	3	2
15.	Fusconaia edgariana	3	2
16.	Lastena lata	3	3
17.	Ligumia recta latissima	3	2
18.	Amblema costata	2	2
19.	Alasmidonta marginata	2	2
20.	Plethobasus cyphyus	2	2
21.	Proptera alata	2	2
22.	Cyprogenia irrorata	1	1
23.	Strophitus rugosus	1	1
The following species were found in qualitative samples only:			
24.	Quadrula pustulosa	0	0
25.	Lampsilis fasciola	0	0
26.	Leptodea fragilis	0	0
27.	Truncilla truncata	0	0
28.	Villosa nebulosa	0	0
29.	Villosa vanuxemensis	0	0

* includes Fusconaia cuneolus

per 10 m^2. Species ranked 17 through 35 in Table II-1 were considered rare at this site. Species numbered 28 through 35 were very rare, reported only from qualitative sampling.

While mussels showed the same pattern of distribution at Speers Ferry (Table II-2) the numbers collected were much lower. The same 5 species were most abundant in quadrats, but abundance was only 25% of that at Kyles Ford. A total of 29 species were recorded from this site. More trips were made to Kyles Ford than to Speers Ferry during the sampling period; thus qualitative records from the former site are based on a greater sampling effort.

Species composition of mussels at Kyles Ford and Speers Ferry was similar; the only difference between the two sites studied, was the presence of six species at Kyles Ford which were not found at Speers Ferry. Since mussel species tend to increase in numbers from the headwaters to the mouth of a river (see Chapter 1), this difference was not unexpected. Speers Ferry is located approximately 20 miles upstream from Kyles Ford, a distance which appears to be sufficient to account for the clinal difference in species composition.

Three of the six additional species reported from Kyles Ford, Cumberlandia monodonta, Elliptio crassidens, and Pleurobema cordatum, are large river species that approach the uppermost limit of their range at this site. Two other species, Dromus dromas and Conradilla caelata, are rare in the Clinch River and may occur in numbers too low to be detected with the sampling effort expended at Speers Ferry; only one live specimen of *C. caelata* was found at Kyles ford during these studies. The sixth species, *Dysnomia torulosa gubernaculum*, was represented in collections only by one freshly dead specimen. This species has not been reported from live collections in recent years, and may be extinct.

Table II-3 shows the percent composition of major species groups in samples taken at both sites for 1973, 1974, and 1975. The species are listed at each site in order of overall abundance at that site. The same 5 species, *Medionidus conradicus*, *Dysnomia capsaeformis*, *Actinonaias carinata*, *A. pectorosa*, and *Ptychobranchus subtentum*, accounted for more than 70 per cent of mussels sampled at both sites. The rank order of species differed, however, at the two sites. At Kyles Ford, the top three species accounted for more than 50 percent of mussels collected, while at Speers Ferry, only two species accounted for this percentage.

The relative rank of the dominant species did not change in samples taken from year to year, however, relative abundance of the species was not constant. At both sites, the first years sampling resulted in a greater proportion of the first ranked species. In subsequent years, the second and third ranked species were better represented in the samples. In samples taken at Kyles Ford, in 1975, the three top ranked species were equally represented in the samples. This difference in results from year to year is probably due to differences in the samples taken each year. Both sites provide a variety of habitat types to be

TABLE II-3

Percent Composition of Major Species Groups Collected in Quadrat Samples from the Clinch River, 1973-1975.

Mussel Species	Percent Composition (by year)		
	1973	1974	1975
Kyles Ford			
Medionidus conradicus	24.4	21.0	19.4
Dysnomia capsaeformis	19.3	15.3	19.0
Actinonaias pectorosa	15.1	14.8	19.2
Ptychobrnchus subtentum	10.9	12.6	15.1
Actinonaias carinata	6.7	10.2	13.0
Speers Ferry			
Dysnomia capsaeformis	34.6	35.5	34.7
Actinonaias carinata	14.8	22.4	14.3
Medionidus conradicus	9.9	6.6	11.2
Ptychobranchus subtentum	0.0	3.9	10.2
Actinonaias pectorosa	4.9	5.3	5.1

sampled, including riffle, shoals, boulder and bedrock. The greatest density and diversity of mussels was found in the gravel shoal habitat. Quadrat samples were taken in a stratified random pattern within the area identified as the mussel "bed". During the first year, samples were distributed over a wide area to determine the limits of the bed. Consequently, there were more non-productive samples than in subsequent years. By the third year, the bed was well defined and most samples were taken within its boundaries. This sampling difference is also reflected in the total number of mussels collected each year.

While the term "mussel bed" is often used to describe mussel assemblages, it has never been well defined. The term has its origins in the commercial mussel industry where it is used to designate well defined "pockets" of mussels which occur in sufficient abundance to support commercial harvest. The density of mussels required to qualify an area as a mussel bed has changed over the years as the resource has declined. While the mussel shoals at Kyles Ford and Speers Ferry are no longer commercially harvested, they have supported commercial harvest in the past, and therefore qualify for designation as mussel beds.

In order to test the statistical significance of the annual differences observed in frequency of occurrence of species at the two sites, data were analyzed using the Kolmogorov-Smirnov test for goodness of fit (Kraft and von Eeden, 1968). This non-parametric test is ideally suited to this application since it allows for comparison of frequency distribution data and is not dependent upon sample size.

Results of the Kolmogorov-Smirnov analysis for Kyles Ford and Speers Ferry data are presented in Tables II-4 and II-5 respectively. Frequency distribution data from 1973 are compared to those from 1974, and 1975. Results indicate that no significant difference in frequency distribution of the six groups among years.

The five most abundant species are of Cumberlandian origin and are widely distributed throughout the Tennessee River system (see Chapter 1). The predominance of *D. capsaeformis* and *Medionidus conradicus* in the samples was unexpected based on qualitative sampling in which *A. carinata* and *A. pectorosa* dominated. This underestimation of *D. capsaeformis* and *M. conradicus* in qualitative samples is most likely due to their small size (20-40 mm) relative to *Actinonaias* (80-120 mm). Both species of *Actinonaias* are large, heavy specimens easily located visually when the water is clear, or tactually by feeling the substrate. The smaller species are more cryptic and may not be collected in proportion to their actual abundance in the community.

Dysnomia capsaeformis is a member of an almost extinct genus commonly referred to as "riffle shells". The reduction in large river shoal habitats has resulted in restriction of most members of this genus to headwater reaches. *D. capsaeformis* is locally abundant in a few areas of the Clinch River and occurs in low abundance elsewhere in the upper Tennessee region. *Actinonaias pectorosa* and *Ptychobranchus subtentum* are also restricted to medium sized streams. Only *A. carinata* has been found in large river habitats of the Cumberland and lower Tennessee Rivers.

TABLE II-4

Comparison of Frequency Distribution of Major Species Groups at Kyles Ford, 1973 - 1975, using the Kolmogorov-Smirnov Test.

	Proportion of mussels in major species groups					
	1*	2	3	4	5	others
Proportion-1973	.25	.19	.15	.11	.07	.23
Cumulative:	.25	.44	.59	.70	.77	1.00
(N =123)						
Proportion-1974	.21	.15	.15	.13	.10	.26
Cumulative:	.21	.36	.51	.64	.74	1.00
(N =373)						
Proportion-1975	.21	.19	.19	.15	.13	.15
Cumulative:	.19	.38	.57	.72	.85	1.00
(N =463)						
Differences in Cumulative Proportions:						
1973-1974:	.04	.08	.08	.06	.03	00
1973-1975:	.06	.06	.02	.02	.08	00

f-value (1973-74) f(.05)= 1.36 x = .14

f-value (1973-75) f(.05)= 1.36 x = .14

Difference is significant if the largest differece in cumulative proportions is equal to or greater than f-value.

* Species: 1. M. conradicus, 2. D. capsaeformis, 3. A. pectorosa, 4. P. subtentum, 5. A. carinata.

TABLE II-5

Comparison of Frequency Distribution of Major Species groups at Speers Ferry, 1973 - 1975, using the Kolmogorov-Smirnov Test.

	Proportion of mussels in major species groups					
	1*	2	3	4	5	other
Proportion-1973	.35	.15	.10	.00	.05	.35
Cumulative:	.35	.50	.60	.60	.65	1.00
(N =81)						
Proportion-1974	.36	.22	.07	.04	.05	.26
Cumulative:	.36	.55	.65	.69	.74	1.00
(N =76)						
Proportion-1975	.35	.14	.11	.10	.05	.25
Cumulative:	.35	.49	.60	.70	.75	1.00
(N =98)						
Difference in Cumulative Proportions:						
1973-74	.01	.05	.05	<u>.09</u>	<u>.09</u>	00
1973-75	.00	.01	.00	<u>.10</u>	<u>.10</u>	00

f-value (1973-74) f(.05)= 1.36 x = .22

f-value (1973-75) f(.05)= 1.36 x = .21

Difference is sigificant if the largest differece in cumulative proportions is equal to or greater than the f-value .

* Species: 1. *D. capsaeformis*, 2. *A. carinata*, 3. *M. conradicus*, 4. *P. subtentum*, 5. *A. pectorosa*.

The Fusconaia barnesiana complex, ranked sixth at Kyles Ford and seventh at Speers Ferry, is a taxon more characteristic of small streams such as the North Fork Holston River, where it may be the dominant component of the mussel community. In small streams, Pleurobema oviforme and Lexingtonia dollabelloides are often lumped with this taxon due to their similarity based on shell characters. At the Clinch River sites, F. barnesiana was seldom found in the main channel of the river, but was most often taken near the shore in shallow shoals under overhanging trees, a habitat more closely approximating the smaller stream environments.

Two other species , Villosa nebulosa and V. vanuxemensis, characteristic of small streams were present but rare at the sample sites. Similarly, a number of species, Quadrula pustulosa, Amblema costata, and Pleurobema cordatum, characteristic of large rivers were found in low abundance at the sample sites.

Most species collected in quadrats were widely distributed among samples, as indicated by the high frequency of occurrence. Two species, however, exhibited highly clumped distribution. Twenty two of the 25 specimens of Fusconaia edgariana collected at Kyles Ford came from one quadrat and 21 of the 26 specimens of Cumberlandia monodonta were found in one m^2 sample. This highly clumped distribution, characteristic of C. monodonta, makes it difficult to find in qualitative samples. For this reason, C. monodonta is often reported as rare, based on qualitative sampling, although its actual numbers may be higher than estimated.

Fusconaia edgariana, listed as an endangered species (Fed. Reg., 1976), is widespread throughout the upper Tennessee River system, although not abundant at any site. There is no evidence to indicate that this species characteristically exhibits the clumped distribution observed at Kyles Ford.

Of the remaining species reported from the sample sites, four (Dromus dromas, Dysnomia brevidens, Lastena lata and Conradilla caelata) which are of Cumberlandian origin appear to be increasingly rare throughout their ranges. Dromus dromas and C. caelata are listed as endangered species (Fed. Reg., 1976) and Lastena lata was proposed for such listing. Dysnomia brevidens remains widespread in the upper Tennessee River drainage where it is a rare component of the fauna. Conradilla caelata is abundant at one site in the Duck River, Tennessee, but rare in the Clinch and Powell Rivers. Although a great deal of effort has been expended in recent years by the Tennessee Valley Authority (Yokley,1975; TVA, 1980) to define the habitat requirements and life history of this, and other, endangered species, reasons for its abundance at one site are still not clear. The remaining species reported here are widespread interior basin species which seldom occur in great abundance.

The mussel communities at Kyles Ford and Speers Ferry are characteristic of those associated with riffle-shoal habitats of large to medium sized streams, where high diversity results from mixing various faunal elements. The mussel community of these shoal areas is a mixture of species ideally suited to medium sized streams (e.g.the 5 most abundant species) as well as species which overlap this region from small and large river habitats. Additionally, in the upper Tennessee region, there is a mixture of Cumberlandian and Ohioan faunal elements. This habitat type supports the greatest mussel diversity remaining in the Tennessee River system.

Table II-6 summarizes quadrat samples taken from selected sites in the Powell River. Species are listed in order of their abundance at all sites combined. The Powell River sites were similar in appearance to those in the Clinch River providing riffle and shoal habitat similar to that at Kyles Ford. Mussel densities ranged from 6.1 to 25 per m^2 sampled; number of species recorded per site ranged from eight to 19. The sampling effort expended here, however, was less than that at the Clinch River sites.

Although mussel species composition at the Powell River sites was generally similar to that of the Clinch River, there was greater variation among sites in species density and in degree of species dominance exhibited. One species, Actinonaias carinata, was most abundant at all sites. The predominance of other species, however, varied widely with site. At Buchannon and McDowell Fords, two species seemed to predominate; at Fletcher Ford, six were very abundant. Data from site 4 are based on only four samples, and are therefore not comparable to other sites.

TABLE II-6

Species and Numbers of Mussels collected from Quadrats taken in the Powell River, Tennessee and Virginia.

Species	Number of mussels collected:			
Sites:	1*	2	3	4
Actinonaias pectorosa	64	22	99	28
Actinonaias carinata	27	5	26	6
Medionidus conradicus	6	11	38	7
Fusconaia barnesiana	4	2	33	3
Elliptio dilatatus	1	5	13	2
Dysnomia brevidens	1	2	10	2
Lasmigona costata	3	1	6	1
Dromus dromas	2	4	0	0
Lampsilis fasciola	1	0	4	1
Amblema costata	1	2	0	0
Dysnomia triquetra	1	0	2	0
Fusconaia edgariana	2	1	0	0
Leptodea fragilis	0	0	3	0
Quadrula intermedia	1	2	0	0
Cyclonaias tuberculata	0	1	1	0
Dysnomia capsaeformis	0	0	2	0
Plethobasus cyphyus	1	1	0	0
Ptychobrachus fasciolaris	1	1	0	0
Ptychobrachus subtentum	2	0	0	0
Quadrla cylindrica	0	1	1	0
Villosa nebulosa	1	0	1	0
Alasmidonta marginata	1	0	0	0
Conradilla caelata	0	1	0	0
Lampsilis ovata	1	0	0	0
Quadrula sparsa	1	0	0	0
Unknown juvinile	0	0	1	0
Totals	121	61	242	50
Area sampled (m^2):	10	10	10	4
No. per m^2 sampled:	12.1	6.1	24.2	12.5
Total no. species (from qualitative samples)	28	36	28	**

* Sites: 1. Buchannon Ford, 2. McDowell Ford, 3. Fletcher Ford, 4. Fletcher Cliff.
** Comparable qualitative data not available.

Table II-7 presents data from quadrat samples taken at several small stream sites in the North Fork and Middle Fork Holston River. The fauna here is typical of a small stream assemblage, differing from the Clinch and Powell sites in species abundance and composition.

In the small streams, the number of species recorded was less than 10 at all sites, with two to three species predominating. The number of mussels collected per square meter was generally less than for large rivers. It is interesting to note that the species which predominated in the small streams (Medionidus conradicus, Villosa nebulosa, and V. vanuxemensis) are small species, generally < 10 mm in length. The large species Actinonaias carinata, abundant in the Clinch and Powell Rivers was absent in small streams. Another large species, A. pectorosa, was rare in these streams.

In general, the pattern of species abundance observed in the study areas consists of two to four dominant species which are Cumberlandian in origin and typical of medium sized stream habitats followed in abundance by seven to 10 species of mixed origin, also typical of medium sized stream habitats. The majority of species are of low occurrance, consisting of rare Cumberlandian forms, Ohioan species and those more typical of small and large streams.

A similar pattern of species dominance has also been observed in recent collections from the lower Tennessee and Cumberland Rivers, and in rivers of the Ohio and Mississippi drainage including the Muskingum River, Ohio, the Allegheny River and French Creek, Pennsylvania, and the

TABLE II-7

Species and numbers of Mussels taken from the North Fork and Middle Fork Holston River, Virginia.

Species	Numbers of mussels collected:		
Sites:	1	2	3
Medionidus conradicus	19	44	5
Fusconaia barnesiana	8	12	11
Villosa nebulosa	18	9	10
Villosa vanuxemensis	2	7	16
Ptychobranchus subtentum	0	8	0
Fusconaia edgariana	2	5	0
Actinonaias pectorosa	0	5	0
Lampsilis fasciola	2	2	1
Ptychobranchus fasciolaris	1	3	0
Elliptio dilatatus	0	0	1
Unknown juvinile	2	0	0
Totals:	54	95	44
Area sampled (m^2)	10	10	5
Number per m^2	5.4	9.5	8.8

* Sites: 1. North Fork at Saltville, 2. North Fork at North Holston Ford, 3. Middle Fork at Craig's Bridge.

Mississippi River, Illinois (Dennis and Bates, unpublished.).

In most large rivers, the dominant species are those of commercial importance. In some areas, the same species have retained their dominant position in the fauna after many years of selective commercial harvest.

Analysis of Mussel Density

The methods by which populations are limited in size have been debated over the years (see Birch, Andrewartha, Nicholsen, Hutchinson, in Cold Spring Harbor Symposium, 1957 ; also Hairston et.al., 1960; Murdoch, 1966; Erlich and Birch, 1967). MacArthur (1958) proposed that animal populations are regulated by two types of factors; those which are independent of population density (i.e.catastrophic events, weather, some predation, some disease) and those which are density dependent (i.e. food availability, space). When density dependent events play a major role in regulating abundance, interspecific relations are important since the presence members of closely related species may have the same effect as the presence of members of the same species. Factors which are reported (Krebs, 1978) to influence density in animal communities include: competition, predation, immigration and emigration as well as such exogenous influences as weather and food availability.

Although population densities maybe observed to shift over time, in mature communities, populations generally reach a condition of stability, referred to as the "balance of nature" by Erlich and Birch (1967). This "balance" is generally attributed to inter or intra-specific competition for limited resources (e.g space, food) or to predator-prey relationships. Freshwater mussel communities consist of populations of many closely related species which exist in seeming equilibrium. While density does not appear to vary widely on a temporal basis, mussel densities do vary significantly among similar sites.

There is evidence that mussel species composition has remained constant over the past 50 years for a number of areas in the upper Tennessee drainage (Bates and Dennis, 1978; Dennis, 1981). Although the absence of quantitative data makes it impossible to compare historical to present density and diversity, data reported here (Table II-8) indicate that mussel densities are much more variable than species composition and diversity on a site specific basis. Although the number of mussels appears to increase with each year, the high averages for 1974 and 1975 are the result of a few quadrats in which mussel densities were exceptionally high (>100 per m^2).

Both species composition and species diversity were similar at Kyles Ford and Speers Ferry, however, mussel densities differed markedly, with 29.7 mussels per m^2 reported at Kyles Ford compared to 7.7 at Speers Ferry. A similar pattern was observed in the Powell River (Table II-9) from 1973-79, in which I identified diverse mussel assemblages at a number of sites, including: Buchannon Ford (RM 99.2) with 28 species,

TABLE II-8

Comparison of Density and Diversity of mussels collected from quadrats taken in the Clinch River at Kyles Ford and Speers Ferry from 1973 through 1975.

	Kyles Ford			Speers Ferry		
Year	1973	1974	1975	1973	1974	1975
No. of Mussels:	123	373	463	81	76	98
Area sampled: (m^2)	10	9	13	11	10	12
Average Density: (mussels per m^2)	12.3	41.4	35.5	7.4	7.6	8.2
Stand. Dev.	11.9	41.5	34.5	8.0	4.6	3.4
Average Density per site:		29.7			7.7	
Species Diversity:		3.26			3.31	

TABLE II-9

Summary of Mussel Densities from Selected Sites in the upper Tennessee River Drainage.

Site Sampled	Area Sampled (m^2·)	Mussel Density (No. per m^2)
Powell River		
Buchannon Ford	10	12.1
McDowell Ford	10	6.1
Fletcher Ford	10	24.2
Fletcher Cliff	4	12.5
North Fork Holston River		
Saltville	10	5.4
North Holston Ford	10	9.5
Middle Fork Holston River		
Craig's Bridge	5	8.8

McDowell Ford (RM 106.6) with 36 species and Fletcher Ford (RM 117.4) with 28 species (Dennis, 1981). Quadrat sampling at these sites revealed widely varying mussel densities ranging from 6.1 to 24.2 mussels per square meter.

All sites appeared similar in habitat type, and the species collected are representative of a riffle-shoal community similar to that of the Clinch River. It is interesting to note that the site with the greatest number of species abundance, McDowell Ford, also exhibited the lowest density. The fact that this site is located between the other sites, with no noticeable pollution source upstream makes the density differences more difficult to understand. While it is possible that habitat disturbances caused reductions in density at Speers Ferry and McDowell Ford, such disturbances are not documented. If pollution or physical disturbances altered the habitat sufficiently to reduce numbers dramatically, why was species abundance not affected?

Table II-9 also includes mussel densities from sites sampled in the North Fork and Middle Fork Holston Rivers. These smaller streams exhibited characteristically lower mussel densities (5 to 10 per m^2). The difference between 29 and seven mussels per m^2 seems great, however, mussel densities of six or seven per m^2 are by no means representative of a depauperate fauna. The high densities of 20 to 30 mussels per m^2 reported for reaches of the upper Tennessee River are, in fact, unusually high when compared to densities elsewhere in the Interior Basin. Most areas which are presently being harvested commercially support mussels in densities of two to eight per m^2. Quantitative sampling on mussel beds in the Muskingum River, Ohio (Bates and Dennis, unpublished) revealed densities of six per m^2. Scruggs (1960) reported densities of approximately six per sq. yard in reaches of the Tennessee River. Isom (in press) reported densities of approximately eight per m^2 on a mussel bed in the Cumberland River in Tennessee. Recent work in the lower Tennessee River by Dennis and Bates (1981) indicate that overbank areas presently being harvested by divers support mussels in densities of approximately two per m^2.

Although factors which limit mussel density are not known, competition for space or food do not appear to be limiting in riffle-shoal communities. While the availability of suitable substrate for colonization is important, overcrowding does not seem to be a problem in shoal areas. At Kyles Ford, mussels varied in density from 0 to 126 mussels per m^2 sampled, with an average of 29.7. Twenty per cent of the quadrats sampled contained greater than 50 mussels. Clearly, the average of 29 mussels per m^2 does not approach the maximum number of mussels possible based solely on available physical habitat. In shoal areas which presently support six to seven mussels per m^2, available physical habitat cannot be the limiting factor.

Allen (1914) reported that an adult fresh water mussel may filter 1.5 liters of water per hour. When considering the large number of mussels which may inhabit a mussel bed, it seems possible that competition for food could be a factor in mussel density. This contention is not supported by experimental data, however. Studies by Weitzel (1970) on phytoplankton populations in the Muskingum River, Ohio, demonstrated that a large mussel bed did not reduce phytoplankton densities at surface, middle or bottom of the water column.

Connell (1975) discussed the role of predation by fish on benthic communities, reporting that the presence of fish is known to cause reductions in benthic fauna. Although there are little published data regarding predation of mussels by fish, I have observed Corbicula in the digestive tracts of catfish taken from the Tennessee River, and small snails and spheriids in the gut of some bottom feeding stream fishes.

The relationship between fish and mussels is complex; fish serve both as a predator on young mussels and as a necessary component of the mussel's reproductive success. This dual role is often combined in the relationship between a mussel and its fish host. A number of species of the genus Lampsilis have developed mechanisms which appear to attract fish to the female mussel at spawning time (Kraemer, 1970). Glochidia are released by some species in packets which are eaten by the fish. Some of the glochidia then attach to gill tissues via the fish's buccal cavity (Chamberlain, 1934; Howard, 1914). The fish is simultaneously providing for and limiting the reproductive success of the mussel species.

Other important predators on freshwater mussels are several small mammals, primarily muskrats and raccoons. These animals have developed methods of locating and opening freshwater mussels for food. Shells left behind in middens indicate that prey selection is not species-specific but tends to be size-specific with preference toward small specimens. Occasionally, a large mussel will be found live in a muskrat midden apparently having escaped by virtue of its ability to resist being opened (S. D. Dennis, unpublished.).

The importance of small mammal predation on mussels is not known, but is probably negligible for the following reasons. Two of the most abundant mussel species collected in the Clinch River (Dysnomia capsaeformis and Medionidus conradicus) were small species, well within the size limits preferred by muskrats. These species in fact comprised the majority of shells found in many middens (S. D. Dennis, unpublished). Since predation seemed to be selective for these smaller species, it is reasonable to assume that this would eventually favor the larger species, giving them a competitive edge. Data indicates, however, that the small species have remained dominant despite this predation. It is probable that the degree of predation was not severe enough to impact community dynamics.

In recent years, there has been an increase in Corbicula populations in the upper Clinch River (Dennis, unpublished), and this small introduced species has almost completely replaced the native mussel species in muskrat middens. Whether this will result in increased abundance of smaller unionid species has yet to be seen.

Age Class Distribution

Data on age class composition of mussels collected from quadrats taken at Kyles Ford and Speers Ferry in 1973, 1974, and 1975 are presented in Tables A-1 through A-7 of Appendix A.

Data from Kyles Ford collections (Tables A-1, A-2, and A-3) demonstrate that, with the exception of the five major species, most species were represented by too few individuals to allow for conclusions as to age class structure of populations. In most cases, however, species seemed to be represented by specimens from all age categories. Cumberlandia monodonta was represented only by specimens in the older categories (8-11 years).

Data on age class composition of mussels collected from Speers Ferry (Tables A-4, A-5, and A-6) show that the two most abundant species (Dysnomia capsaeformis and Actinonaias carinata) had a predominance of specimens in the youngest age class (0-3 years). The majority of species recorded from quadrat samples were represented by one or two specimens per year. These single observations account for most of the mussels recorded for the 6-7 year and 8-9 year age classes.

For comparative purposes, limited sampling was conducted in a selected pool area adjacent to the shoal sampled at Kyles Ford. Results of this sampling are presented in Table A-7 and Figure II-6. Unlike the shoal sites, collections were dominated by individuals in the older age classes. Actinonaias carinata and A. pectorosa comprised 78% of the specimens collected at this site, and almost 70% of these specimens were over 11 years of age. Of the remaining 15 species recorded, most were in the 8-10 year category.

Data on age frequency distribution of mussels from Kyles Ford and Speers Ferry are presented graphically in Figures II-4 through II-6. All species were lumped and divided into four age class categories. The per cent of mussels in each age class is presented for each of the three years sampled.

Age frequency distributions of mussel communities at Kyles Ford and Speers Ferry were compared using the Kolmogorov-Smirnov Test (Kraft and van Eeden, 1968). Comparisons were made between the two shoal communities (Table II-10 and between the shoal and pool community at Kyles Ford (Table II-11). In both cases, a significant difference was demonstrated between age frequency distributions.

The Speers Ferry community (Fig. II-5) was skewed heavily toward the younger age classes, while that at Kyles Ford (Fig. II-4) exhibited a more uniform distribution among age classes. The age class distributions represented in both of these figures are characteristic of stable populations described by Krebs (1978) as "stationary" and "stable" age class distributions. The stationary distribution illustrated in Figure II-4 is similar to that described by Krebs for a mature population of maximum size in which the birth rate equals the death rate. The stable distribution illustrated by Figure II-5 represents a rapidly growing population.

It should be noted that the oldest age class, labeled 11+, is not equal in size to the others. Due to the difficulty of ageing mussels which are over 12 years old all mussels over 10 years old have been lumped into one category which includes mussels which range from 11 to 30+ years. If more age classes could be defined, the oldest age category would be considerably smaller than represented in the histograms (Figs II-4 and II-5).

The difference in the shape of the age class curves for Kyles Ford and Speers Ferry may reflect a difference in past environmental conditions. Two industrial spills have been documented (Cairns et. al., 1970, 1971) from a power plant 45 miles above Speers Ferry, Va. On June 10, 1967, a fly ash spill occurred and on June 19, 1970, an acid spill was reported from the same site at Carbo, Va. Cairns, et al. (1970, 1971) reported that deleterious effects on benthos were observed for 77 miles below Carbo and that all molluscs were eliminated for 11.7 miles as a result of the spills. Specific data on freshwater mussels were not reported for the study area except to note that recovery of mussels and snails did not occur within the period of the follow up studies.

Since fish kills resulting from the spills were reported as far downstream as the Tennessee State line (9 miles below Speers Ferry), it is probable that the spills had some effect upon mussels in this river reach. Presence-absence information alone, however is not adequate to document the impact. Quantitative data taken during the present study, however tend to support the hypothesis that the area of Speers Ferry was

TABLE II-10

Comparison of Age Frequency Distribution of Mussel Populations at Speers Ferry and Kyles Ford using the Kolmogorov-Smirnov Test.

	Age Class				
	0-3	4-5	6-7	8-10	11+
Kyles Ford (#1)					
No. collected Total N=945	241	255	177	142	130
Proportion	.26	.27	.19	.15	.14
Cumulative:	.26	.53	.72	.87	1.01
Speers Ferry (#2)					
No. collected: Total N=255	118	60	30	30	17
Proportion:	.46	.23	.12	.12	.07
Cumulative:	.46	.69	.81	.93	1.00
Difference in Cumulative proportions:					
	.20	.16	.19	.06	.01

f(.01) = 1.63 x = .11 .20< .11 Diff. is Sig.

difference is significant if largest difference between cumulative proportions is equal to or greater than f-value.

TABLE II-11

Comparison of Age Frequency Distribution of Mussels Collected from pool and riffle areas of the Clinch River at Kyles Ford, using the Kolmogorov-Smirnov Test.

	Age Class (years)				
	0-3	4-5	6-7	8-10	11+
Riffle (#1)					
Cumulative Proport. (Table II-17)	.26	.53	.72	.87	1.01
Pool (#2)					
No. Collected: Total N=145	6	29	20	31	59
Proportion:	.04	.20	.14	.21	.41
Cumulative	.04	.24	.38	.59	1.00
Difference in Cumulative Proportions:					
	.24	.29	.34	.28	.01

f(.01) = 1.63 x = .26 .34> .26

Difference is significant if largest difference between cumulative proportions is equal to or greater than f-value.

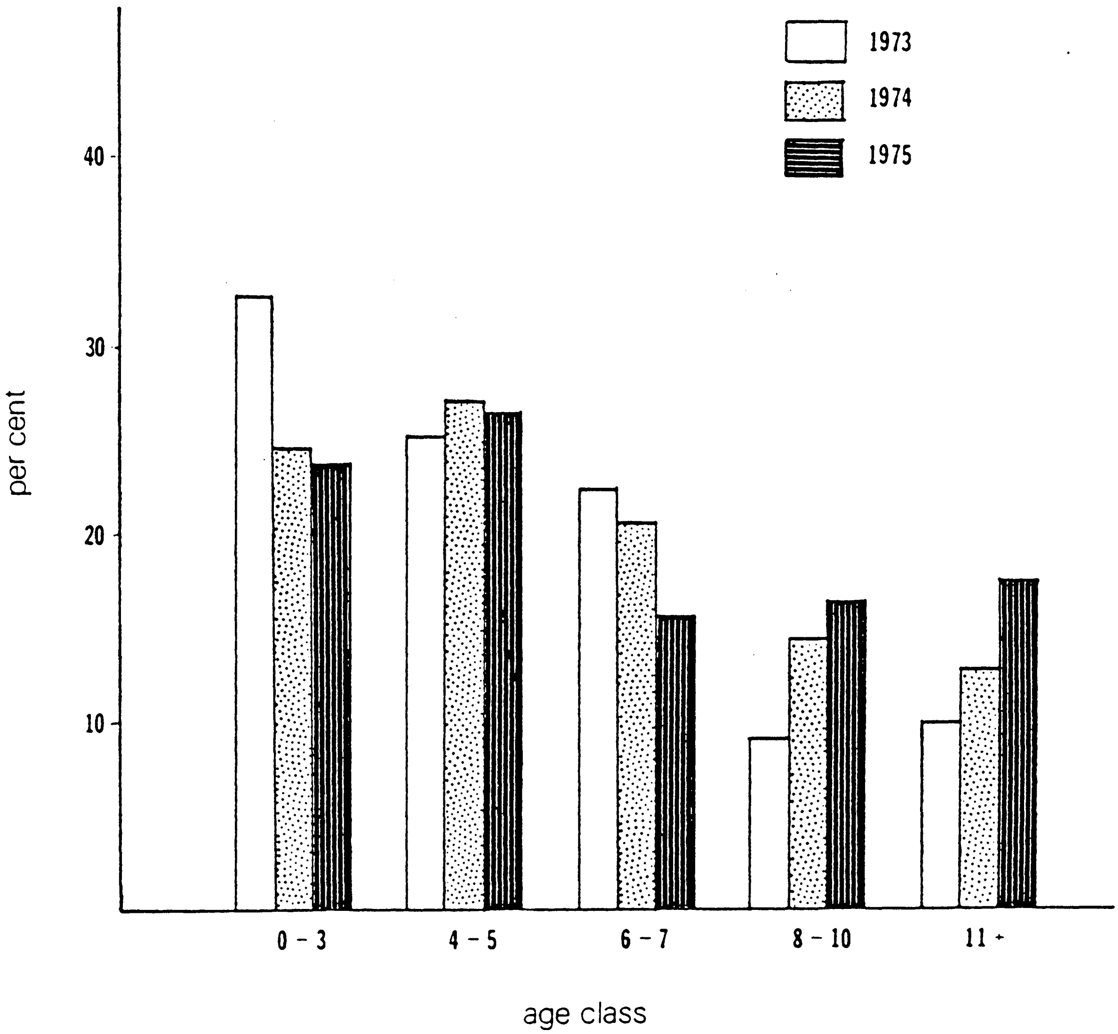


FIGURE II-4. AGE CLASS STRUCTURE OF MUSSELS SAMPLED IN M² QUADRATS FROM THE CLINCH RIVER, KYLES FORD, 1973-75

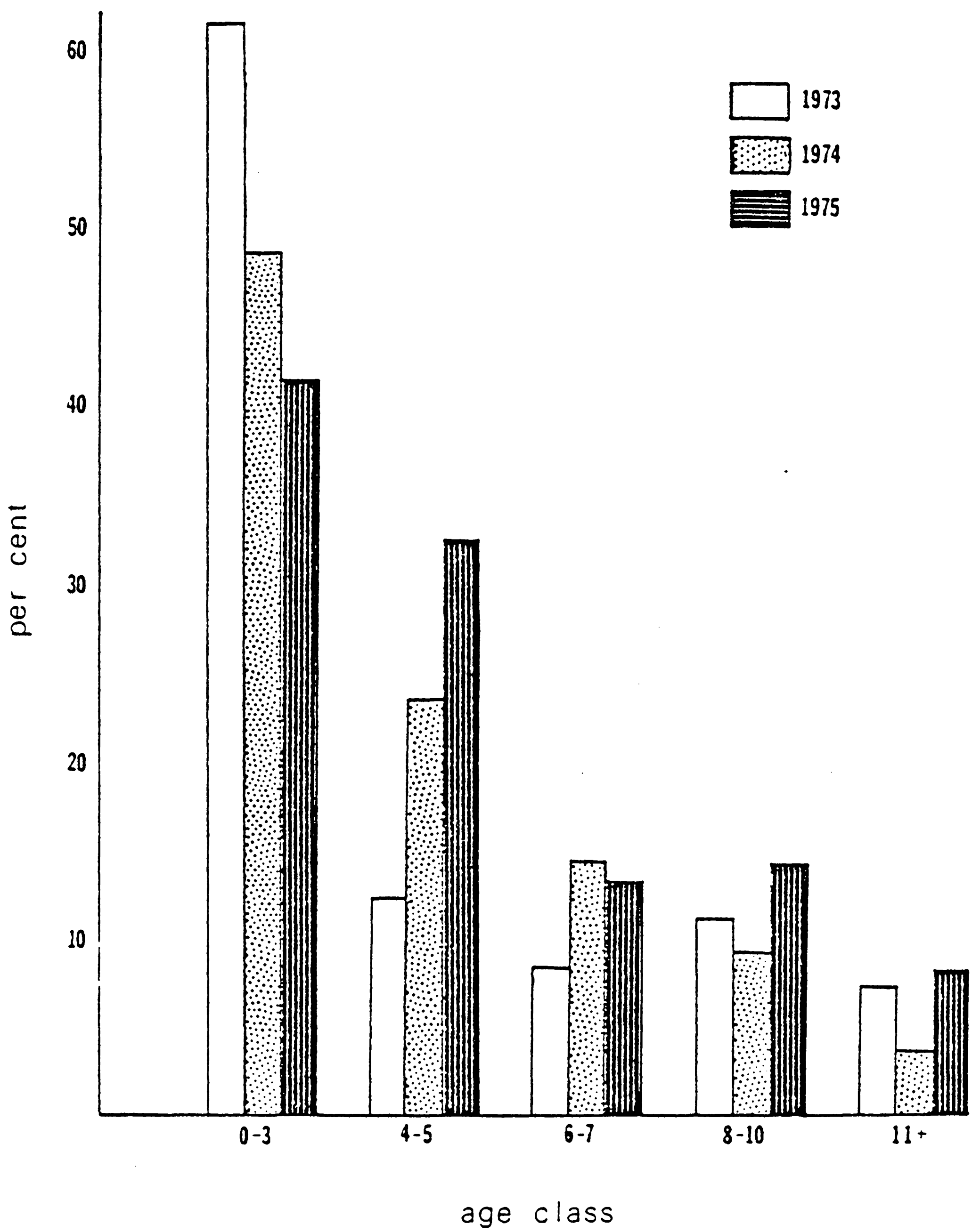


FIGURE II-5. AGE CLASS STRUCTURE OF MUSSELS SAMPLED IN M^2 QUADRATS FROM THE CLINCH RIVER, SPEERS FERRY, 1973-75

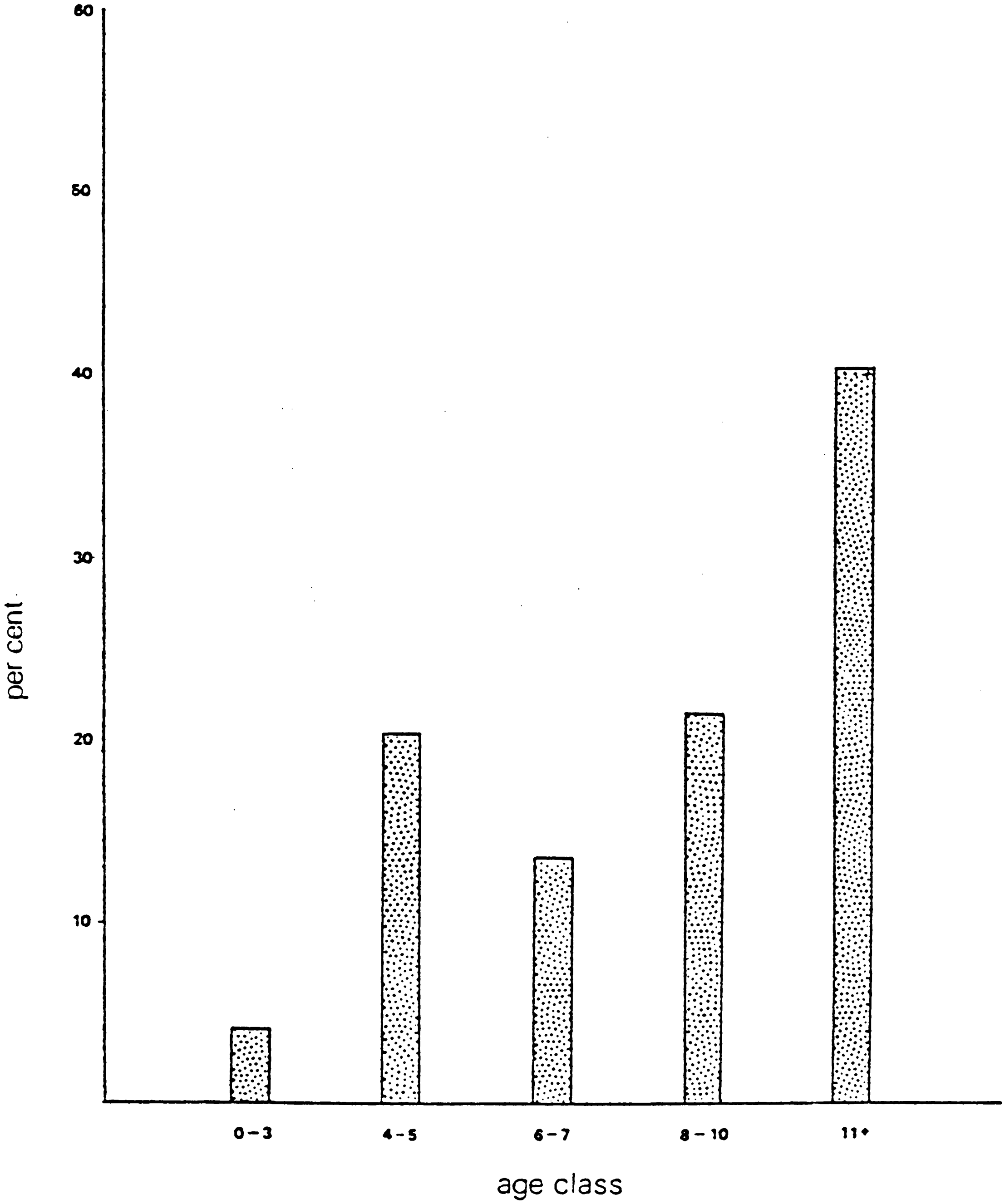


FIGURE II-6. AGE CLASS STRUCTURE OF MUSSELS SAMPLED WITH SCUBA FROM A POOL OF THE CLINCH RIVER, KYLES FORD, 1975 impacted. This would account for the high proportion of young specimens indicative of rapid growth in the community.

Species Abundance and the Niche

The pattern of species abundance observed at Kyles Ford and Speers Ferry in the Clinch River was also observed at other sites throughout the upper Tennessee River system. Data presented in Tables II-2, II-3, II-4 and II-5 show that at most sites, greater than 50 per cent of mussels collected were individuals of two species. The dominant species varied from site to site both within and among streams.

Collections from the Powell River (Table II-6) exhibited a pattern similar to that of the Clinch River, with *Actinonaias carinata*, *A. pectorosa*, and *Medionidus conradicus* dominating the collections. *Dysnomia capsaeformis* and *Ptychobranchus subtentum*, which were abundant in the Clinch River, were rare in the Powell, where they were replaced in numerical rank by *Fusconaia barnesiana* and *Elliptio dilatatus*.

Species composition in the North Fork and Middle Fork Holston River (Table II-7) differed markedly from that of the Clinch and Powell Rivers due to differences in stream size. *Medionidus conradicus* was abundant in the North Fork, as were members of the genus *Villosa* and the *F. barnesiana* complex. *Villosa vanuxemensis* and *V. nebulosa* were dominant in collections taken from the Middle Fork. The abundance of these species is indicative of small stream conditions.

The concept of species dominance assumes that certain species are better adapted to a given habitat at a given time than others. Given a wide variety of species, each occupying a specific niche, the dominant species in an area may vary over time as environmental conditions change, first favoring one species, then another. There is, unfortunately, little quantitative data available from historic collections with which to detect such shifts in freshwater mussel communities.

Evidence of shifts in mussel dominance resulting from habitat alteration can be seen in examining records of commercial harvest in the Tennessee River since its impoundment. In the river reach below Pickwick Dam, *Pleurobema cordatum* was once the dominant commercial species, comprising 40% of the catch in 1939 (Bates and Dennis, 1981). When sampled in 1980, this species comprised 1.6% of the mussels taken at this site. It is no longer considered an important commercial species here. With the decline in numbers of *P. cordatum*, there has been an increase in abundance of another commercial species, *Fusconaia ebenus*. This species has increased from 4.2 to 29.8% of the population during the same time period (Bates and Dennis, 1981).

The habitat below Pickwick Dam is favorable for riverine mussel species; there is a swift current with gravel substrate. Several riverine species, including *Quadrula metanevra* and *Q. pustulosa*, have maintained stability in relative abundance over the years; each comprises approximately 10% of the fauna. The change in dominance from

P. cordatum to F. ebenus is most likely due to changes in fish species composition resulting from construction or operation of the dam. Fish species records available for this area (primarily sport and commercial catch records) are not complete enough to reveal any comparable change.

In the area of New Johnsonville, Tennessee, effects of impoundment by Kentucky Dam are obvious. The Tennessee River is widened into a lake, with extensive backwaters, overbanks and shallow sandy flats. Here, both species dominance and location of the fauna have changed drastically. The riverine P. cordatum has all but disappeared, replaced by species inhabiting the overbanks. Amblema costata and Quadrula quadrula, which were rare in the riverine assemblage are dominant species in overbank areas along with Fusconaia undata which has moved in from the Ohio River. Since 1958, Q. quadrula has increased in abundance from <1 to 23.5% of the commercial catch. In the lower reservoir, in Kentucky, this species now comprises 54% of the fauna. Whether it is the mussel species themselves, or their fish hosts which prefer the overbank reaches is unknown, since these species are also common members of riverine communities.

Analysis of recent quantitative data from a number of locations indicate that species dominance is characteristic of mussel communities. The reason for one species' success over another is, however obscured by our lack of knowledge of the biology of these organisms. Factors which are thought to control populations, such as natality, mortality, emigration, migration, predation, feeding and reproductive behavior, have not been reported for fresh water mussels. The cryptic behavior and complicated life history of these organisms makes interpretation of population data difficult. Additionally, specific habitat requirements have not been established for any species.

In order to understand the success of a species in a community, something must be known of that species' niche. Hutchinson (1958) defined the "fundamental niche" of an organism as the total set of environmental conditions that permit a species to exist, and the "realized niche" as that subset of conditions that an organism shares with no other species.

Since neither the actual nor realized niche can be defined accurately for most species, Pielou (1975) suggested a measure of "niche width" to define the physical relationships among species. The concept of niche width involves a weighted measure of niche parameters in terms of success to the species. Pielou (1975) suggested that in evaluating the niche of organisms, habitat factors be chosen which can be interpreted in terms of niche width and overlap. In this application she acknowledged that mean habitat span and habitat overlap would be more precise terms. The problem with the use of this measure to define the niche of fresh water mussels is in the choice of habitat factors for study. In a mussel shoal community, 30 or more species appear to share the same habitat.

The occurrence of many species together in a small area may be interpreted in two ways. Either each species has a narrow niche width allowing many species to be packed into a small area, or each species has a wide niche and it is the ability of niches to overlap without exclusion that allows for high diversity. Pielou (1975) suggested that it is niche narrowness or niche overlap which permits closely related species to live together.

While it is impossible to calculate niche width for fresh water mussels due to lack of information as to habitat requirements, preliminary observation supports the hypothesis that it is niche overlap which permits diversity in mussel communities. The apparent random distribution of mussels within a shoal or bed, the close proximity of closely related species, and the inability to define separate habitat requirements tends to support this assumption.

One key to understanding this relationship lies in the association between freshwater mussels and their fish hosts. If each mussel has a specific fish host which it shares with no other, the niche narrowness theory would be supported. If however, the fish-mussel relationship is not species specific, the niche overlap theory is most likely operative. There is some indication, based on available information, that both cases may exist.

One case in which host specificity has been identified is that of _Simpsonichoncha ambigua_, which has as its host the mud puppie, _Necturus maculosa_. The relationship has been clearly demonstrated (Howard, 1914, 1922) and no other mussel is known to share this host. The realized niche of Simpsonichonca is thus defined by this relationship. The distribution and habitat preference of this mussel can be related to that of its host. In most cases, however, the fish-host relationship is not so well defined. As a result of early life history studies, several common fish species (e.g. Poxomis annularis, Lepomis cyanellus, Ictalurus punctatus) have been implicated as hosts for many freshwater mussels. The White crappie (P.annularis) is listed as host to 16 species of mussels from three sub-families (Fuller, 1974).

Most early studies on the life history of fresh water mussels were done by workers attempting to propagate mussels by artificially infecting fish. Results of the studies by Coker and others were summarized by Fuller (1974). Much of this work was speculative and many fish hosts were "implicated" rather than proved. There is still considerable question as to the validity of host specificity in this relationship.

Fresh water mussels have been lumped generally into species groups associated with certain habitat types such as riffle, pool, creek, river, pond lake, and into more specific habitats such as gravel shoal, sand bar and mud slough. A generalized "niche" is thus defined for assemblages of species rather than for individual species.

An example of such an assemblage characterization involves members of the genus Anodonta (A. grandis, A. suborbiculata, A. imbecillis) which are common inhabitants of ponds and backwaters. These light weight, thin shelled mussels are noted for their ability to colonize new habitats such as farm ponds and fish hatcheries, where they are able to live in soft mud with no water flow (Bates and Dennis, 1982). They may be found with Uniomerus tetralasmus in ditches and borrow pits which are subject to periodic dewatering Manning, in press). In large rivers, they may be found in muddy backwaters with members of the genus Leptodea (Bates and Dennis, 1981). These species, while not always found together constitute a slack water, soft substrate "community".

Another species which appears to be defined as to its niche is Lampsilis anodontoides, the Yellow Sand Shell. This is one of the few species which has been successful in colonizing sand bars and is often the only species to occupy this habitat. While I have found this species in abundance in sandy drainage ditches in Mississippi, and on sand flats in the White River, Arkansas, It also appears as a minor component of riverine gravel communities, indicating that the sand is not necessary to its survival. The sand bar alone is not enough to define its niche.

It is clear that the niche of freshwater mussels cannot be characterized in terms of habitat alone. Until life history of mussel species can be worked out, definition of the niche for individual species is unlikely.

CONCLUSIONS

Intensive quantitative sampling of freshwater mussels at two sites in the Clinch River showed differences not apparent based solely on species composition data. The only differences observed as a result of qualitative sampling could be attributed to size differences between the two sites, and rarity of some species. Examination of quantitative data, however, revealed significant differences in mussel densities. Results of quantitative sampling throughout the drainage indicated that density was more variable than species composition on a site to site basis. Mussel densities seemed unrelated to species abundance; one site in the Powell River showed both the greatest diversity, and the lowest density.

Comparison of age class structure of mussel communities at the two study sites showed considerable differences. The Speers Ferry site contained an unusually high percentage of young mussels compared to Kyles Ford. The rapid growth of the mussel community at this site might be the result of recovery from detrimental effects of two documented pollution spills at Carbo Virginia, 45 miles upstream.

At both sites, the majority of specimens sampled belonged to one of five species. These species did not, however hold the same rank at both sites. At some sites sampled in other rivers (Powell, North Fork Holston) species dominance was also noted. The number and identity of most abundant species varied from site to site.

Attempts to explain the relative success of some species over others were impeded by a basic lack of information regarding niche requirements of any mussel species. The key to understanding the niche of freshwater mussels lies in the relationship between the mussel and its fish host (or hosts). This information is not available for most mussel species.

CHAPTER 3

SILTATION AS A LIMITING FACTOR TO FRESHWATER MUSSEL DISTRIBUTION IN THE TENNESSEE RIVER SYSTEM

FOREWARD

Siltation has long been identified as detrimental to freshwater mussels, based primarily on the work of Ellis (1931, 1936). Recent literature is, however, vague as to specific effects of siltation. There are no recent data regarding specific silt levels which are deleterious to mussels, and little distinction is made between effects of suspended and deposited silt. The mechanism by which silt is limiting to mussels has not been clearly addressed.

Literature on marine bivalves provides considerable information on feeding and filtration in commercially important species, but is of little help in evaluating effects of siltation. While the influence of suspended material on feeding and assimilation is often addressed, the levels of suspended material tested generally fall short of levels which would be considered excessive.

Observations as to mussel distribution patterns in the upper Tennessee River system led me to conclude that siltation was a serious limiting factor to mussel survival in this drainage. This was especially apparent in the Powell River where the presence of freshwater mussels appeared to be inversely related to the degree of siltation from strip mine runoff.

In order to determine if and how siltation could be limiting to mussel distribution, a two part study was initiated. In the first part, effects of siltation on mussels in a natural setting were investigated by transplanting mussels into habitats of varying degrees of siltation. The second part involved laboratory experiments designed to examine effects of siltation on uptake of food by mussels.

Field and laboratory studies are presented separately as parts one and two, each including its own introduction, methods and materials, results and discussion sections.

PART 1

FIELD EVALUATION OF EFFECTS OF SILTATION ON FRESHWATER MUSSELS

INTRODUCTION

Most recent literature dealing with effects of siltation on aquatic organisms is based on observation, with little quantification of silt levels involved, and often little indication of species effected. Cordone and Kelly (1961) reviewed the literature on effects of siltation on benthos. Most of the studies they reviewed (e.g. Bartsch, 1970) dealt with alteration of habitat by deposition of silt from a clearly defined source. Changes in density were reported with little indication of changes in species composition, making it impossible to tell if some species were replaced by more silt tolerant species.

Chutter (1968) noted that most of the literature concerned with effects of silt on aquatic fauna dealt with cases where partial or complete smothering of the habitat resulted. In a study of the benthic fauna of an African River subject to severe seasonal erosion, Chutter (1968) characterized the fauna as to habitat, defining erosional and depositional assemblages. He further defined the depositional assemblages as to those inhabiting stable and unstable substrates. He did not, however report actual silt levels occurring in the river, nor did he report any mollusks in his samples.

Muncey et al. (1979) reviewed the literature on effects of suspended solids on young warmwater fishes, noting the general lack of distinction made between suspended and deposited solids. They observed that inferences made by authors were generally not supported by evidence, and that cause and effect relationships were not well documented.

Siltation has long been associated with reductions in freshwater mussel assemblages. Bartsch (1916) noted effects of heavy siltation on mussels when he described the Missouri River as a faunal barrier due to its heavy load of mud and silt. Coker (1914) predicted the demise of riverine mussel species in favor of a "river-lake" fauna due to the accumulation of silt following impoundment of the Mississippi River. Ellis (1931, 1936) documented deleterious effects of erosion silt on freshwater mussel populations in the Tennessee, Ohio, and Mississippi Rivers where he noted the smothering effect of silt that settled out behind obstructions in the rivers. Ellis (1936) presented field and laboratory data on effects of suspended silt, noting that 1/4 to 1 inch of deposited silt caused high mortality in mussels. He speculated that in high concentrations, silt interfered with feeding of freshwater mussels.

Most reports of siltation effects, however, are based on observation and inference, with little actual supporting data. Scruggs (1960) reported dead mussels in place in the substrate in silted areas of Chikamauga Reservoir (Tennessee River) and, he noted that recruitment in the commercial species Pleurobema cordatum declined steadily in Wheeler Reservoir since impoundment. He attributed both these observations to effects of siltation. Bates (1962) also reported effects of siltation resulting from impoundment on mussel stocks of Kentucky Lake, Tennessee River. Negus (1966) observed that young mussels were found only in sand and gravel substrates in the Thames River, never in silt.

More recent reports on this topic are contradictory and confusing. A study by Coon, Eckblad and Trygstad (1977) attributed recent decline in mussels of the Mississippi River to siltation from channel maintenance dredging, while a study by Fuller (1978) stated that such dredging has little adverse affect on mussels in the Mississippi River.

Suspended silt, due primarily to erosion appears to be increasing as mussel resources decline. This has been observed throughout the Mississippi River drainage (Ellis, 1936; Thiel, 1981) and particularly the Tennessee River system (Isom 1969; Bates and Dennis 1978; Dennis, 1981). While it has been demonstrated that heavy silt deposition, such as occurs behind riverine impoundments, has a smothering effect on mussels (Scruggs, 1960; Bates, 1967; Isom, 1969), the effects of suspended silt are not so well documented, and the mechanism by which silt may be limiting to mussels is only speculated. Mechanisms most often suggested in the literature involve interference with respiration and or feeding due to clogging of gills with silt. Ellis (1936) observed that heavy concentrations of suspended silt caused excessive mucous secretions in freshwater mussels. He proposed that silt interfered with feeding in mussels by causing them to remain closed much of the time and that silt could suffocate mussels by clogging gills.

To examine effects of siltation on freshwater mussels in a field situation, mussel transplants were made to river reaches exhibiting varying degrees of siltation. The Powell River in Virginia was chosen for the mussel transplant studies because it provided habitats ranging from heavily silted to non-silted. The upper reaches of this river (PRM 141-180) have been heavily silted by runoff from unreclaimed strip mined lands in the headwaters, resulting in complete elimination of the mussel fauna (Dennis, 1981). Below River Mile 140, mussel species gradually increase in numbers downstream to a maximum of 36 species at PRM 106.6.

The objectives of the experimental transplant were first, to determine if adult mussels could survive in silted reaches of the Powell River; secondly, to document, if possible, effects of siltation on mussel feeding, reproductive activity, and general health; and finally, to correlate mussel survival with habitat parameters. Studies carried out over a one year period involved physical characterization of transplant sites and examination of transplanted mussels.

Habitat characteristics chosen for examination were those most closely related to siltation levels. Substrate particle size was examined at each site to determine if this varied significantly among sites and if it could be related to mussel survival. Particulate organic material (POM) analysis were made on water sampled from each site to determine if there was a significant difference in size composition or organic content among sites. A higher percentage of inorganic material in suspension at silted sites would implicate starvation as a possible limiting factor in these areas. For the same reason, organic content of fine particulates from substrate samples was determined for each site.

Transplanted mussels were observed for signs of starvation, clogging of the gills or siphons with silt, or interference with reproductive activity.

METHODS AND MATERIALS

Three stations in the Powell River, Virginia were chosen for mussel transplant studies based primarily on the degree of siltation observed during previous years sampling. Site 1, Big Stone Gap (PRM 175), was the most heavily silted; site 2, Swing Bridge (PRM 146.2), was moderately silted, and site 3, White Shoals (PRM 127.2), showed little evidence of siltation. An additional transplant site was established in the Clinch River at Speers Ferry, Virginia (CRM 211) as a control. Location of transplant sites are shown in Figure III-1.

Mussels were collected from the Clinch River at Kyles Ford, Tennessee (CRM 189.6) and transplanted in early August, 1979. The transplant sites were similar in appearance, each having a shoal area with gravel and rock substrate, swift flow, and water depths of approximately 1/2 meter at low flow. An attempt was made to choose areas with limited public access to avoid disturbance of transplants by fishermen or campers. At each site, a transplant plot of approximately $6m^2$ was marked by pounding a length of steel pipe into the river bottom at each corner.

The mussel chosen for the transplant was Actinonaias carinata gibba, a form restricted to the upper Tennessee River Drainage, where it is widespread and locally abundant in shoal areas. Its relative abundance in the Clinch River at Kyles Ford, TN, allowed for collection of large numbers of young specimens in a reasonable length of time, and

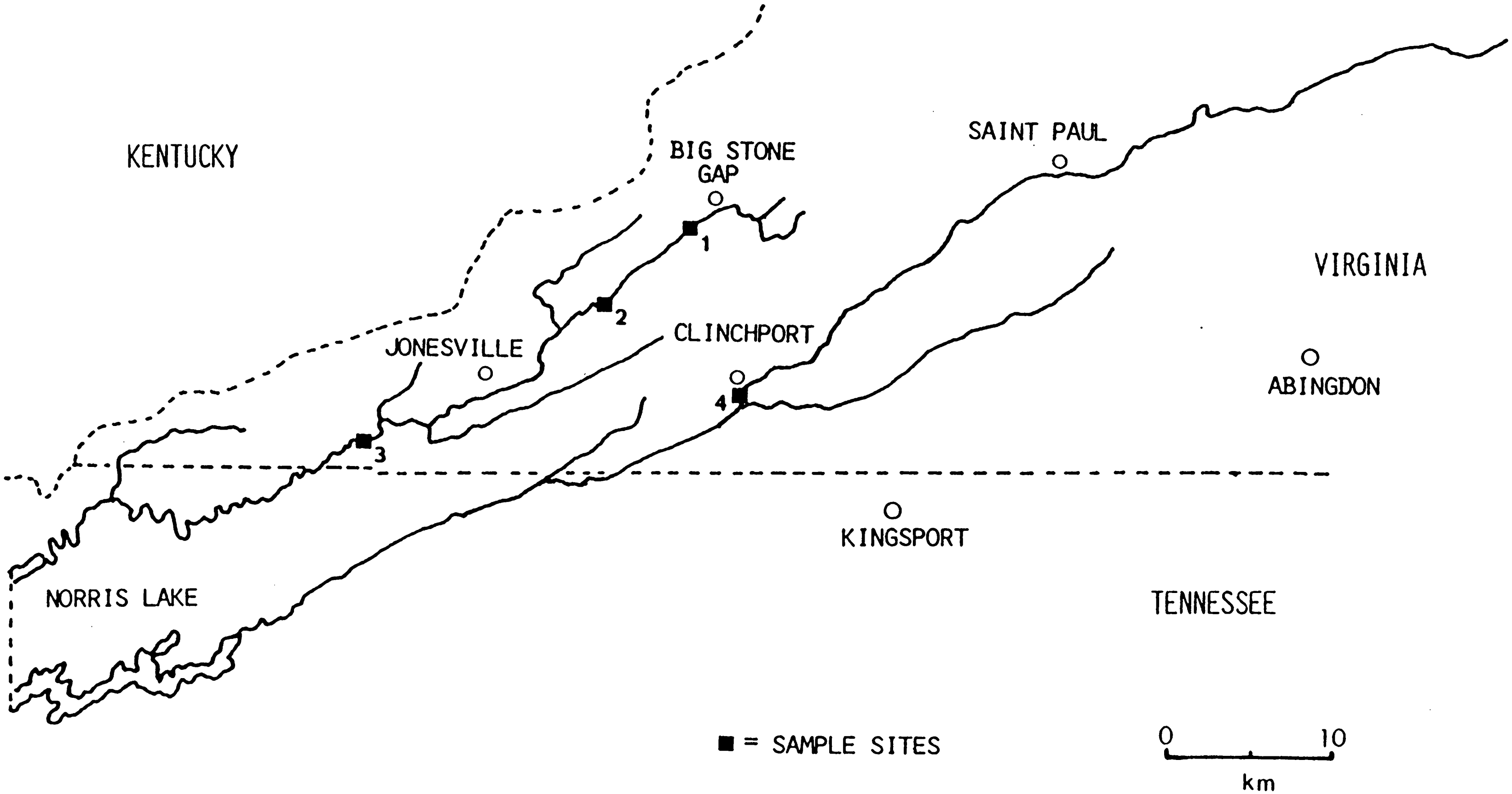


FIGURE III-1. MAP SHOWING LOCATION OF TRANSPLANT SITES without damage to the population. The large size of this mussel made it easy to work with, and previous experience with this species indicated that it would withstand transport and relocation well. Two species (Medionidus conradicus and Dysnomia capsaeformis) which occurred in greater numbers than A. carinata at Kyles Ford were too small and fragile to withstand the transplant process.

A new method of marking mussels was developed for this study since methods used in previous studies were found to be unsatisfactory. Small (5mm) numbered plastic fish tags (Floy Mfg. Co.) were attached to the mussel shells using a cyanoacrylate glue (Super Glue®; Krazy Glue®). The fast drying time and water resistance of this glue made it ideal for this purpose.

Eighty mussels ranging in age from three to 11 years were selected for transplant to each site. Following their collection at Kyles Ford, mussels were placed on their sides in shallow water with only a portion of shell exposed to the air. When the exposed shell was dry, a tag was applied with a drop of glue and allowed to dry for two to three minutes. After tagging, each mussel was measured, aged and weighed, then placed in a wet cloth bag in preparation for transport.

The age of mussels was estimated by counting growth arrests following the methods described by Chamberlain (1931). Weights were recorded to the nearest 0.1 gram using an Ohaus triple beam balance. Length was measured with a caliper at the longest axis and recorded to the nearest 0.01 millimeter.

Mussels were transported in wet cloth bags in a cooler to the transplant site where they were hand positioned in the substrate within pre-determined plots. During transplant and recovery a yellow polyethylene rope was stretched between the pipes marking the corners of each plot to aid in locating the mussels.

Mussels were transplanted August 10-12, 1979. Ten mussels were collected from each plot on September 28 and October 30, 1979 and examined for accumulation of silt or mud on gills, mantle flaps and siphons. Shell and body weights (wet) were recorded separately. The remaining mussels were left to overwinter. In July, 1980, ten mussels were collected from each plot for examination. Remaining mussels were collected in August, 1980, approximately one year following their transplant.

At each of the transplant sites, the substrate was characterized as to particle size and organic content, and water samples were analyzed for particulate organic material. Substrate samples were collected using a coring device illustrated in Figure III-2. Samples were wet sieved through a No. 10 (2mm) USGS sieve screen. The fraction passing through the No. 10 screen was air dried and weighed to provide the fine particulate (<2mm) size fraction. Material retained in the sieve was air dried and run through a series of screens of the following mesh sizes: 19.0, 12.5, 9.5, 6.35, and 4.75 millimeters. Each of these fractions was weighed, and reported as percent of total weight (all fractions combined).

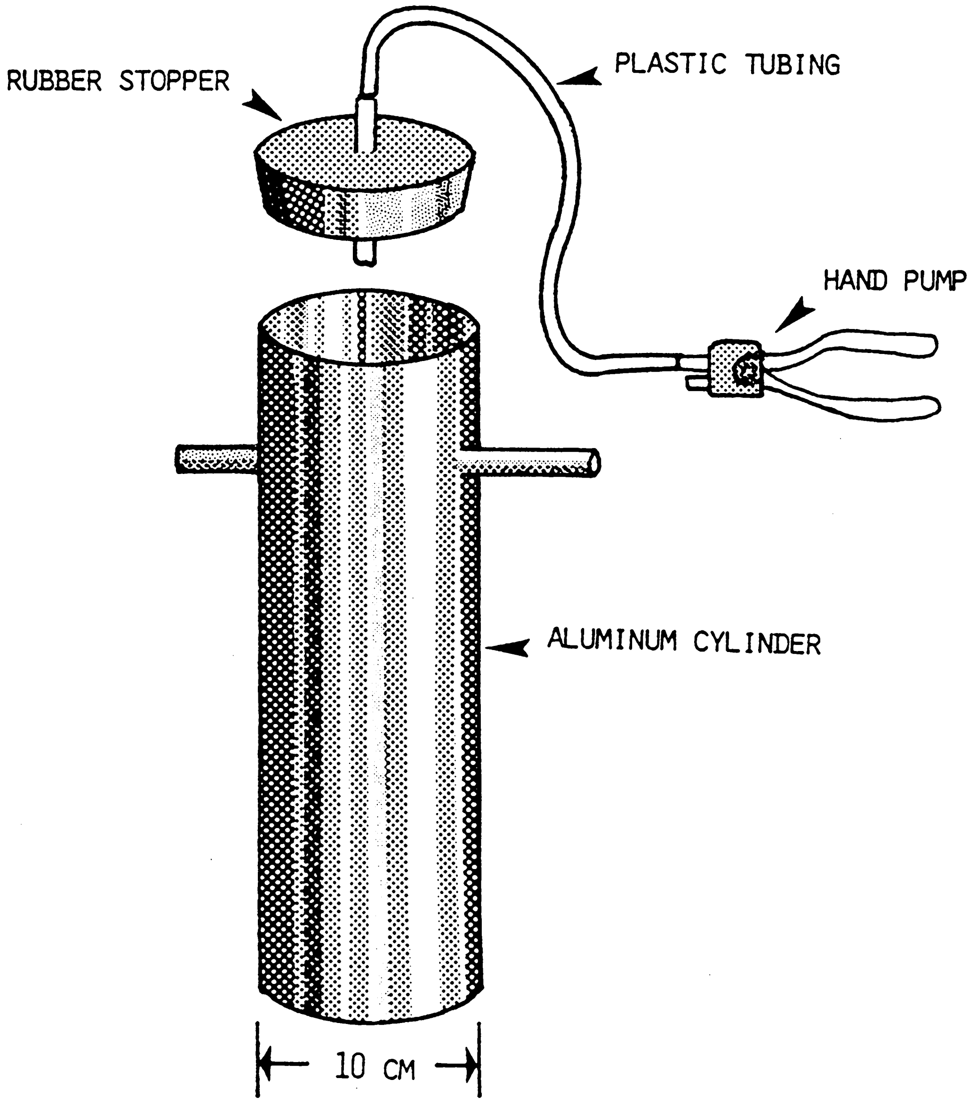


FIGURE III-2. CORING DEVICE USED TO COLLECT SUBSTRATE SAMPLES

Whole water samples and plankton net samples were collected for analysis of POM using a wet filtration technique outlined by Gurtz et al. (1980). Measured volumes of water and suspended net samples were filtered through a series of stainless steel sieves of the following sizes: Medium large (ML)= >234 um, Small (S)= 105-234 um, Fine (F)= 43-105 um, and Very Fine (VF)= 25-43 um. An aliquot of material passing through the VF screen was filtered through a glass fiber filter (0.5um) to provide an Ultrafine fraction (UF= 0.5-25 um). Samples were oven dried at 50°C for 24 hours, desiccated for 24 hours, weighed, ashed at 500°C for 15 minutes, re-wetted, dried, desiccated, and weighed. From dry weight and ash-free weight, percent composition by weight and percent organic matter were calculated for each size fraction.

RESULTS AND DISCUSSION

Mussel Transplant

There are few reports of controlled field studies using freshwater mussels primarily because of the difficulty of marking and recapture of specimens. The first documented attempt at marking mussels was reported by Isely (1913) in studies related to mussel growth and migration. After trying to scratch numbers on the shell, he resorted to drilling a hole near the edge of the shell and attaching a tag with a wire. He noted, however, that some injury to the mantle tissue often occurred. Scruggs (1960) also drilled a hole in mussel shells, this time, through the thick shell of the umbo, attaching a plastic fish tag with a nickel pin. This method, while successful with adult specimens of thick shelled species, would not work with thin shelled specimens. Another drilling technique was employed by Yokley and Gooch (1976) who used a template to drill shallow holes in the mussel shells in patterns representing numbers.

Finding the tagged mussels following relocation was a problem in all cases, but more so in large river habitats (Scruggs, 1960; Yokley and Gooch, 1976) where divers were used to retrieve the specimens. Yokley and Gooch (1976) were unable to recapture any tagged mussels from one transplant site. Allen (1921b) transplanted mussels into a soft substrate where migration was a problem. Isely (1913) attempted to avoid this problem by enclosing mussels in "pens" in some habitats. Foster and Bates (1978) used mussels suspended in wire baskets in short term monitoring studies, eliminating contact with the substrate altogether.

The success of the mussel transplants conducted in the present studies is due to development of a marking technique which is permanent and non-deleterious to the mussels, and to accuracy of the transplant and recovery techniques. Because of the habitat type and species involved, losses due to migration or inability to relocate transplant plots were virtually eliminated. Shock to the mussels resulting from the transplant and marking process was kept to a minimum. Once transplanted, mussels occupied a habitat similar to the one they came from and were situated in the substrate in their normal feeding posture.

Results of the transplant study are presented in Table III-1. Percent recovered represents the percent of mussels collected live from each transplant plot during the study and is interpreted here as percent survival. It is assumed that mussels not recovered died and were washed out of the transplant plots during high water. It is unlikely that live mussels washed out of the plot as they were placed securely in the substrate and were observed to be positioned normally (buried with only siphons visible) following the transplant. It is also unlikely that mussels migrated from the plots since riverine species inhabiting hard gravel substrates are generally sessile throughout their lifetimes (Isely, 1913).

TABLE III-1

SURVIVAL OF TRANSPLANTED MUSSELS

Site Number	Number Recovered 1979	Number Recovered 1980	% Gravid 1980	% Recovered 1980 (of 60)	Total % Recovered (of 80)
1	20	22	0	36.7	52.5
2	20	49	20.4	81.7	86.3
3	20	36	38.9	60.0	70.0
4	20	45	20.0	75.0	81.3

The transplant plots were examined in September and October, 1979 when specimens were collected for examination. During these visits, no mortalities were observed, and all mussels appeared to be well anchored in the substrate. Had mussels died during this period, shells would have remained in the area because of absence of high water during this period.

Of the eighty mussels transplanted to each site, 20 were collected for examination during 1979, leaving 60 in each plot to overwinter. The percentage recovered in 1980 represents the percentage of mussels which survived the winter and spring high water periods. This is probably a better indication of mussel survival at the transplant sites than the total percentage recovered.

Recovery was lowest at site 1, where only 36.7% of mussels survived over winter. The percent survival at site 2 was higher than expected considering its location relative to the sources of siltation and the absence of a mussel fauna in the area. A number of environmental factors may have contributed to this result. The mussels were placed in an area of very swift current where turbulent flow could prevent accumulation of silt on or near the bottom. Additionally, there is indication, based on other data collected, that there may be a source of organic input at this site which would provide a greater food source for the mussels.

Recovery was expected to be similar at sites 3 and 4 since these habitats showed the greatest similarity and both sites supported native mussel populations. Because of the scenic nature of these sites, however, they were most subject to disturbance by vandalism.

While site 3 was accessible only through private property, campers were observed on one occasion near the transplant plot. Site 4 was accessed often by fisherman and TVA biologists. During the late summer of 1979, TVA personnel reported collecting tagged mussels from my transplant plot and returning them to the river. If not properly replaced, these specimens could have washed out of the plot. Since I did not learn of the incident until well after the fact, It was impossible to determine if the disturbance was consequential.

Mussels collected from the transplant plots were examined for reproductive activity, and the percentage of mussels found gravid reported for the 1980 collections. Gravidity is not reported for mussels collected in 1979 since these mussels could have become gravid prior to the transplant. Mussels collected in 1980 had spent an entire reproductive season at the transplant site. It should be noted that the percentage gravidity is reported for all mussels and not for females only. Since A. carinata does not exhibit external sexual dimorphism, the exact proportion of males to females transplanted is unknown. It has been demonstrated, by histological work with this species (Bates and van der Schalie, unpublished), that the sexes typically occur in equal numbers in natural populations. It is likely then, that both males and females were included in the transplants to each site. Actinonaias carinata is bradytictic (a long term breeder) and females are typically gravid during late summer and early fall months, the time of my final collections. In considering the importance of gravidity, it should also be noted that little information is available as to the exact mechanism of fertilization. It is known that sperm are released into the water and siphoned in by female mussels to fertilize eggs in the marsupia. It is not known, however, whether a critical number of male mussels is necessary to induce gravidity or how important is the relative position of males to females. It is likely that female mussels transplanted to sites 3 and 4 would stand a better chance of becoming gravid by native mussels of the same species outside the transplant plots. Given the unknowns regarding the fertilization process and the proportions of males and females transplanted, the gravidity data should be taken only as evidence that reproduction occurred. While the significance of the percentages recorded cannot be determined at this time, the absence of any gravid mussels at site number one is considered meaningful.

Mussels collected from the transplant plots were examined for condition of gills, mantle cavity and digestive tract. A crystalline style was observed in all mussels examined, indicating active feeding, and there was no evidence of silt accumulation in the mantle cavity or on the gills. Accumulation of mud and silt was observed, however, in the lower gut and on the excurrent siphons of several of the mussels from site number one, indicating that this material was being discharged in large amounts from the intestinal tract.

In order to compare weights of mussels of different sizes and ages, I used a ratio similar to the condition factor used by fisheries biologists. The body and shell of each mussel were weighed (wet weight) separately, and the ratio of body weight to total weight (B/T ratio) determined for each mussel. It was anticipated that emaciation of starved mussels would be revealed as lower than average B/T ratios. The B/T ratios for mussels collected in the fall of 1979 are presented in Table III-2. Statistical analysis of these data, presented in Table III-3, indicate a higher value for mussels taken from site number 2, with no difference among other sites. The higher B/T ratios for mussels taken at site 2 and the high survival rate here, supports the hypothesis that there was a source of organic input at this site. A number of potential sources of organic input were located here, including a residence and a farm.

The B/T ratios for mussels collected in July 1980 are presented in Table III-4. Statistical analysis of these data show no significant difference among sites; however, all values were lower than for 1979 collections. For comparative purposes, B/T ratios were also calculated for mussels from the Clinch River at Kyles Ford (control) and for mussels held in a Living Stream (Fridgid Systems, Inc.) for eight months without feeding (starved). While there were no statistical differences among B/T ratios data for 1980, it is interesting to note that the average ratio for mussels taken from Kyles Ford, Clinch River (.166) is exactly the same as that for those transplanted to the control site (no.

Table III-2

B/T Ratios for Mussels Collected from Transplants, 1979

	Site No.			
Mussel No.	1	2	3	4
1	.170	.375	.178	.210
2	.182	.140	.150	.200
3	.181	.236	.188	.146
4	.176	.196	.189	.180
5	.189	.240	.148	.183
6	.164	.218	.203	.148
7	.168	.197	.172	.241
8	.160	.429	.198	.220
9	.180	.168	.184	.123
10	.156	.158	.199	.157
11	.153	.283	.140	.184
12	.174	.245	.180	.168
13	.174	.170	.196	.204
14	.170	.262	.149	.172
15	.147	.230	.174	.138
16	.208	.436	.207	.149
17	.179	.204	.180	.193
18	.156	.283	.199	.168
19	.174	.151	.181	.190
20	.208	.274	.225	.155
$\overline{X}$	.173	.245	.182	.175

TABLE III-3

STATISTICAL ANALYSIS OF B/T RATIOS DATA FOR MUSSELS
COLLECTED FROM TRANSPLANTS, 1979

I. Analysis of Variance: Comparison of means 1, 2, 3, and 4

ANOVA Table

Source of Variation	df	SS	MS	F
$\bar{Y}-\bar{Y}$ Among groups	3	.06	.02	4.44
$Y-\bar{Y}$ Within groups	76	.34	.004	
$Y-\bar{Y}$ Total	79	.40		

f(.01) =4.10 f(.05) =6.10

Conclusion: Reject hypothesis that all means are the same
at = .001, Do not reject at =.01

II. Duncan's Multiple Range Test for means 1, 2, 3, 4

Group No.	A	B	C	D
$\bar{X}$	.173	.176	.182	.244
Site No.	1	4	3	2

Conclusion: No difference among means for sites 1, 4, and 3
Mean for site 2 sigificntly diferent from others =.01

TABLE III-4

B/T Ratios for Mussels Collected from Transplants July, 1980

Mussel No.	Site No. 1	2	3	4
1	.146	.120	.177	.200
2	.157	.191	.142	.179
3	.179	.176	.146	.165
4	.144	.183	.165	.160
5	.173	.180	.176	.167
6	.137	.201	.143	.139
7	.154	.198	.171	.152
8	.147	.159	.141	.159
9	.146	--	.165	.172
10	.156	--	--	.166
$\overline{X}$	.153	.176	.158	.166

Ave. for mussels taken from Kyles Ford (not transplanted)= .166

Ave. for mussels kept in laboratory for 7 months (starved)= .150

Sites: 1= Big Stone Gap
2= Swing Bridge
3= White shoals
4= Speers Ferry

4) in the same river. Also, the average value for mussels taken at site 1 was only slightly higher than that for mussels which were held under conditions of starvation.

Gut samples taken from the transplanted mussels collected in July, 1980 were analyzed for organic content. These data, presented in Table III-5, show no significant differences in percentage organic content of gut samples among sites.

Habitat Characterization of Freshwater Mussels

Water Quality:

Environmental parameters considered critical to freshwater mussels include pH, temperature, available calcium, oxygen, substrate type, and siltation. Information on water quality requirements of freshwater mussels is, however, generally lacking.

Fuller (1974) reviewed the literature on habitat requirements of freshwater mussels, summarizing what has been reported on the importance of various chemical and physical constituents of the environment. The information he was able to assemble was generally inconclusive and often conflicting. As Fuller (1974) aptly stated "we do not know the limits of tolerance by a single species for a single chemical parameter." The same, unfortunately, can be said of most physical variables as well.

TABLE III-5

Organic Analysis of Gut Contents of Mussels taken from Transplants, July 1980.

I. Percent Organic Content of Gut Samples by Site

Mussel No.	Site No. 1	2	3	4
1	20.1	17.9	17.8	22.9
2	20.7	19.0	22.9	20.9
3	21.7	16.4	24.6	18.7
4	25.9	14.9	21.1	19.9
5	16.4	19.5	19.1	17.1
X	21.0	17.5	21.1	19.9

II. Analysis of Variance: Comparison of Means 1, 2, 3, 4

ANOVA TABLE

Source of Variation	df	SS	MS	F
$\bar{Y}-\bar{Y}$ Among groups	3	40.65	13.55	1.96
$Y-\bar{Y}$ Within groups	16	110.59	6.91	
$Y-\bar{Y}$ Total	19	151.24		

f(.05) = 3.24 f(.01)= 5.29

Conclusion: No difference among means at =.01

Coker et al. (1921) discussed what was known at that time of habitat requirements of freshwater mussels. The authors characterized faunal assemblages of various habitat types including streams, lakes, ponds and sloughs, and artificial channels. They compiled information as to species associated with bottom types (sand, gravel, mud, rocks, clay, and combinations of these) and degrees of current (little to strong).

Coker et al. (1921) also summarized available information on water quality requirements of freshwater mussels. The authors assembled data on a number of relevant parameters including turbidity, suspended material, bicarbonate, total dissolved solids, and a number of ionic constituents for river reaches which supported mussels (productive) and for those which did not (nonproductive). A portion of these data (taken from Dole, 1909) are presented in Table III-6. While these data help to characterize optimum habitat for commercial mussel species, they are not definitive. No set of chemical or physical characteristics has been put forth which can aptly define freshwater mussel habitat.

The nonproductive sites fell into two categories which I have listed in Table III-6 as groups A and B. The sites listed in group B exhibited lower values than the productive sites in all parameters tested. Significant among these are readings for calcium, magnesium and bicarbonates indicating soft water with low buffering capacity for a number of sites. Coker considered these sites nonproductive due to the low calcium readings.

TABLE III-6

CONTENTS OF WATERS OF CERTAIN PRODUCTIVE MUSSEL STREAMS
AND OTHER NONPRODUCTIVE STREAMS (from Coker, et.al, 1921)

Productive Rivers	Turbid.	Suspend. Matter	Ca.	Ma.	Bicarb.	TDS
Wabash, Vincennes, Ind.....	172	193	61	22.0	230	336
Illinois, La Salle, Ill....	159	136	50	22.0	203	278
Illinois, Kampsville, Ill..	188	145	47	20.0	203	278
Fox, Ottawa, Ill..........	94	87	60	32.0	275	335
Sangamon, Springfield, Ill.	74	39	52	24.0	247	276
Cumberland, Nashville, Tenn	126	94	26	3.6	92	119
Cumberland, Kuttawa, Ky....	176	165	28	4.3	100	124
Des Moines, Keosauqua, Iowa	542	642	58	21.0	216	312
Grand, Grand Rapids, Mich..	37	43	56	19.0	214	258
Cedar, Cedar Rapids, Iowa..	64	61	48	16.0	209	228
Maumee, Toledo, Ohio.......	143	112	57	16.0	143	298
Mississippi, Moline, Ill...	117	106	33	13.0	152	179
Mississippi, Quincy, Ill...	173	119	36	16.0	175	203
$\overline{X}$	159	149	47	17.6	191	247
sd	125	155	12	7.7	53	73

TABLE III-6 (Continued)

CONTENTS OF WATERS OF CERTAIN PRODUCTIVE MUSSEL STREAMS AND OTHER NONPRODUCTIVE STREAMS (from Coker, et.al, 1921)

	Turbid.	Suspend. Matter	Ca.	Ma.	Bicarb.	TDS
Nonproductive Rivers (A)						
Savannah, Augusta, Ga......	172	143	5.7	0.8	30	60
Cape Fear, Wilmington, N.C.	73	21	5.0	1.5	25	57
Wateree, Camden, S.C.......	259	214	6.3	1.8	34	73
James, Richmond, Va........	90	71	14.0	3.0	60	89
Hudson, Hudson, NY.........	13	16	21.0	3.8	73	108
Potomac, Cumberland, Md....	28	29	24.0	4.6	36	130
Shenandoah, Millville, W.Va	31	39	32.0	8.2	132	140
$\overline{X}$	95	76	15.4	3.4	56	94
sd	90	75	10.6	2.5	38	33
Nonproductive Rivers (B)						
Mississippi, Memphis, Tenn.	556	519	36.0	12.0	129	202
Mississippi, Chester, Ill..	858	634	44.0	16.0	174	140
Red, Shreveport, La........	790	870	74.0	17.0	135	561
Missouri, Ruegg, Mo........	1931	1890	52.0	16.0	178	346
$\overline{X}$	1034	981	51.5	15.3	154	312
sd	662	624	16.4	2.2	26	187

While a few mussel species can inhabit soft water, most commercially important, heavy shelled species are not found in this habitat type. Members of the family Margaritiferidae, however, are common in poorly buffered streams of the eastern drainages (Harman, 1969). Clarke and Berg (1959) did not report mussels from water with less than 47 ppm hardness (Calcium carbonate), while Harman (1969) reported some species from as low as 21 ppm. One soft water stream in the Tennessee River drainage, the Little Tennessee River, supported a diverse mussel fauna (prior to its impoundment) under conditions of low hardness (7-23 mg/l) and pH (6.0-6.7)(Dennis, unpublished).

The streams in group B (Table III-6) are similar to the productive streams in all parameters except for turbidity and suspended matter. Coker et al. (1921) believed siltation to be limiting to mussel survival in these river reaches. The Missouri River, in particular, has been considered a faunal barrier to migration of mussels into headwater reaches because of its heavy silt load.

Recent data on water quality sheds little additional light on habitat requirements of freshwater mussel species. In preparing a handbook of distribution and water quality requirements of freshwater mussels, for the U.S. EPA, Bates, Dennis and Isom (in preparation) reviewed water quality and mussel distribution records for all major drainage basins in the United States. Because of the wide range of tolerance of mussels, no correlations could be made between species distribution and chemical-physical conditions of the water. Information regarding past and present suspended silt loads in natural waters is practically non-existent. The limited data available are difficult to interpret.

Ellis (1936) documented effects of erosion silt in riverine habitats using an index of siltation which he devised. This index, called the millionth intensity depth (m.i.d.) was defined as the depth at which light was reduced to one millionth of its surface intensity. While Ellis (1936) reported the results of m.i.d. measurements from extensive surveys throughout the Interior Basin, his data, based on a light meter of his own design, cannot be easily compared with data from other sources.

There is also an absence of consistency in data reported from government monitoring programs (e.g. U.S.G.S, and TVA). While turbidity measurements are occasionally reported, the units are often not comparable and the method of analysis is not given. Turbidity measurements cannot be interpreted readily in terms of actual silt loads by conversion to a weight to volume measurement. While a measurement of suspended solids is somewhat more useful in this regard, methods for determination of this parameter are often not consistent. Most often, only dissolved solids are reported, leaving no indication of suspended silt loads.

Substrate:

There seems to be some confusion regarding the importance of substrate to freshwater mussels. That the substrate is important is often taken for granted, yet there are no data available regarding specific characteristics of the substrate. There have been many studies on the relationship of substrate type to benthic fauna, most dealing with insect assemblages. Many studies correlate insect species with substrate type including Wiene (1970) working with midge larvae, Lenduska (1942) with mayflies, Scott (1958) with caddisflies.

Throupe (1966) proposed a stream classification system based on substrate type, recognizing that in this application, substrate type is a reflection of other ecological parameters. It is a function of current velocity and flow volume, and influences oxygen content and food conditions of the water column. He noted that certain benthic organisms are associated with certain substrate types e.g., Ancylus, Epeorus, and Heptagenia, with stony bottoms; oligochaetes and certain Chironomidae with muddy bottoms.

Percival and Whitehead (1929) recognized seven basic substrate types and found certain animal species associated with each. Pennak and van Gupen (1947) described the benthic faunas associated with four substrate types in a mountain stream. Moon (1939) articulated the "erosion-deposition" concept stating that in rapidly flowing water (erosional) fine substrate is washed away; animals living here are adapted for clinging or current avoidance, while in reduced flow (depositional) animals are adapted for life in fine substrates.

A number of workers have looked at substrate particle size in relation to benthic fauna, including Scott (1960), Kamler and Riedel (1960), Eriksen (1964, 1966), and Cummins (1961, 1964a, 1964b, 1966). Cummins (1964b) reviewed the literature on organism-substrate relationships in streams, pointing out the absence of experimental field data.

Cummins and Lauff (1969) used a laboratory stream to test responses of 10 stream invertebrates (nine insects and one gastropod) to various substrate particle sizes and flow regimes, categorizing the organisms as fast or slow water species. They speculated as to the importance of four general environmental factors: particle size of the substrate, current velocity, food, and other physical-chemical parameters (such as temperature and oxygen content), concluding that benthic organisms respond to all four simultaneously. Of the species tested in laboratory streams, they found that four exhibited primary habitat selection based on substrate type, while four insects and the snail (*Helisoma anceps*) responded to substrate type as of secondary importance. Cummins and Lauff (1969) also tested selection for silted versus non-silted substrates, reporting that siltation had little effect. The degree of siltation tested (approximately one mm of silt on the surface of the substrate) was slight, however, and effects of suspended silt were not examined.

Analysis of size class structure of sediment samples taken during the present study is presented in Table III-7, and organic analysis of fine particulates in Table III-8. The only apparent difference among sites was a high percentage of fine (<2 mm) material at site 1, consistent with a higher level of siltation. Organic analysis of particulates was difficult to interpret because of the abundance of coal fines in substrate samples from the upper Powell River. The low percentage of organic material observed in sediments from site 4 may reflect the relative absence of coal fines at this site.

Water samples from each site were analyzed for particulate organic material (POM) and the results presented in Tables III-9 and III-10. These data are extremely variable, with no apparent trend among sites.

Results of mussel transplant and habitat evaluation indicate that silt loads in the Powell River may be limiting to mussel populations in the extreme headwaters, near Big Stone Gap, Virginia, but that lower reaches may be suitable for re-establishment of a mussel fauna. There is no evidence, on the basis of data collected, that food availability or substrate type is the limiting factor in the upper river.

Certain freshwater mussels can be found which have adapted to most substrate types including soft mud (*Anodonta*, *Leptodea*, *Amblema*), sand (*Lampsilis anodontoides*), firm gravel (*Plagiola*, *Quadrula*, and many others) and even bedrock ledges (*Actinonaias carinata*). The substrate type in these cases is closely related to other important parameters such as stream gradient, current velocity, type and amount of available

TABLE III-7

Size Class Distribution of Sediments Taken from Transplant Sites

Seive Size (mm)	Percent Composition by Site			
	1	2	3	4
19.00	63.0	60.7	73.3	59.7
12.50	7.7	13.0	6.7	9.4
9.5	4.7	6.3	3.9	4.8
6.35	4.8	6.4	4.3	5.9
4.75	2.3	2.9	2.3	3.3
2.00	4.3	4.8	5.0	6.9
<2.00	13.2	5.8	4.2	9.9

Sites: 1= Big Stone Gap
2= Swing Bridge
3= White shoals
4= Speers Ferry

TABLE III-8

Organic Content of Fine Sediments (<2mm)
from Transplant Sites

Site No.	% Organic
1	3.75
2	3.75
3	2.40
4	1.60

Sites: 1= Big Stone Gap
2= Swing Bridge
3= White shoals
4= Speers Ferry

TABLE III-9

Size Composition of Particulate Organic Material (POM) from Water Samples taken at Transplant Sites

Size (um)	% Composition (dry weight) by Site				
	1	2	3	4	5*
ML (>234)	.10	.37	.23	.26	.73
S (105-234)	.20	.35	.48	.49	4.00
F (43-105)	.81	1.30	1.10	6.60	7.00
VF (25-43)	2.60	3.10	2.00	7.60	9.90
uF (.5-25)	96.30	94.80	96.10	84.70	78.10

* Clinch River, Kyles Ford, source of transplanted mussels.

Sites: 1= Big Stone Gap
2= Swing Bridge
3= White shoals
4= Speers Ferry

TABLE III-10

Organic Content of Fine fractions of Particulate Organic Material (POM) from water samples taken at Transplant Sites

Size (mm)	% Organic (each fraction)			
	1	2	3	4
F (43-105)	81.3	45.1	82.0	85.9
VF (25-43)	85.4	93.4	88.9	92.4
uF (.5-25)	96.2	93.8	91.4	92.5

food, and associated fish species. The actual degree of dependence of mussel species on the substrate is unknown. In a few cases, mussels may be physically limited as to substrate choice. Members of the genera Anodonta and Leptodea, for instance, have thin, fragile shells which could be easily damaged in a rocky environment. Their light weight and buoyancy, however, allows them to move freely in soft muddy substrate which would bury heavier species.

Most riverine mussel species, however, seem to be able to occupy a variety of substrate types. Mussels have been kept successfully suspended in baskets without any substrate for extended periods of time (Howard, 1922; Foster and Bates, 1978). It is likely that the main functions of the substrate are to protect the mussel shell from the scouring effect of swift currents and to hold it in place for efficient feeding and reproduction. As long as the mussels are able to maintain their proper posture, the size class structure of the substrate may be of little significance except as a reflection of other environmental conditions.

Poor survival of transplanted mussels at site 1 was probably related to silt loads carried during periods of high run off. The heavy accumulation of mud and silt on the excurrent siphon of mussels from Big Stone Gap may indicate that a high energy expenditure was involved in the filtering process at this site.

PART 2

LABORATORY EVALUATION OF EFFECTS OF SILT ON FEEDING IN FRESHWATER MUSSELS

INTRODUCTION

Allen (1914) described the details of ciliary movement and its role in mussel feeding, and reported the results of qualititaive examination of gut contents of various species of freshwater mussels. In a subsequent publication (Allen, 1921a), he reported results of experiments on feeding behavior in adult freshwater mussels. Speculating on the function of feeding organs, he proposed that the cilia on gills and palps exercised a high degree of qualitative sorting of food. This conclusion was based on the observation that inert substances (carmine, starch and carborundum) when administered to adult mussels rarely entered the digestive tract. In examining stomach contents of free living mussels, he found little sand and mud and concluded that these items were sorted out by palps and gills. When he observed an abundance of pyrenoid bodies in the crystaline style of mussels fed mascerated algae, he concluded that mussels were capable of selecting very small food particles.

In summary, Allen concluded that: 1. Under normal conditions mussels feed constantly, the ciliary mechanism operates continuously and siphoning is constant; 2. a crystalline style is always present when mussels are feeding normally; 3. much food passes through the digestive tract without being digested; and 4. mussels are capable of a high degree of qualitative sorting of food particles.

Churchill and Lewis (1924) expanded on Allen's work, supporting most of his conclusions. They disagreed, however, with the suggestion that mussels are capable of qualitative sorting of food. In working with young mussels, Churchill and Lewis (1924) observed that carmine and other inert materials were not sorted out, but passed through the digestive tract. Mussels 18-25 mm long took in everything small enough to enter the mouth. Adult mussels were observed to control the ingestion of "distasteful" substances such as carmine by closing the valves and ceasing siphoning. Instances were cited in which sand and silt were observed in mussel stomachs and intestines.

Churchill and Lewis also reported, based on laboratory experiments, that mussels fed in the presence of heavy silt loads did not select food material and reject silt, but took in limited amounts of all material present. They concluded that mussel gills and palps were not used in size selection, but served as quantitative regulators of ingestion. Coker et al. (1921) also concluded, based on examination of gut contents of freshwater mussels, that there was little discrimination of material ingested. They noted an abundance of what was described as "organic remains" along with inorganic material, algae and diatoms in gut samples examined.

In recent studies, however, Ten Winkel and Davids (1982) reported that the freshwater mussel Dressenia polymorpa exercised selection of food based both on size and chemical composition. They compared particle content of ambient environment to particle composition found in the mantle cavity and stomach of mussels, and observed a positive selection of particles of the size range 15-45 u. They noted that this selection was not observed when mussels were starved for 16 hours, an observation not reported in other studies.

There have been numerous publications on feeding, filtration rate, and particle retention by commercially important marine bivalves. While much of these data are not directly applicable to freshwater mussels a number of studies are worth noting because of techniques employed and/or results reported. Reviews of the literature on suspension feeding in marine bivalves by Jorgensen (1955) and Winter (1978) indicate no qualitative selection of particles ingested. This is documented by Foster-Smith (1975b) who reported that when alumina was added to algal cultures fed to marine bivalves the feeding organs did not select the algae over the alumina particles, and that the alumina had little effect on the proportion of algae digested.

The question of food selection by marine bivalves has been controversial and there is much conflicting data in the literature. There has also been an absence of agreement as to whether feeding rates are constant or related to the concentration of food in suspension. Jorgensen (1949) looked at the rate of feeding in different kinds of suspensions by Ostrea and Mytilus, speculating that filtration efficiency was not constant. Oysters were observed to ingest 10 to 30% of bacteria; they retained 15 to 80% of Nitzschia and Euglena (approx. 60 u in diameter); while for Chlorella (5 u) the value varied from 0 to 92% retention.

Jorgensen (1975) in a review of suspension feeding in marine invertebrates asserted that marine bivalves maintain feeding currents independent of concentration of food and other particles below certain concentrations (naturally occurring levels). He attributed the contradictory findings in the literature to effects of laboratory experiments themselves, contending that different laboratory set ups affect results in a different ways, making results non comparable.

Winter (1978) observed that filtration rate decreased with increasing concentration of food. He assumed that the mussels altered the rate of intake to maintain a constant food supply. He also concluded that assimilation efficiency depends on the quality and quantity of food ingested. Jorgensen (1975) disagreed with Winter's earlier (1969, 1970, 1973) conclusions to this effect, suggesting that the food concentrations Winter used were above "incipient limiting levels".

Confusion arises in determining the relationship between assimilation and food supply. If mussels alter filtration rate to maintain a constant food supply, and if assimilation is related to quality and amount of food, then ingestion and assimilation are both independent of ambient concentration of food according to Winter's work.

The above mentioned studies were carried out using food concentrations within the range found in natural sea water. Winter (1969) showed that filter feeding activity of Mytilus edulis was highly stimulated by low quantities of suspended silt (12.5 mg/l). This increase in filtration rate also increased ingestion and resulted in tissue weight gain. Effects of higher concentrations of suspended silt on ingestion and assimilation of food by mussels have not been documented.

METHODS AND MATERIALS

Feeding Studies

Freshwater mussels (Actinonaias carinata and A. pectorosa) were collected from the Clinch River at Kyles Ford, Tennessee in early December, when mussels are generally inactive and metabolic requirements are low. Specimens were placed in a cooler with river water and a small amount of ice, transported to Virginia Tech, and placed in a holding tank (Living Stream). Water temperature was maintained at 15°C, approximating river conditions from which mussels were removed. Flourescent lights were set on a 10L:14D photoperiod.

Plastic pans full of river gravel provided substrate for the mussels, which positioned themselves in normal feeding posture, i.e., buried except for siphons. Mussels were fed twice weekly with a commercially available marine invertebrate food (MIF). Periphyton sloughed from the substrate and sides of the holding tank provided an additional food source. Approximately two weeks prior to initiation of the feeding studies, the water temperature in the holding tank was allowed to warm to room temperature (21°C) and cultured algae (Selenastrum capricornutum Prinz) was added to the diet.

Culture and Tagging of Algae:

<u>Selenastrum capricornutum</u> Prinz was cultured in accordance with procedures outlined by Miller et al. (1978), with the exception that cultures were not incubated in a continuous shaker, but shaken once a day.

A one liter Erlenmeyer flask containing 500 ml of sterile culture medium was innoculated with 5 ml of algae (from stock cultures held under refrigeration at Virginia Tech) 4 to 5 days prior to use and incubated at 24°C under flourescent illumination. Prior to tagging, the culture was passed through a Foerst-type plankton centrifuge, and the concentrated algae re-suspended in approximately 300 ml of dechlorinated tap water. In order to maintain consistant algal densities in cultures, the volume of each culture was adjusted to achieve a constant spectrophotometer reading of 550-650 at an optical density of 663.

Algae were labelled by adding 5 uCi of C-14 tagged bicarbonate (from New England Nuclear) and incubating samples at 24°C for three hours. To determine optimum incubation time, a preliminary experiment was run in which algae were sampled after 3, 5, 7, and 16 hour exposures to the tagged bicarbonate. The samples were filtered (Millipore) and the filters placed in scintillation vials with Aquasol (New England Nuclear) solubilizer and radioactivity determined (Beckman Instrument LS3150T).

Mussel Feeding:

Feeding experiments were conducted in 1 liter beakers containing 600 ml of water under constant aeration. Water from holding tanks was used to minimize shock to the mussels and promote normal feeding behavoir. Initial experiments were designed to determine optimum feeding time and choice of mussel tissues to be analyzed for C-14 uptake. Mussels were fed 30 ml of C-14 tagged algae for periods of 2, 3, 6, and 16 hours, then dissected and various tissues analyzed for C-14 uptake. On the basis of these results, a three hour feeding time was established, and gill and mantle tissues selected for analysis.

Silt used in feeding experiments was obtained from river sediments collected from the Clinch, Powell and North Fork Holston Rivers for analysis of particle size distribution. The finest fractions (<2 mm) of these samples were further seived using a No. 230 (62.5 um) USGS screen and pooled for use in feeding experiments.

Prior to initiation of the feeding experiments, silt (10 to 100 ml dry volume) was added to the feeding beakers with 600 ml of water and aerated for one hour to allow for stabilization of material in suspension. Silt concentration in the test beakers was determined by filtering water samples on tared (pre-weighed) glass fiber filters, drying (25°C for 24 hours) and weighing filters. Silt concentration was recorded as mg dry wt./ml. No silt was added to one beaker which served as a control. Two mussels were placed in each beaker, and 30 ml of tagged algae added to each. After three hours, mussels were dissected and tissues analyzed for C-14.

Analysis of Mussel Tissues:

Mussel tissue samples were dissected from live mussels and rinsed well in dilute hydrochloric acid solution to remove any surface adsorbed C-14. Tissues were then dried (25°C) for 24 hours, desiccated for 24 hours and weighed. Dried tissues were then placed in 5 ml scintillation shell vials and frozen. The frozen shell vials were placed in scintillation vials to which 2 ml of phenethylamine had been added as a carbon dioxide absorbant. One or two ml of oxidizer (Potassium dichromate in concentrated sulfuric acid) was carefully added to the tissues in the shell vial and the scintillation vial capped. Vials were placed in a boiling water bath for 3 hours, alowed to cool and refridgerated. Carbon-14 released from the tissues during oxidation was absorbed by the phenethylamine in the scintillation vial.

Prior to counting, shell vials were removed and 5.4 ml of scintillation coctail (460 ml toluene, 270 ml methanol, 1.4 g PPO, 0.1 g POPOP) added to each vial. The vials were refrigerated for 48 hours to allow chemoluminescence to subside, then counted. Counting efficiency was determined by computing channels ratios for standards of known activity. A quench curve was generated by plotting channels ratio against counting efficiency for the standards. Scintillation vials without tissues were prepared and run to determine background radiation levels.

RESULTS AND DISCUSSION

Feeding Studies

Table III-11 shows C-14 uptake by the alga Selenastrum capricornutum at different exposure times. Data are reported as counts per minute (CPM) for 10 ml of algal culture. Results indicate that the average CPM increased slightly from 3 to 5 hours, then dropped sharply at 7 hours exposure, probably due to respiration of the C-14 as carbon dioxide by the algae. The 3 hour exposure time was selected for use in subsequent experiments to avoid the problem of respiratory loss of C-14 from the algae during the course of the feeding experiments.

Results of initial experiments established optimal feeding time for mussels and indicated the most suitable mussel tissues for C-14 analysis. Table III-12 compares C-14 uptake for various mussel tissues at different exposure times. Results are presented as average disintegrations per minute (DPM) X 10^3 per gram (dry weight) of mussel tissue.

Of the four tissues analyzed, mantle and gill exibited the greatest uptake of C-14 at all exposure times and gave the most consistant results. Foot tissue showed the lowest level of uptake of C-14; gonadal and digestive gland tissues gave inconsistant results, possibly due to contamination of samples with undigested food from the digestive tract. In fresh water mussels, the gut winds through the gonadal tissue from

TABLE III-11

Uptake of Carbon-14 by Selenastrum capricornutum

for Different Exposure Times

Exposure Time (hours)	Counts per Minute (CPM)	Average CPM
3	9334.0	
	13366.0	11350.0
5	17372.0	
	11696.4	14534.2
7	9961.6	
	1792.0	5876.8

TABLE III-12

Carbon-14 Uptake for Different Mussel

Tissues and Exposure Times

Tissue	Ave. Uptake (DPM/g X 10^3) at exposure times			
	2 hour	3 hour	6 hour	16 hour
Foot	0.22	3.11	--	--
Gonad	1.78	39.23*	28.28*	9.78
Mantle	20.09	38.68	9.91	11.67
Gill	21.81	74.32	6.44	12.44
Digestive gland	--	--	18.22	5.36

* High average due to one large value

-- = No data available

which it is very difficult to separate.

The three hour exposure time resulted in the highest uptake of C-14 for gill and mantle tissues. This finding agrees well with those of Sorokin (1968) who suggested 2 to 3 hour exposure times to isotope tagged food for the European freshwater mussel Dressenia. The Dressenia tested averaged 17-28 mm in length, however; the 3 hour exposure time appears equally well suited to the larger (80-120 mm) mussels used in the present study. The lower C-14 content observed for longer exposure times is, again, probably due to respiration of C-14 as carbon dioxide.

Results of the experiments on siltation effects are presented in Figure III-3, where C-14 uptake by mussels is plotted against silt concentration. Analyses of gill and mantle tissue were averaged for each mussel, and each graph point represents the average DPM per gram (dry weight) of tissue X 10^3 for one mussel.

In Table III-13, data are grouped into four silt ranges based on observed effect. Group A was the control, fed only algae; group B was fed in low concentrations of silt (.029-.119 mg/ml); group C was fed in an intermediate silt range (.211-.820 mg/ml); and group D fed in a high silt range (.996-3.28 mg/ml).

At low levels of silt, the average uptake of C-14 was slightly higher than for the control group, indicating that silt in low concentrations may have a stimulatory affect on feeding. This phenomenon has also been reported for marine bivalves by Winter (1975) who looked at the influence of suspended silt added to unialgal cultures

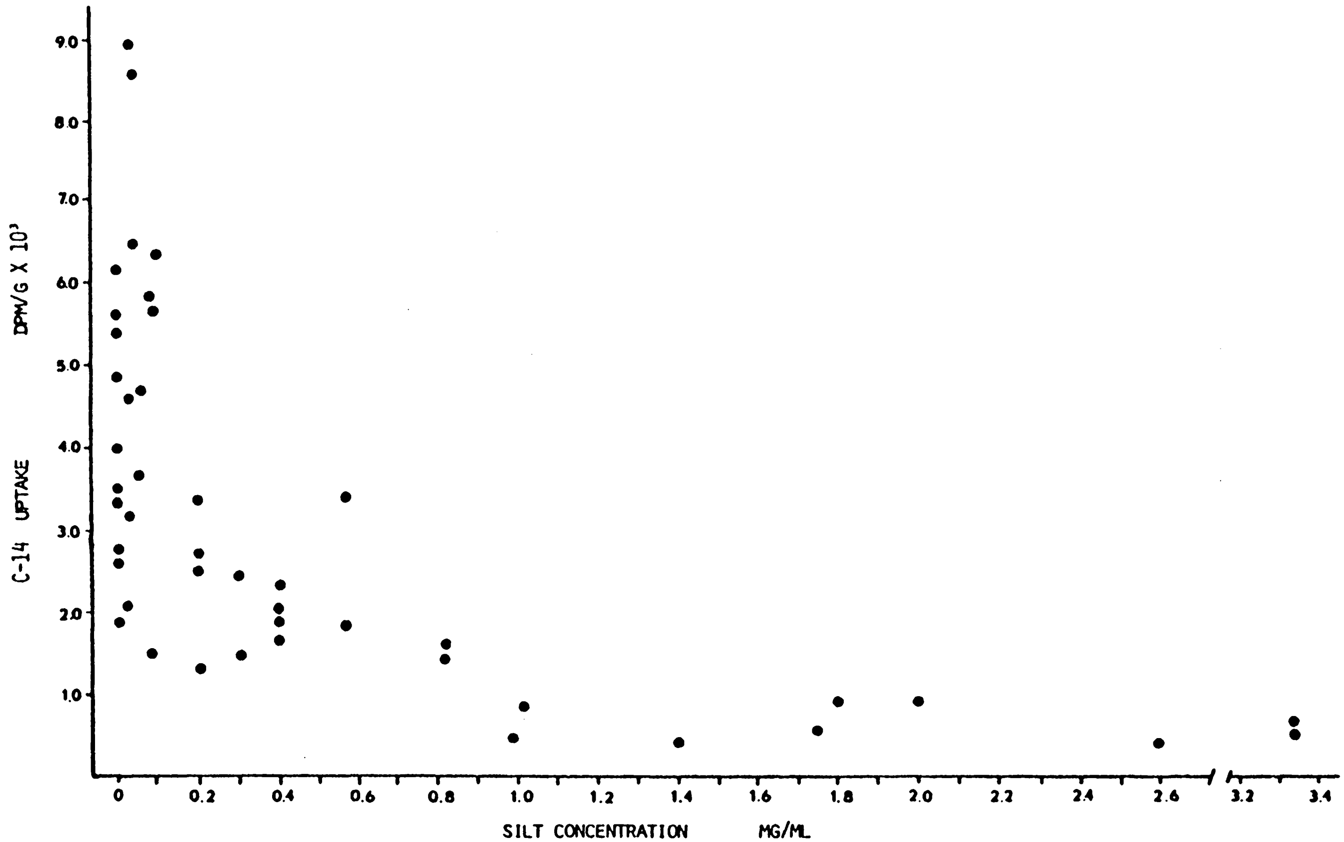


FIGURE III-3. UPTAKE OF C-14 BY MUSSELS VERSUS SILT CONCENTRATION IN FEEDING VESSELS

TABLE III-13

CARBON-14 UPTAKE BY MUSSELS AT 3 SILT RANGES

Uptake (DPM/g x 10^3) at silt ranges A-D

	A 0	B .029-.119	C .211-.802	D .996-3.28
	6.16	3.14	1.26	0.45
	5.59	2.03	2.47	0.83
	5.44	8.98	2.65	0.43
	4.88	4.67	3.38	0.94
	4.30	8.57	1.49	0.59
	3.23	6.46	2.43	0.94
	3.49	4.77	1.80	0.43
	2.68	3.69	2.32	0.59
	2.64	1.45	1.98	0.78
	1.89	5.72	1.65	
		5.84	1.75	
		6.36	3.44	
			1.59	
			1.45	
$\overline{X}$	4.03	5.14	2.12	0.66

Silt Concentrations = mg/ml

on the feeding activity of the marine bivalve Mytilus edulis. He observed that additions of silt at 12.5 mg/l resulted in an increase in filter feeding activity, food ingestion, and growth of these mussels.

Statistical analysis of data (Table III-14) indicates no significant difference in C-14 uptake between mussels in the control (A) and low silt (B) groups. These two groups did differ significantly, however, from the intermediate (C) and high (D) silt groups. The C-14 uptake at intermediate silt ranges averaged less than half that for the low silt group. Uptake of C-14 at silt levels greater than 1 mg/ml averaged less than 15 percent that for the low silt group.

A few works of particular relevance to the present studies deal with the effect of suspended silt on marine bivalves. Winter (1975) determined that low concentrations of silt added to the food of Mytilus edulis increased feeding activity. Jorgensen (1955) reported on the effects of silt on the pumping rate of oysters, and Loosanoff (1961) looked at effects of turbidity on larval and adult oysters. In most cases, results of studies on effects of siltation are not directly comparable because levels of silt are reported in non-comparable terms (e.g. particle density, light penetration, weight to volume ratio). Two studies were found, however, in which results reported are comparable to those of the present study.

H. C. Davis (reported in Loosanoff, 1961) examined effects of suspended silt on mortalities of larval oysters, reporting silt concentrations as mg/l. His findings, summarized in Table III-15 show a

TABLE III-14

STATISTICAL ANALYSIS OF CARBON-14 UPTAKE DATA

Analysis of Variance: Comparison of means A, B, C and D

Anova Table

Source of variation	df	ss	MS	F_s
$\bar{Y}-\bar{Y}$ Between groups	2	118.66	59.33	26.84
$Y-\bar{Y}$ Within groups	42	92.64	2.21	
$Y-\bar{Y}$ Total	44	211.30		

$f_{.01\ (2,42)} = 5.18$ $f_{.001\ (2,42)} = 8.25$

Conclusion: Reject hypothesis that all means are the same

II. Student-Newman Keuls test: Least Significant range test for means A, B, C, D =.05

Groups	LSR	Difference between means	Significant difference
B,D	2.55	4.48	yes
B,C	2.16	3.02	yes
A,B	1.92	1.11	no
A,C	1.85	1.91	yes

TABLE III-15

Effect of Suspended Silt on Development of Oyster Larvae
(H.C. Davis, from Loosanoff, 1961)

% of oyster larvae which developed	mg/l silt
95	125
73	250
31	500
3	1000
none	>1000

remarkable similarity to those observed in the present studies. Detrimental effects are noted at silt ranges comparable to my intermediate range, with severe effects at levels greater than 1000 mg/l. In both cases, silt levels less than 125 mg/l were not deleterious.

In another study, Arruda et al. (1983) looked at the effects of suspended sediment on nutrition of zooplankton in turbid reservoirs. In studies involving ingestion and incorporation of C-14 tagged Chlorella by Daphnia parvula and D. pulex, they determined that both ingestion and incorporation rates were reduced in the presence of suspended sediments. At low sediment concentrations (<1 mg/l) they reported a slight reduction in ingestion of Chlorella; at concentrations of 10-100 mg/l they noted a greater reduction; and at the highest concentration used (2451 mg/l) they reported an ingestion rate of only 0.8% that of the control. Likewise, incorporation rates decreased with increased sediment concentrations from approximately 70% (of control) at 10 mg/l to less than 10% at 2451 mg/l.

Similar results have been reported for freshwater fishes, although reports are often contradictory. Muncy et al. (1979) reviewed the literature on effects of suspended solids on young warmwater fishes reporting that inferences made by authors were often not supported by evidence, and that cause and effect relationsips were not well documented. Citing studies by Morgan et al. (1973), Schubel et al. (1973) and Auld and Schubel (1978), they pointed out contradictions in the literature regarding silt levels causing mortality in fish eggs.

In examining effects of suspended silt on viability of Striped Bass (Morone saxatilis) eggs, Morgan et al. (1973) reported that the eggs were unaffected by concentrations of 20-2300 mg/l. Schubel et al. (1973) reported that sediment concentrations of 1000 mg/l lowered hatching success of this species, while Auld and Schubel (1978) reported normal development in all concentrations tested.

Similar contradictory results were reported for the white perch (Morone americana). Morgan et al. (1973) reported no reduction of hatching success at silt levels of 50-5250 mg/l, while Auld and Schubel (1978) reported no effect from 25-500 mg/l, but a significant reduction in hatching success at 1000 mg/ml. Likewise, for the yellow perch (Perca flavescens) Schubel et al. (1973) reported that 1000 mg/l suspended sediment caused significant increases in mortality of eggs, while Auld and Schubel (1978) later reported that egg survival was unaffected by that level.

Muncy et al. (1979) concluded that chronic siltation can be detrimental to fish reproduction, and that high concentrations of silt may cause significant mortality in embryos. They suggested that the effects of suspended solids on fish reproduction are relative to spawning behavior and timing. The fish best adapted to survive in silted environments are those that spawn at times other than periods of highest turbidity. They also concluded that there was evidence, although sparse, that species composition was altered by siltation.

Suggested Mechanism by Which Suspended Silt is Limiting to Freshwater Mussels:

Ellis (1936), Collinson and Rees (1978) and others have suggested that silt causes mortality in mussels by clogging gills and interfering with respiration. Ellis (1936) reported that high levels of suspended silt caused excessive mucous secretions in fresh water mussels, an observation not unexpected since mucous secretions are important in collection and excretion, as pseudofaeces, of material which cannot be ingested because of its size or abundance. He also noted that 1/4 to 1 inch of deposited silt caused high mortality in mussels, and that after death the mussels contained silt in mantle and gill cavities.

Ellis (1936) also reported that silt interfered with food uptake in mussels, but believed that this was a result of the mussel closing up and ceasing filtration in high silt concentrations. In the present study, mussels were observed to continue filtration in all silt concentrations. When mussels were dissected at the termination of the experiments, the digestive organs were examined for silt accumulation. In the highest concentrations of silt, an accumulation of silt was observed on the excurrent siphon, but not in the mantle cavity or on the gills. Accumulations of mud in the lower digestive tract confirm that the feeding process was not discontinued. It is apparent that at least for the three hour exposure times used in these studies, the mussels were able to handle the large volume of suspended material by passing it through the gut or expelling it as pseudofaeces, without any accumulation within the mantle cavity.

Since the feeding vessels were well aerated, and gill function did not appear to be impaired by the suspended silt. Interference with respiration is not a likely cause of the reduced C-14 uptake at high silt levels. It is more likely that the silt interfered directly with the uptake of food by the mussels.

If Allen's (1921a) conclusions that mussels are capable of sorting food from non-food items were true, an explanation could be put forth that the energy required to sort large amounts of silt from suspended food is greater than the food value gained, resulting in a net energy loss. If such sorting were in operation, however, the stomach and gut of mussels fed in the presence of silt would show little silt accumulation. This was not the case, however, in mussels examined following the feeding studies. Present observations support the conclusion of Churchill and Lewis (1924) that freshwater mussels exibit little ability to sort food items qualitatively.

Since food items cannot be selected over inorganic particles, all material in suspension is ingested in proportion to its concentration in the ambient environment. The mechanism by which silt limits food assimilation is apparently one of dilution of the food to levels below the critical minimum necessary to sustain the animal. Examination of the digestive tracts of test mussels supports this hypothesis. Mussels fed in algal cultures alone contained concentrations of algae throughout the digestive tract after three hours of feeding, while mussels fed in the same algal concentrations with silt added contained "mud" throughout the digestive tract.

If the uptake of food is based primarily on the proportion of edible material ingested, then the relative proportion of organic to inorganic material in suspension in a river may be more important to mussel survival than the concentration of suspended material alone. This would help to explain why some rivers which are known to carry heavy silt loads are able to sustain freshwater mussel populations while others are not.

Another consideration not often addressed in considering effects of suspended silt is the organic content of the suspended material. Arruda et al. (1983) looked at survival, growth and reproduction in Daphnia fed only silt (clay mineral) to which organic material had been adsorbed (amended), as compared to those fed unamended (without organics) silt and those fed cultured yeast. They found that growth and survivorship was greater with the yeast and ammended sediments than with unamended sediments. While most of the Daphnia fed yeast produced eggs, those fed the amended and control sediments did not. The authors suggested that while suspension feeders are believed to be unable to use dissolved organic material directly as a food source (Jorgensen, 1975), they may be able to use this material if it is adsorbed to clay particles.

In the experiments reported here, the density of food was held constant while inorganic silt concentrations were varied. Future experiments in which food concentration is varied in proportion to silt concentration will shed more light on this problem. Also worth exploring is the nature of the suspended silt. Experiments in which the organic content of the silt is varied will aid in evaluating possible deleterious effects of suspended silt on mussel populations.

CONCLUSIONS

The mussel transplants conducted in conjunction with the present studies suggest that heavily silted headwater reaches of the Powell River were at the time of these studies unsuitable for re-establishment of a freshwater mussel fauna. Observing survival of mussels over a one year period provided information as to the suitability of the habitat which could not be determined by physical and chemical measurements alone. Substrate characterization by particle size and organic content was not useful to predict survival of mussels at a given site.

Laboratory studies showed that suspended silt can interfere with feeding in freshwater mussels. Food uptake was reduced to approximately 50% (of control) at silt levels of 211 to 820 mg/l, and to approximately 80% at silt levels over 1000 mg/l.

It was concluded based on short term laboratory studies that the mechanism by which silt is limiting to freshwater mussels is one of dilution of the food source rather than direct interference in filtration or respiration.

GENERAL SUMMARY

The Tennessee River drainage presently supports one of the richest freshwater mussel faunas in the world. Of the 71 freshwater mussel species extant in this drainage, approximately 25% are endemic to the Cumberlandian region. Although a number of species, primarily members of the genus *Dysnomia*, have been extirpated from this drainage within the past 60 years, the number of extant species remains high. The major impact of man's activities over the past half century has been the reduction of available habitat for mussel species.

The mussel fauna of the Tennessee River system can be divided into species assemblages based on stream size. Once exibiting a continuous gradation from one size category to the next, these assemblages now exist in isolated communities separated by river reaches made uninhabitable for mussels. Factors which have contributed to this isolation of communities include: impoundment; erosion silt from land development, gravel dredging and strip mining; and pollution from industrial sources.

Comparison of recent and historic species distribution records documents these reductions in mussel habitat over the past 60 years. The absence of quantitative collection data from most early collections, however, makes it impossible to document more subtle changes over time in mussel community structure.

Intensive quantitative sampling at two sites in the Clinch River showed differences not apparant based solely on species composition data. While qualitative sampling showed similar species composition at the two sites, examination of quantitative data revealed significant differences in mussel densities. Results of quantitative sampling throughout the drainage indicated that density is more variable than species composition on a site to site basis. In addition, examination of age class structure of mussel communities at the two study sites showed differences which might be attributed to environmental perturbations at one of the sites.

The hypothesis that suspended silt may be limiting to mussel distribution in the Tennessee system was supported by laboratory and field studies on the effects of suspended silt on freshwater mussels.

Experimental mussel transplants to three areas of the Powell River showed the heavily silted headwater reaches of this river to be unsuitable for re-establishment of a freshwater mussel fauna. Mussels transplanted to the uppermost site showed poor survival compared to other sites and exibited an inhibition of reproductive activity.

Laboratory studies demonstrated that suspended silt can interfere with feeding in freshwater mussels. Food uptake was reduced to approximately 50% (of control) at silt levels of 211 to 820 mg/l, and to approximately 80% at silt levels over 1000 mg/l. It was concluded based on these laboratory studies that the mechanism by which silt is limiting to freshwater mussels is one of dilution of the food source rather than direct interference in filtration or respiration.

The Cumberlandian mussel fauna has decreased in range within the past 50 years, resulting in the listing of a number of these mussel species as endangered. Information gathered in the present studies will contribute to our understanding of factors limiting freshwater mussel distribution. Such information is needed for the preservation and management of this steadily declining resource. The analysis of community structure will provide a basis for evaluating future changes in the fauna of the Clinch and Powell Rivers. The studies on effects of siltation identify this as a potential threat to the continued existance of freshwater mussels.

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APPENDIX A

QUADRAT DATA FROM THE CLINCH RIVER,

KYLES FORD, TENNESSEE AND SPEERS FERRY, VIRGINIA

TABLE A-1

Age class composition of Mussels from m^2 quadrat samples taken from the Clinch River at Kyles Ford, Tennessee, 1973.

Species	Number	Age Class (years) A 0-3	B 4-5	C 6-7	D 8-10	E 11+
Medionidus conradicus	29	8	11	9	1	-
Dysnomia capsaeformis	23	12	6	4	1	-
Actinonaias pectorosa	18	8	2	4	2	2
Ptychobranchus subtentum	13	4	3	3	2	1
Actinonaias carinata	8	-	1	1	2	4
Fusconaia barnesiana	8	1	2	1	1	3
Elliptio dilatatus	5	2	1	2	-	-
Fusconaia edgariana	3	2	1	-	-	-
Lasmigoa costata	3	1	-	1	-	1
Truncilla truncata	3	-	2	-	1	-
Ptychobranchus fasciolaris	2	-	-	1	1	-
Dysnomia triquetra	1	-	1	-	-	-
Lampsilis ovata	1	1	-	-		-
Proptera alata	1	-	-	-	-	1
Strophitus rugosus	1	-	-	1	-	-
Unidentified young (<1 yr)	4	4	-	-	-	-
Totals:	123	43	30	27	11	12

TABLE A-2

Age Class Composition of Mussels from m^2 quadrat samples taken from the Clinch River at Kyles Ford, Tennessee, 1974.

Species	Number	Age Class (years)				
		A 0-3	B 4-5	C 6-7	D 8-10	E 11+
Medionidus conradicus	78	21	31	17	7	2
Dysnomia capsaeformis	57	22	16	18	1	-
Actinonaias pectorosa	55	9	10	15	14	7
Ptychobranchus subtentum	47	18	12	10	3	4
Actinonaias carinata	38	5	7	5	9	12
Cumberlandia monodota	22	-	-	-	4	18
Fusconaia edgariana	22	10	11	1	-	-
Elliptio dilatatus	12	-	4	4	4	-
Fusconaia barnesiana	9	2	-	2	2	3
Alasmidonta marginata	5	1	3	-	1	-
Cyclonaias tuberculata	5	1	1	-	1	1
Lasmigona costata	5	1	1	1	1	1
Ptychobranchus fasciolaris	3	-	1	2	-	-
Dysnomia brevidens	2	-	1	1	-	-
Lampsilis fasciola	2	-	1	-	1	-
Lampsilis ovata	2	-	-	1	1	-
Truncilla truncata	2	-	-	-	2	-
Cyprogenia irrorata	1	1	-	-	-	-
Dromus dromas	1	-	1	-	-	-
Dysnomia triquetra	1	-	1	-	-	-
Lastena lata	1	-	-	-	1	-
Plethobasus cyphyus	1	1	-	-	-	-
Quadrula cylindrica	1	-	-	-	1	-
Villosa iris	1	-	-	-	1	-
Totals:	373	92	101	77	54	43

TABLE A-3

Age Class Composition of Mussels from m^2 quadrat samples taken from the Clinch River at Kyles Ford, Tennessee 1975.

Species	Number	Age Class (years)				
		A 0-3	B 4-5	C 6-7	D 8-10	E 11+
Medionidus conradicus	90	36	29	14	10	1
Actinonaias pectorosa	89	5	13	14	25	32
Dysnomia capsaeformis	88	35	37	7	9	-
Ptychobranchus subtentum	69	19	13	19	15	3
Actinonaias carinata	60	4	11	8	3	34
Fusconaia barnesiana	18	1	8	1	3	5
Lasmigona costata	11	1	2	1	6	1
Alasmidonta marginata	6	1	2	1	1	1
Elliptio dilatatus	6	-	3	2	1	-
Cumberlandia monodonta	4	-	-	-	-	4
Truncilla truncata	4	-	1	2	1	-
Lampsilis fasciola	3	-	1	1	1	-
Cyclonaias tuberculata	2	1	1	-	-	-
Cyprogeia irrorta	2	1	1	-	-	-
Dromus dromas	2	1	-	-	-	1
quadrula cylindrica	2	-	2	-	-	-
Dysnomia brevidens	1	-	-	1	-	-
Dysnomia triquetra	1	1	-	-	-	-
Lampsilis ovata	1	-	-	-	1	-
Ligumia recta latissima	1	-	-	-	1	-
Ptychobrachus fasciolaris	1	-	-	1	-	-
Villosa iris	1	-	-	1	-	-
Totals:	462	106	124	73	77	82

TABLE A-4

Age Class Composition of mussels from m^2 quadrat samples taken from the Clinch River at Speers Ferry, Virginia, 1973.

Species	Number	Age Class (years)				
		A 0-3	B 4-5	C 6-7	D 8-9	E 11+
Dysnomia capsaeformis	28	23	3	2	-	-
Actinonaias carinata	12	8	2	-	1	1
Medionidus conradicus	8	7	1	-	-	-
Actinonaias pectorosa	4	4	-	-	-	-
Cyclonaias tuberculata	4	2	-	-	1	1
Dysomia brevidens	4	1	2	-	1	-
Lasmigona costata	3	-	-	-	1	2
Lampsilis ovata	3	3	-	-	-	-
Fusconaia barnesiana	2	-	-	-	1	1
Ligumia recta latissima	2	-	-	1	1	-
Ptychobranchus fasciolaris	2	-	1	-	1	-
Quadrula cylindrica	2		-	1	-	-
Alasmidonta marginata	1	-	-	1	-	-
Amblema costata	1	-	-	1	-	-
Elliptio dilatatus	1	-	-	1	-	-
Lastena lata	1	-	-	1	-	-
Plethobasus cyphyus	1	-	-	-	-	1
Proptera alata	1	-	-	-	1	-
Ptychobranchus subtentum	1	1	-	-	-	-
Totals:	81	50	10	6	9	6

TABLE A-5

Age Class Composition of mussels from m^2 quadrat samples taken from the Clinch River at Speers Ferry, Virginia, 1974.

Species	Number	Age Class (years)				
		A 0-3	B 4-5	C 6-7	D 8-10	E 11+
Dysnomia capsaeformis	27	16	7	3	1	-
Actinonaias carinata	17	10	2	2	1	2
Dysnomia brevidens	5	3	2	-	-	-
Medioidus conradicus	5	3	1	1	-	-
Actinonaias pectorosa	4	1	1	2	-	-
Fusconaia edgariana	3	2	1	-	-	-
Ptychobrachus subtentum	3	2	1	-	-	-
Elliptio dilatatus	2	-	1	1	-	-
Quadrula cylindrica	2	-	1	1	-	-
Cycloaias tuberculata	1	-	-	-	-	1
Cyprogenia irrorata	1	-	-	-	1	-
Dysnomia triquetra	1	-	-	1	-	-
Fusconaia barnesiana	1	-	-	-	1	-
Lampsilis ovata	1	-	-	-	1	-
Lasmigona costata	1	-	-	-	1	-
Ptychobranchus fasciolaris	1	-	-	-	1	-
Strophitus rugosus	1	-	1	-	-	-
Totals:	76	37	18	11	7	3

TABLE A-6

Age Class Structure of Mussels from m^2 quadrat samples taken from the Clinch River at Speers Ferry, Virginia 1975.

Species	Number	Age Class (years)				
		A 0-3	B 4-5	C 6-7	D 8-10	E 11+
Dysnomia capsaeformis	34	13	18	1	1	1
Actinonaias carinata	14	5	1	3	3	2
Medioidus conradicus	11	4	3		1	-
Ptychobranchus subtentum	10	6	1	2	-	1
Actinonaias pectorosa	5	-	4	1	-	-
Fusconaia barnesiana	5	-	2	-	1	2
Dysnomia brevidens	3	1	1	-		-
Cyclonaias tuberculata	2	-	1	-	-	1
Dysnomia triquetra	2	-	-	1	1	-
Lastena lata	2	-	-	1	1	-
Alasmidonta marginata	1	1	-	-	-	-
Amblema costata	1	-	-	-	1	-
Elliptio dilatatus	1	1	-	-	-	-
Lampsilis ovata	1	-	-	-	1	-
Lasmigona costata	1	-	-	-	1	-
Ligumia recta latissima	1	-	-	-	1	-
Plethobasus cyphyus	1	-	-	-	1	-
Proptera alata	1	-	-	-	-	1
Ptychobranchus fasciolaris	1	-	-	1	-	-
Totals:	98	31	32	13	14	8

TABLE A-7

Age Class Composition of Mussels from quadrats taken in a pool region of the Clinch River at Kyles Ford, 1974.

Species	Number	Age Class (years)				
		A 0-3	B 4-5	C 6-7	D 8-10	E 11+
Actinonaias carinata	49	2	6	6	7	28
Actinonaias pectorosa	18	-	-	-	-	18
Elliptio dilatatus	13	-	4	1	8	-
Medionidus conradicus	13	2	7	4	-	-
Dysnomia capsaeformis	12	1	6	3	2	-
Fusconaia barnesiana	12	-	5	2	2	3
Lasmigona costata	5	-	-	1	2	2
Amblema costata	4	-	-	-	1	3
Cyclonaias tuberculata	3	-	-	-	1	2
Pytchobranchus subtentum	3	1	-	-	2	-
Truncilla truncata	3	-	-	2	1	-
Cyprogenia irrorata	2	-	-	1	1	-
Ptychobranchus fasciolaris	2	-	-	-	-	2
Quadrula cylindrica	2	-	-	-	2	-
Quadrula pustulosa	2	-	1	-	1	-
Dysnomia brevidens	1	-	-	-	-	1
Lampsilis ovata	1	-	-	-	1	-
Totals:	145	6	29	20	31	59

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