COMMUNITY STRUCTURE OF FRESHWATER MUSSELS
(BIVALVIA: UNIONIDAE) IN COASTAL PLAIN STREAMS
OF THE SOUTHEASTERN UNITED STATES

By

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Abstract of Dissertation Presented to the Graduate School
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The North American freshwater mussel (*Bivalvia*: *Unionidae*) fauna is the richest in the world, and the southeastern United States has more species than any other region. Freshwater mussels are also one of the most imperiled faunal groups in North America, and a precipitous decline in freshwater mussel populations has been documented throughout the southeastern region, including the Apalachicola, Chattahoochee, and Flint (ACF) River basin of Alabama, Georgia, and Florida. The decline in freshwater mussel populations in many river basins has been attributed, in part, to land-use modifications that cause changes in sediment regimes. The specific associations that mussels have with streambed sediments, however, are poorly understood, making it difficult to assess the impacts that changes in sedimentation rates have on unionid mussels. In addition, the biotic and abiotic attributes that define suitable habitats of individual mussel species are

poorly understood. Ecosystem-level studies of freshwater mussels are few, and it is unclear what factors should be measured, and at what spatial and temporal scales, to elucidate meaningful relationships between mussels, suitable habitat, and community structure. In this study quantitative methods were used to evaluate the relative importance of fish and abiotic characteristics on mussel community structure in the ACF basin. Over 2,500 mussels, 7,200 fish, and 2,600 sediment cores were sampled at 30 locations in the basin. The response of four mussel species to catastrophic burial by sand and fine sediments was also determined through laboratory experiments. Significant relationships were detected between mussel and fish assemblage structure and macro- and micro-habitat descriptors, but not between mussel and fish assemblage structure. Mussel community structure was closely related to stream size and streambed substrate properties, including stream order, link magnitude, substrate porosity, substrate sorting, percentage of fine sediments, and mean sediment particle size. This study suggests that in the ACF basin, freshwater mussels are habitat specialists whose distributions are tied to suitable habitat defined by a combination of macro- and micro-habitat variables. In addition, covering mussels with as little as 14 cm of sediments significantly decreased their chances of extricating themselves from burial, suggesting that the fouling of North American streams by erosional sediments may be a factor in the current decline of unionid mussels.

CHAPTER 1 INTRODUCTION

The North American freshwater mussel fauna is the richest in the world and historically probably numbered over 300 species (Stansbery 1971). Within North America, the southeastern United States has more freshwater species than any other region, with about 80% of the fauna (Burch 1973). North America's freshwater mussel fauna is in decline, however, with 7% of the species presumed extinct, 40% considered endangered or threatened, 24% of special concern, 24% stable, and about 5% undetermined (Williams and Neves 1995). There appears to have been a precipitous decline in freshwater mussel populations throughout the southeastern region, including the ACF basin, in the past 40 years (Heard 1975, Williams et al. 1993).

The ACF rivers form one of the largest drainages in the eastern Gulf of Mexico and drain portions of east Alabama, west Georgia, and northwest Florida. Eastern Gulf of Mexico river systems, including drainages from the Suwannee River west to the Escambia River, are important areas for molluscan speciation and endemism, with about 56% of the fauna comprised of endemics (Butler 1989). Within this area, the ACF rivers contain the greatest total number of mollusk species as well as endemics (Clench and Turner 1956).

Mollusks are one of the best sampled invertebrate groups largely because of the interest of shell collectors beginning in the 18th century (Barnes 1980). These

collections, many of which were made by private individuals and were later donated or purchased by natural history museums, form the backbone of our historical knowledge of unionid mussels. Collections from the ACF rivers date back to 1833, when Timothy A. Conrad traveled through the ACF basin, passing over both the Flint and Chattahoochee rivers. Conrad (1834) was the first to note that freshwater mussels from rivers draining the Gulf of Mexico differed from those of the Atlantic slope region, and that in the ACF Basin, some mixing of these two faunal groups occurred. Later, van der Schalie (1938a) also reported that the ACF basin consisted of a "strikingly peculiar fauna" that was distinct from the Alabama drainage to the west and the Atlantic coastal drainages to the east. The biological uniqueness of the basin is due to a combination of factors including its geographic location, physiographic and geologic diversity, and unglaciated status during the last glacial period (Adams and Hackney, 1992). Its relatively isolated geographic location, between the Alabama Basin to the west and the southern Atlantic Slope drainages to the east, is especially important, as faunal elements representing both regions are present in the basin. In addition, the unique geological features that occur where the upper Coastal Plain Physiographic Province meets the Piedmont has produced a diverse animal fauna that includes both Coastal Plain (southern) and Piedmont (northern) forms.

Although isolated collections have been made in the ACF Basin for over 160 years, a comprehensive survey of the three major rivers of the basin and their tributaries was not conducted until the early 1990s (Brim Box and Williams 1999). They determined that the conservation status of ACF Basin mussel species included 13 (39%) species that were

currently stable, six (18%) species were of special concern, three (9%) that were threatened, seven (21%) that were endangered, two that were extirpated (6%) and two (6%) that were extinct. Their assessment of the conservation status of the 33 species of mussels that occur in the ACF Basin revealed a picture of significant decline during the past 30 years. In addition 11 of the 33 species (33%) had a reduced conservation status within the basin compared to their range-wide status (Brim Box and Williams in press, Williams et al. 1993).

The causal factors for the decline of freshwater mussel faunas are poorly understood (Fuller 1974, Bogan 1993, Williams and Neves 1995), and much of the information that links mussel declines to changes in their physical habitats is based on anecdotal or descriptive information. One of the most ubiquitous factors that may adversely affect mussel populations is excessive sedimentation caused, in part, by poor land-use practices. Excessive sedimentation has been suspected as a cause of unionid mussel declines since the late 1800s (Kunz 1898). The US Environmental Protection Agency (1990) cited sediments as the number one pollutant of rivers in the United States, impairing > 40% of the nation's river miles. This estimate is nearly 50% higher than the next pollutant. Sediment production is closely tied with changes in land use, and increased sediment production is thought to negatively impact unionid mussels. Although sedimentation is often cited as a cause of the cataclysmic decline experienced by the majority of North America's freshwater mussels, the role of streambed substrate composition in defining suitable habitat for unionid mussels is unclear, and results are contradictory regarding the

strength of associations between streambed substrates and freshwater mussel distributions.

Attempts to address causal factors of mussel declines are hampered by the lack of knowledge of even basic aspects of their life histories and habitat requirements. The biotic and abiotic attributes that define suitable habitats for individual mussel species are poorly understood. Freshwater mussel communities reportedly are structured by three types of environmental factors: 1) the distribution and availability of their host fish (Haag and Warren 1998, Watters 1992), 2) drainage-level characteristics (e.g., stream area) (Strayer 1983), or 3) micro-habitat variables, including substrate composition (Harman 1972, Leff et al. 1990, Layzer and Madison 1995). Much ambiguity remains over the role of these three groups in structuring freshwater mussel communities, and results are often contradictory concerning their usefulness in predicting the occurrence or density of unionids in streams (Holland-Bartels 1990, Bauer et al. 1991, Strayer and Ralley 1993, Di Maio and Corkum 1995). In order to address causal factors of freshwater mussel declines, however, a better understanding must be gained of how such ecological factors structure mussel communities.

The purpose of this study was to evaluate the relative importance of fish and abiotic characteristics on mussel community structure. Mussel and fish assemblage structures were correlated to each other and to macro- and micro-habitat descriptors at the site level. The strength of associations were tested between properties of streambed substrate composition, including bulk density, porosity, sediment sorting, the percentage of fine sediments, and mean particle size, and the distribution of individual mussel species at 30

stream sites in the ACF Basin of the eastern Gulf of Mexico. Finally, the responses of four species of unionid mussels from the ACF basin to catastrophic burial by both fine sediments and sand were evaluated.

CHAPTER 2 STUDY AREA

The ACF rivers form one of the largest drainages in the eastern Gulf coastal plain, and drain portions of southeast Alabama, southwest Georgia, and northwest Florida. The ACF basin encompasses approximately 50,800 km² (Leitman et al. 1983) and drains parts of the Blue Ridge, Piedmont, and Coastal Plain physiographic provinces. The basin is one of the largest and longest in the southeastern region and wholly or partially encompasses 59 Georgia counties, 10 Alabama counties, and 8 Florida counties.

The Apalachicola River originates at the confluence of the Chattahoochee and Flint rivers just north of the Florida/Georgia border. It is 182 km long and lies entirely within the Coastal Plain physiographic province. It drains approximately 6,200 km², about half of which drains the Chipola River subbasin (Mattraw and Elder 1984). It is the largest river in Florida, with monthly mean discharges of approximately 25,000 cubic feet per second (cfs) and seasonal highs approaching 100,000 cfs (Livingston 1974). The river has been named an Outstanding Florida Water (Florida Department of Natural Resources 1989). A distinctive feature of the Apalachicola River is its dense bottomland hardwood forest that contains more than 1,500 trees per hectare (Mattraw and Elder 1984). The average annual litter fall produced by this vegetation makes the Apalachicola floodplain forest one of the most productive in warm temperate regions.

The Chipola River is the major tributary to the Apalachicola River and is the fourth largest river in the basin, draining approximately 1,649 km². The Chipola River begins in extreme southeastern Alabama, flows 177 km south into Florida, and empties into the Apalachicola River, near Sumatra (Florida Department of Natural Resources 1989). The river is considered a springfed river, containing many small spring runs as well as a first magnitude spring, and is designated as an Outstanding Florida Water (Florida Department of Natural Resources 1989). Two Chipola River tributaries were used in this study: Baker and Spring (Merritt Mill) creeks, Jackson County, Florida.

The Chattahoochee River originates in the Blue Ridge Mountains of northern Georgia and flows approximately 702 km to its confluence with the Flint River at Lake Seminole on the tristate boundary. For much of this distance it forms the border of Alabama and Georgia. The Fall Line, near Columbus, Georgia, marks the boundary of the Coastal Plain and the Piedmont physiographic provinces. Nine Chattahoochee River tributaries were used in this study: North Fork Cowikee Creek, Barbour County, Alabama; Hog Creek, Clay County, Georgia; Kirkland and Sawhatchee creeks, Early County, Georgia; Little Uchee Creek, Lee County, Alabama; Pumpkin Creek, Randolph County, Georgia; Hatchechubee and Uchee creeks, Russell County, Alabama; Lime Spring Creek, Stewart County, Georgia.

The Flint River originates in the crystalline rocks of the Piedmont physiographic province, just south of Atlanta, and flows 564 km south to its confluence with the Chattahoochee River. Approximately 193 km of the Flint River lies in the Piedmont province, while the remaining 371 km are in the coastal plain, all within the state of

Georgia. Nineteen Flint River tributary sites were used in this study: Coolewahee and Ichawaynachaway creeks, Baker County, Georgia; Swift and Cedar creeks, Crisp County, Georgia; Spring Creek, Decatur County, Georgia; Hogcrawl Creek, Dooly County, Georgia. Kiokee Creek, Dougherty County, Georgia; Muckalee Creek (two sites), Lee and Sumter counties, Georgia; Aycocks Creek, Miller County, Georgia; Chocee and Lime creeks, Sumter County, Georgia; Patsaliga Creek, Taylor County, Georgia; Chickasawhatchee Creek, Terrell County, Georgia; Kinchafoonee Creek, Webster County, Georgia; Jones and Abrams creeks, an unnamed tributary to Abrams Creek, and an unnamed tributary to Mill Creek, Worth County, Georgia.

CHAPTER 3 STREAMBED SUBSTRATE PROPERTIES

Introduction

Freshwater mussels (Bivalvia: Unionidae) are considered the most endangered faunal group in North America, with over 70% of the approximately 280 species considered imperiled or extinct (Neves et al. 1997). Extinction rates for freshwater mussels are an order of magnitude higher than expected background levels (Nott et al. 1995). Reasons for the decline of freshwater mussel populations in the past century throughout North America and especially the southeastern United States are poorly understood. Although decreases in freshwater mussel populations can sometimes be attributed to specific factors (e.g., dams and pollution), the importance of other factors is less clear. Much of the information that links mussel declines to changes in their physical habitats is based on anecdotal or descriptive information (Fuller 1974, Bogan 1993, Williams and Neves 1995).

Attempts to address causal factors of unionid mussel declines are hampered by the lack of knowledge of even basic aspects of their life histories and habitat requirements. For example, freshwater mussels' life histories are complex and include a glochidial stage that parasitises a host fish, undergoes metamorphosis, and drops off to become a free-living juvenile mussel. Many aspects of this relationship are unknown, and only about a third of the fish hosts for North American unionids have been discovered

(Watters 1994a). In addition, the degree of host specificity (i.e., the number of host fish per mussel species) probably varies from mussel species to species.

The biotic and abiotic attributes that define suitable habitats for individual mussel species are also poorly understood. Freshwater mussel communities reportedly are structured by three types of environmental factors: 1) the distribution and availability of their host fish (Haag and Warren 1998, Watters 1992), 2) drainage-level characteristics (e.g., stream area) (Strayer 1983), or 3) micro-habitat variables, including substrate composition (Harman 1972, Leff et al. 1990, Layzer and Madison 1995). Much ambiguity remains over the roles of these three general factors in structuring freshwater mussel communities, and results are often contradictory concerning their usefulness in predicting the occurrence or density of unionids in streams (Holland-Bartels 1990, Bauer et al. 1991, Strayer and Ralley 1993, Di Maio and Corkum 1995). It is imperative, however, in the face of current mussel declines, that a better understanding be gained of how such ecological factors structure mussel communities, especially because resource managers must increasingly delineate suitable habitat in recovery plans for imperiled mussel species.

One of the most ubiquitous factors that may adversely affect mussel populations is excessive sedimentation caused, in part, by poor land-use practices (Brim Box and Mossa 1999). The US Environmental Protection Agency (1990) cited sediments as the main pollutant of rivers in the United States, affecting > 40% of the nation's river miles. This estimate is nearly 50% higher than the next pollutant. Excessive sedimentation has been suspected as a cause of unionid mussel declines since the late 1800s (Kunz 1898).

Excessive amounts of sediments, especially fine particles, that wash into streams can potentially affect mussels in many ways, although empirical studies examining the effects of eroded sediments on invertebrates are lacking (Waters 1995). In addition, although sedimentation is often cited as a cause of the cataclysmic decline experienced by the majority of North America's freshwater mussels (Bogan 1993, Williams and Neves 1995, Neves et al. 1997), the role of streambed substrate composition in defining suitable habitat for unionid mussels is unclear, and results are contradictory regarding the strength of associations between streambed substrates and freshwater mussel distributions. This relationship, however, must be understood before the impact of anthropogenic sources of erosional sediments on existing mussel populations can be evaluated.

There are several possible reasons why meaningful relationships between unionid mussel distributions and micro-habitat descriptors, such as streambed composition, have eluded researchers: 1) mussels may be habitat generalists, occurring in many types of substrate indiscriminately, 2) relationships between mussels and substrate composition may be species-specific, although much of the literature refers to multiple species when describing habitat preferences, and 3) there are several methodological problems with the sampling designs used to elucidate meaningful relationships between mussels and suitable habitat, including the number of samples collected, how samples are processed, and statistical considerations for nonparametric data.

In this study we tested the strength of associations between properties of streambed substrate composition, including bulk density, porosity, sediment sorting, the percentage of fine sediments, and mean particle size, and the distribution of individual mussel

species at 30 stream sites in the Apalachicola, Chattahoochee, and Flint (ACF) basin of the eastern Gulf of Mexico. Currently, over 60% of the mussel fauna of the basin are either endangered (four species federally listed), threatened (two species federally listed), of special concern, extirpated, or extinct. Only 13 of the 33 species known from the ACF basin have populations regarded as stable (Brim Box and Williams, in press). Erosional sediments were implicated early on (van der Schalie 1938a, Clench 1955) for mussel declines in the basin, but most of that information is based on anecdotal evidence. The objective of this study was to quantify relationships between streambed substrate composition and the distribution of individual unionid mussel species in the ACF basin. We also determined whether species could be regarded as habitat generalists or specialists based on streambed substrate composition.

Methods

Mussels and sediments were collected from 30 sites in the Coastal Plain Physiographic Province of the ACF basin (Fig. 3-1). These 30 sites represent a subset of 150 ACF tributary streams originally surveyed for mussels from 1991 to 1992 (Brim Box and Williams, in press). Measurements of species diversity at each of the original 150 sites indicated that these sites included a wide range of mussel richness. Therefore, each of the original 150 sites was assigned to one of six species richness categories (very low = 1-2 species; low = 3-4 species; medium = 5-6 species; medium high = 7-8 species; high = 9-10 species; very high = 11-12 species). Sites that were not in the coastal plain or where no mussels were found were excluded from further consideration. From the remaining

Figure 3-1. Study area: Thirty sampling sites in the coastal plain of the Apalachicola, Chattahoochee, and Flint basin.

pool of 62 sites, five sites were randomly selected from each of the six species richness categories to be the 30 sites used in this study. At each of the 30 sites, a 100-meter reach was delineated and stratified for sampling into bank, slope, and channel habitats. These habitats were defined by a combination of physical and geomorphic attributes of the channel morphology. The bank habitat extended from the shoreline to the point in the channel where the depth began to increase, indicating the beginning of the slope habitat. The slope habitat ended where the gradient leveled out, indicating the beginning of the channel habitat. Visible changes in substrate (e.g., mud to sand) also were used to demarcate these habitats and generally coincided with changes in gradient. Previous sampling in the New River, Florida, a Suwannee River tributary that also drains into the Apalachicola Region, indicated that mussel species composition and densities differed significantly among these three habitats (J. Brim Box and L. Arvanitis, unpublished data).

Quadrats were used to collect samples of mussels and sediments from the bank, slope, and channel habitats. In each habitat, 32 quadrats (0.25 m^2) were selected randomly from a grid for collecting mussels. This number was based on a method from Downing and Downing (1992), given a 95% level of confidence and a precision of 20% of the true mean number of mussels per m^2 . All mussels falling within or touching the sides of the quadrats were placed into dive bags (noting quadrat number and habitat type), identified to species, and returned to the substrate.

At each site and each quadrat a 4.7 cm-diameter core was collected from the top 8.5 cm of sediment for determination of bulk density, porosity, and sediment particle size composition. Bulk density is the ratio of mass to volume (g/cm^3) of the bed material and

varies with composition and compaction of the sediments (Gordon et. al. 1992). Porosity is inversely related to bulk density and is the ratio, in percent, of the volume of void space to the total volume of the sample (Friedman 1992). We were unable to collect sediment cores from 195 quadrats that contained predominantly rock, and were unable to sieve 24 additional samples because of processing errors; therefore our total sample size was limited to 2661 quadrats.

There are no standard methods for characterizing sediments in freshwater streams in ecological studies (Bovee 1982, Gordon et al. 1992), but samples typically are divided into a set of particle-size categories, and the relative proportion (by weight) in each of these categories is measured. In this study, each quadrat sample was divided into 19 sediment particle-size categories that corresponded to 0.5 phi intervals of the Wentworth scale (Wentworth 1922), and included pebble to clay-sized particles. The choice of particle size categories was guided by standard methods of fluvial geomorphology (Mudroch and Azcue 1995) and to avoid the lack of resolution that can occur with fewer size categories. The composition of sediment particle sizes larger than silt was determined using a series of nested sieves (Folk 1980). The amount of silt and clay (i.e., fine sediments < 0.063 mm) in each sample was determined by pipette analysis (Folk 1980).

Statistical parameters of grain size are typically derived from a cumulative frequency plot or measures of moments calculated from the weight of sediment in each size class (Lindholm 1987, Gordon et al. 1992). In this study, we back-calculated the number of particles present in each of the 19 size classes by assuming the density of each particle

was approximately 2.65 g/cm^3 (the approximate density of quartz and sandy, siliceous particles with little organic matter), and that each particle was spherical. These estimates were then used to determine the mean particle size, sorting, and percentage of fine sediments of each sediment core sample, by using a method of moments derived for grain-size calculation (Lindholm 1987). Sorting, defined as the standard deviation of each core divided by the mean particle size (Lindholm 1987), is a measure of the spread of particle sizes in the substrate. Sorting classes usually range from very well sorted to very poorly sorted (Gordon et al. 1992).

Species-specific associations between mussels and sediment were explored statistically by testing whether the presence of mussels was independent of streambed substrate properties, including bulk density, porosity, sorting, mean particle size, and percentage of fine sediments. Presence was analyzed instead of mussel density owing to the low number of mussels typically found in each 0.25 m^2 quadrat. In each analysis the number of quadrats in which mussels were present was computed for each of 10 categories of streambed substrate properties. The boundaries of these categories were defined by 10 equally spaced percentiles (i.e., 10%, 20%, etc.) of the observed distribution of each substrate attribute. In this way all categories included an approximately equal number of quadrats (264 or 265 quadrats). Under the null hypothesis of independence between mussels and substrate properties, the number of quadrats with mussels present was expected to be equal in each of the 10 categories. Departures from this equiprobable (null) model were tested using the deviance test statistic, D , for binomial responses (Collett 1991):

$$D = 2 \sum_i (y_i \log \left(\frac{y_i}{\hat{y}_i} \right) + (n_i - y_i) \log \left(\frac{n_i - y_i}{n_i - \hat{y}_i} \right)).$$

Here, n_i is the number of quadrats in the i th substrate property category; y_i and $\hat{y}_i$ are the observed and expected numbers of quadrats with mussels present in the i th substrate category. Under the equiprobable model, $\hat{y}_i = n_i \hat{p}$, where $\hat{p}$ is the maximum-likelihood estimate of a constant probability of occurrence of mussels in substrates of different compositions, i.e.,

$$\hat{p} = \frac{\sum_i y_i}{\sum_i n_i}$$

Like Pearson's χ^2 statistic, the distribution of the deviance is approximately χ^2_v (where v = number of substrate property categories minus one) assuming: 1) the equiprobable model is correct, 2) the number of quadrats in each substrate property category is reasonable large, and 3) the expected number of quadrats with mussels present is not too small (Collett 1991). Ten substrate property categories were used to ensure that assumptions two and three were satisfied for all species of mussels found in at least 1% (=26) of the 2661 quadrats. Under the equiprobable model, the 26 quadrats were expected to be divided equally among the 10 bulk substrate property categories and, on average, each category was expected to include about three quadrats with mussels ($\hat{y}_i = 2.6$). Simulations have shown that the distribution of deviance and Pearson's test statistics are nearly χ^2_v when $\hat{y}_i$ is at least two (Read and Cressie 1988). Therefore, for each of the mussel species found in at least 1% of the samples, observed differences in the presence of mussels at different levels of substrate properties were considered to have more than chance outcomes (i.e, to have statistical significance) when the deviance test statistic D exceeded the chi-squared critical value $\chi^2_v(\alpha)$.

The categories used to define the 10 equally spaced percentiles of each of the five substrate attributes were also used to examine relationships among these five sediment properties. Spearman's rank correlation coefficient (ρ) was used to determine whether these five properties were correlated. An alternative form of Spearman's rank correlation coefficient, the Hotelling-Pabst test (Conover 1971), was used to test the null hypothesis that substrate attributes were mutually independent. The alternative hypothesis of this two-tailed test is that there is a tendency for a substrate attribute to be either positively (or negatively) correlated with one of the other four substrate properties.

Results

Significant correlations were found among the five substrate properties measured (Table 3-1). As expected, bulk density was almost perfectly inversely related to porosity (Fig. 3-2); to reduce redundancy, only porosity was used in further analyses. Substrate samples fell into three broad categories: 1) substrates that were well sorted, consisting of small particle sizes (including a high percentage of fine sediments), with high porosity (Fig 3-3a, b, c), 2) substrates that were moderately sorted, with larger particle sizes (i.e., sand), moderate porosity, and a low percentage of fine sediments (Fig 3-4 a, b, c, d), and 3) substrate that were poorly sorted, consisting of both large and small particles with a high percentage of fine sediments present, and low porosity (Fig. 3-4 a, b, c, d). In this study, samples with large mean particle sizes were either inundated with fine sediments (Fig. 3-5a) or lacked a high percentage of fines (Fig. 3-5b). In the former case, those substrates were also poorly sorted with low porosity. If samples were well sorted, then

Table 3-1. Spearman rank values (ρ) for correlations of streambed substrate properties. P-values are given in parenthesis, and relationships were considered significant at the $\alpha = 0.05$ level.

sediment property	porosity	sorting	percent fines	mean particle size
porosity		-0.97 ($p < 0.001$)	0.67 ($p=0.033$)	-0.99 ($p < 0.001$)
sorting	-0.99 ($p < 0.001$)		0.27 ($p = 0.446$)	0.73 ($p=0.016$)
percent fines	0.76 ($p = 0.111$)	0.27 ($p = 0.446$)		-0.99 ($p < 0.001$)
mean particle size	-0.89 ($p = 0.005$)	0.98 ($p < 0.001$)	-0.99 ($p < 0.001$)

Figure 3-2. Scatter plot of 2,661 substrate samples. This plot demonstrates the inverse relationship between sediment bulk density and sediment porosity.

Figure 3-3. Correlations between streambed substrate properties: a) mean particle size and sediment sorting, b) porosity and sediment sorting, and c) porosity and mean particle size.

Figure 3-4. Correlations between streambed substrate properties: a) mean particle size and porosity, b) mean particle size and sediment sorting, c) porosity and percent fine sediments, and d) sediment sorting and percent fine sediments.

Figure 3-5. Cartoon depiction of the three main substrate categories found in this study.

samples with smaller particle sizes had higher porosities than samples with large mean particle sizes (Fig. 3-5c). If samples were poorly sorted, than porosity was lowest in substrates that contained both large and small particles.

A total of 2,563 mussels were collected in the 2661 quadrat samples of the ACF basin (Table 3-2). Of the 25 species of mussels collected, the majority were Elliptio (70%) or Villosa (16%). Nine mussel species, Elliptio complanata, E. crassidens, E. icterina, Toxolasma paulus, Unio merus carolinianus, Utterbackia imbecillis, Villosa lienosa, V. vibex, and V. villosa were found in at least 1% of the 2661 quadrats. These nine species were used to test whether mussel presence was associated with the following differences in sediment composition: porosity, mean particle size, percentage of fine sediments, and sediment sorting.

This study of mussels and microhabitat in the ACF basin revealed statistically significant associations between mussel presence and substrate properties for eight of the nine most abundant species encountered (Table 3-3). Six species were most common in substrates with high porosity: Elliptio complanata, E. icterina, Toxolasma paulus, Utterbackia imbecillis, Villosa vibex and V. villosa (Table 3-4).

A significant difference between mussel presence and sediment sorting was detected for six of the nine most abundant mussel species: Elliptio complanata, E. crassidens, Villosa lienosa, Toxolasma paulus, Unio merus carolinianus, and Utterbackia imbecillis (Table 3-3). Of these six species, only E. crassidens was more common in poorly- sorted substrates; the other five species were more common in well-sorted substrates (Table 3-4).

Table 3-2. Number of mussels collected and number of quadrats with mussels in 2,661 quadrat samples of sites within the ACF basin.

Species	Common name	Number of mussels	Number of quadrats with mussels
<u>Anodonta sp.</u>		1	1
<u>Anodontoides radiatus</u>	Rayed creekshell	3	3
<u>Elliptio arcata</u>	Delicate spike	8	5
<u>Elliptio complanata</u>	Eastern elliptio	1,495	458
<u>Elliptio crassidens</u>	Elephant ear	70	30
<u>Elliptio icterina</u>	Variable spike	195	88
<u>Elliptio purpurella</u>	Inflated spike	20	14
<u>Elliptio sp.</u>		21	16
<u>Lampsilis claibornensis</u>	Southern fatmucket	6	5
<u>Lampsilis subangulata</u>	Shinyrayed	6	6
<u>Medionidus penicillatus</u>	pocketbook	6	3
<u>Megalanaia nervosa</u>	Gulf moccasinshell	1	1
<u>Pleurobema pyriforme</u>	Washboard	17	12
<u>Pyganodon grandis</u>	Oval pigtoe	1	1
<u>Quincuncina infucata</u>	Giant floater	13	11
<u>Strophitus subvexus</u>	Sculptured pigtoe	4	3
<u>Toxolasma paulus</u>	Southern creek mussel	97	69
<u>Unio merus carolinianus</u>	Iridescent lilliput	52	37
<u>Utterbackia imbecillis</u>	Florida pondhorn	82	47
<u>Utterbackia peggyae</u>	Paper pondshell	41	20
<u>Villosa lienosa</u>	Florida floater	266	121
<u>Villosa vibex</u>	Little spectaclecase	91	57
<u>Villosa villosa</u>	Southern rainbow	60	43
<u>Villosa sp.</u>	Downy rainbow	3	3
Unidentified		4	2
Total		2,563	

Table 3-3. Tests of lack of associations between mussel presence and five streambed substrate properties. P-values are associated with the deviance test statistic.

	Bulk density	Porosity	Mean particle size	Sorting	Percent fines
Species	P-value	P-value	P-value	P-value	P-value
<u>Elliptio complanata</u>	<0.001	<0.001	0.2	<0.001	<0.001
<u>Elliptio crassidens</u>	0.23	0.29	<0.01	<0.01	0.15
<u>Elliptio icterina</u>	0.04	0.04	0.19	0.45	0.31
<u>Toxolasma paulus</u>	0.03	0.03	0	<0.001	<0.001
<u>Unio merus carolinianus</u>	0.57	0.62	0.06	0.05	0.32
<u>Utterbackia imbecillis</u>	0.02	0.02	0.28	0.04	0.03
<u>Villosa lienosa</u>	0.12	0.14	<0.001	<0.001	<0.001
<u>Villosa vibex</u>	0.05	0.05	<0.001	0.1	0.08
<u>Villosa villosa</u>	<0.01	<0.01	0.85	0.16	0.06

Table 3-4. Descriptions of the relationships between the nine most abundant species in this study, and the four substrate properties tested. Not significant means P-values > 0.05 associated with the deviance test statistic.

Species	Porosity	Sorting	Fines (%)	Mean size
<u>Elliptio complanata</u>	high	well	low	not significant
<u>Elliptio crassidens</u>	not significant	poor	not significant	large particles
<u>Elliptio icterina</u>	not significant	not significant	not significant	not significant
<u>Villosa lienosa</u>	high	well	high	small particles
<u>Villosa vibex</u>	high	not significant	high	small particles
<u>Villosa villosa</u>	high	not significant	low	not significant
<u>Toxolasma paulus</u>	high	well	low	intermediate sizes
<u>Uniomereus carolinianus</u>	not significant	well	not significant	intermediate sizes
<u>Utterbackia imbecillis</u>	high	well	low	not significant

A significant difference between mussel presence and the percentage of fine sediments was detected for six species: Elliptio complanata, Toxolasma paulus, Utterbackia imbecillis, Villosa lineosa, V. vibex, and V. villosa (Table 3-3). Villosa lienosa and Villosa vibex were most common in substrates with a high percentage of fine sediments present, while the other four species were most common in substrates with a low percentage of fine sediments (Table 3-4).

Mean particle size had the least predictive power of the four substrate properties examined (Table 3-3). A significant difference between mussel presence and particle size was detected for Elliptio crassidens, Villosa lienosa, V. vibex, Toxolasma paulus, and Unio carolinianus. Of these species, E. crassidens was most common in substrates consisting of predominantly larger particle sizes, V. lienosa and V. vibex were most common in small particle sizes, and T. paulus and U. carolinianus were most common in substrates consisting of particles of intermediate sizes (Table 3-4).

Discussion

This study of mussels and microhabitat in the ACF basin revealed statistically significant associations between mussel presence and substrate properties for eight of the nine most abundant species encountered. Elliptio icterina was the only species that was not associated with any of the four substrate properties tested. This was not surprising, given that E. icterina has been reported from a variety of substrates in slight to moderate current, and in streams, lakes, reservoirs, ponds, and large rivers (Johnson 1970, Heard 1979). In the ACF basin, E. icterina was found in a variety of habitats, including sand,

gravel, and silt deposits between rocks (Jenkinson 1973). Based on the results of this study, *E. icterina* can be considered a habitat generalist.

Eight species (*Elliptio complanata*, *E. crassidens*, *Toxolasma paulus*, *Uniomereus carolinianus*, *Utterbackia imbecillis*, *Villosa lixiosa*, *V. vibex*, and *V. villosa*) were most common in one of four broad substrate types; *E. complanata*, *U. imbecillis*, and *V. villosa* were most common in highly porous, well-sorted substrates, with a low percentage of fines. *Villosa lixiosa* and *V. vibex* were most common in highly porous, well-sorted substrates, with a high percentage of fines. *Toxolasma paulus* and *U. carolinianus* were most common in well-sorted substrates of intermediate particle sizes, and *E. crassidens* was most common in poorly-sorted substrates with large particle sizes.

Elliptio complanata, *U. imbecillis*, and *V. villosa* were more common in quadrats with a low percentage of fine sediments. In the ACF basin *E. complanata* was reported from sites with sand and limestone rock substrates, sand and fine sediments, and sand (Brim Box and Williams 1999). In South Carolina, *E. complanata* densities were significantly greater in sand and sand/mud substrates than in sand/gravel substrates (Leff et al. 1990). However, in New York it was reported in a wide variety of substrates except soft mud (Clarke and Berg 1959). Kat (1982) found that *E. complanata* grew slower in muddy substrates, and speculated that these fine particle sizes may result in reduced feeding efficiencies through interfering with filter feeding. The results of this study are consistent with previous observations that this species is less common in substrates that contain a high percentage of fine sediments.

The occurrence of Utterbackia imbecillis and Villosa villosa also decreased progressively as the percentage of fine sediments per quadrat increased. This was unexpected, in that previous studies have consistently documented the presence of U. imbecillis in slackwater areas in mud or muddy sand (Clench and Turner 1956, Johnson 1970, Brim Box and Williams in press). In addition, U. imbecillis is thin-shelled, unsculptured, and with no dentition, which are three morphological characters thought to increase buoyancy in fine sediments (Watters 1994b). Villosa villosa had previously been reported from muddy waters (Johnson 1970), mud and muddy sand (Heard 1979), murky water and muddy substrates (Butler 1989), and sandy substrates (Brim Box and Williams 1999). There was not a significant relationship between the presence of Elliptio complanata, U. imbecillis, or V. villosa and particle size, and it appears these three species can be found in a variety of substrate sizes excluding fine sediments, as long as these substrates are well sorted with corresponding high porosities. Based on the results of this study, Elliptio complanata, U. imbecillis, and V. villosa can be considered habitat specialists.

Villosa lienosa and V. vibex were most common in high porous, well-sorted substrates, and were the only species that were most common in substrates with a high percentage of fine sediments present. This is consistent with descriptive studies, in which V. lienosa was found in soft mud (Jenkinson 1973), in muddy substrates in detrital areas (Clench and Turner 1956), and in substrates ranging from mud to sand and clay (Brim Box and Williams 1999). Villosa vibex has also been reported from mud or soft sand, especially in detrital areas (Johnson 1970, Heard 1979), and sandy mud bottoms

(Williams and Butler 1994). These species can also be considered habitat specialists, because they were most common in well-sorted substrates with high porosity, a high percentage of fines, and small mean particle sizes.

Toxolasma paulus and Uniomerus carolinianus were most common in well-sorted substrates of intermediate particle sizes. In the ACF basin, T. paulus was reported from a wide variety of habitats, from fine sand to rocky substrates (Jenkinson 1973), in mud and sand (Heard 1979), and sand and rock, sand and clay, and sandy substrates (Brim Box and Williams 1999). Little is known about the habitat preferences of U. carolinianus, other than that it has been found in muddy sand and sand in slight current (Heard 1979), and in substrates ranging from sand and clay to sand and limestone rock (Brim Box and Williams 1999). In this study, although T. paulus was most common in substrates of intermediate particle sizes (i.e., sands), these substrates were also well sorted with a low percentage of fines present. In contrast, there was not a significant relationship between the presence of U. carolinianus and porosity or percentage of fine sediments present. This suggests that this species is less habitat-specific than T. paulus, although it too was most common in well-sorted sediments of intermediate sizes.

Elliptio crassidens was the only species that was most common in poorly-sorted substrates with large particle sizes. In the ACF basin E. crassidens was found in mid-channel areas of moderate to strong currents, in substrates ranging from muddy sand, sand, to rock (Johnson 1970, Heard 1979, Brim Box and Williams in press). Elliptio crassidens, based on this study, can also be considered a habitat specialist.

This study suggests that individual mussel species can either be habitat specialists or generalists in regard to streambed substrate properties. That habitat preferences differed among species was not surprising, although specific examples of habitat requirements for individual species based on empirical studies are rare. Habitat requirements are usually based on observational or descriptive data (Clench and Turner 1956, Heard 1979), and the same species have been judged tolerant or intolerant to changes in sedimentation regimes in different studies (e.g., Stein 1972, Houp 1993). The species-level differences found between mussels and substrate properties in this study are consistent with the ambiguity concerning the relationship between mussels and micro-habitat descriptors. For instance, some studies suggested strong habitat specificity (Kat 1982, Leff et al. 1990), whereas others (Holland-Bartels 1990, Strayer et al. 1994, Layzer and Madison 1995) failed to find statistically significant relationships between mussels and habitat descriptors. Part of this ambiguity is also a result of the paucity of studies (e.g., Huehner 1987, Bailey 1989) that have empirically tested for species-specific habitat preference and specificity, although habitat-specific sampling is often required to determine invertebrate production and function in streams (Smock et al. 1992).

Substrate particle size has been considered an important micro-habitat descriptor when assessing associations between mussels and their physical habitats (Bronmark and Malmqvist 1982, Salmon and Green 1983, Leff et al. 1990), although meaningful relationships between unionid mussels and substrate composition have not always been found (Lewis and Riebel 1984, Strayer and Ralley 1993, Layzer and Madison 1995, Di Maio and Corkum 1995). For example, Strayer and Ralley (1993) concluded that

microhabitat-mussel associations, as estimated from discriminant analysis, were weak, and that larger spatial scales might be more useful in predicting mussel occurrence. They also suggested that descriptions of habitat based on fluvial geomorphology might be more informative. Others have suggested that substrate stability, not composition, is important in predicting mussel occurrence. In the Holston River, Virginia, the greatest species densities were associated with stable mixed sand, gravel, and pebble substrates (Neves and Widlak 1987). Freshwater mussels of the lower Cumberland River, Kentucky, were abundant only in stable habitats composed of gravel in firm sandy clay (Sickel 1982). Kat (1982) suggested that streambeds can be divided into high- and low-quality microhabitats. High-quality microhabitats are characterized by stable substrates, uncrowded conditions, and protection from scour; low-quality microhabitats are characterized by unstable substrates and a significant reduction of energy input available for growth and reproduction. Hydrologic variables such as the type of stream flow or shear stress, or macrohabitat descriptors such as stream size may be more useful than substrate composition in predicting mussel occurrence (Layzer and Madison 1995, Di Maio and Corkum 1995).

Although relationships among four substrate properties and nine mussel species were tested in this study, only one species (Toxolasma paulus) had a significant relationship with all four substrate properties. In addition, although Elliptio icterina was the third most common species collected, its presence was not significantly related to any of the four measures of substrate. Factors other than sediment composition are probably important in defining the physical habitat of E. icterina and other mussel species. For

example in Ohio, water velocity was a better predictor of the distribution of E. dilatata than sediment type (Huehner 1987), and in Great Lake tributaries E. dilatata was associated with streams that were considered hydrologically stable (Di Maio and Corkum 1995).

The lack of correlation between substrate particle size and mussel distributions in some studies may also be a result of inadequate sampling effort and improper substrate particle size analysis. Associations between substrate composition and the aquatic fauna are often evaluated based on a limited number of samples (e.g., 30) or particle-size classes (e.g., 6). One hundred to 300 samples may be necessary to characterize adequately the substrate at a particular site in rivers with spatially heterogeneous beds (Wolcott and Church 1991). In addition, in this study substrate size had the least predictive value of the five substrate properties originally measured. This is surprising, in that substrate size is one of the most important sediment characteristics and has a direct influence on sediment mobility (Hjulström 1935). Historically, relationships between benthic animals and substrate were based on sediment granulometry, and the main impact of streambed sedimentation on benthos was thought to be a disruption of the positive relationship between these animals and increasing substrate particles size (Waters 1995). Substrate heterogeneity was later considered more important than substrate particle size, because the abundance of aquatic insects was least in homogenous (i.e., well sorted) substrates, and greatest in heterogeneous gravel, pebbles, and cobbles (Minshall 1984). Minshall's (1984) hypothesis may not be true for unionid mussels. Five of the nine species tested were most common in well-sorted or homogenous substrates.

Mussels may be more common in well-sorted substrates because of the high porosity associated with well-sorted sediments. In this study, although two species were most common in fine sediments, six of the nine most common species were more common in high-porosity substrates than low-porosity substrates. None of the nine species tested was significantly more common in low-porosity substrates. This is consistent with Minshall's (1984) assertion that substrates consisting of gravel, pebble, and cobbles can have a high abundance of aquatic animals. Presumably, these substrates have fairly high porosities (as long as sands and fine sediments are absent), an observation consistent with the distribution of mussels in this study.

The effects of fine sediments on freshwater mussels have been well documented through descriptive studies (Ellis 1936, Chutter 1969, Stein 1972, Hartfield and Hartfield 1996, Neves et al. 1997). Excessive amounts of sediments, especially fine particles, that wash into streams can affect mussels in many ways. Larger particles can become surrounded or covered by finer sediments, and this embeddedness can reduce interstitial flow rates (Hamilton and Bergersen 1984). Silt and clay particles can clog the gills of mussels (Ellis 1936), interfere with filter feeding (Kat 1982, Aldridge et al. 1987), or affect mussels indirectly by reducing the light available for photosynthesis and the production of unionid food items (Davies-Colley et al. 1992, Kanehl and Lyons 1992). Erosional sediments were implicated early on in the disappearance of nearly all species of freshwater mussels in the main stem of the Chattahoochee River, which historically was one of the most productive sites for collecting mussels in the entire eastern Gulf of Mexico (Clench and Turner 1956, Brim Box and Williams in press). However, a positive

association was found between fine sediments and V. lienosa and V. vibex, two of the species that disappeared from the river. This suggests that factors other than changes in sediment composition were also responsible for eliminating the mussel fauna in the main stem of the Chattahoochee River. Some possibilities include increases in pollution and changes in hydrology induced by impoundments.

Although 25 species from 12 genera were collected in samples from the ACF basin, some mussels were not present in sufficient numbers to assess their association with sediment composition. Prior to this study we hypothesized that the mussel fauna of the ACF basin comprised fine-sediment tolerant and fine-sediment intolerant species, and that historical changes in sedimentation rates in the basin may have been responsible for the current rarity of fine-sediment intolerant species, including six that are federally threatened or endangered (USFWS 1998). We attempted to determine if the presence of five rare species (Anodontoides radiatus, Lampsilis subangulata, Medionidus penicillatus, Pleurobema pyriforme, Strophitus subvexus) varied significantly among different substrate properties; however, these five species were present in only 27 of the 2661 quadrats sampled. In future studies of mussel-sediment associations in the ACF basin, novel sampling designs are recommended to facilitate collecting rare species in greater numbers than those encountered in this study.

The results of this study suggest that mussel communities in the ACF basin are structured, in part, by properties of streambed substrate composition. Substrate porosity, sorting, and the percentage of fine sediments present were useful in elucidating meaningful relationships between mussel distributions and microhabitat. Substrate

particle size had the least predictive power of the five substrate properties measured.

These results suggest that the fouling of North American streams by erosional fine sediments may be a factor in the current decline of unionid mussels and should be explored as a causal factor of decline. In addition, because species may be habitat specialists or generalists with regard to streambed substrate properties, other ecological factors that may control mussel abundance and distribution, including the availability of host fish, may also control mussel community structure in the basin and should be examined.

CHAPTER 4

ROLE OF ECOLOGICAL FACTORS AT THREE PERSPECTIVES

Introduction

Freshwater bivalves are a highly specialized group of organisms, dominated by only a few taxonomic groups, including the Unionidae, an exclusively freshwater family whose greatest diversity (> 280 species) is found in North America. Freshwater mussels, in contrast to most marine bivalves, have highly specialized life histories, including a life stage called a glochidia that parasitises a fish host, undergoes metamorphosis, and drops off to become a free living juvenile mussel. The mussel/fish relationship is often species-specific, in that only certain fish species can serve as suitable hosts for a particular mussel species (Brunderman and Neves 1993, Haag and Warren 1997). Consequently, anthropogenic changes that affect either member in this relationship are likely to have a serious impact on the diversity and abundance of freshwater mussels.

Since the early part of this century, 7% of the native North American mussel fauna have become extinct, and an additional 72% of the fauna is considered endangered, threatened, or of special concern (Williams et al. 1993), making freshwater mussels one of the most imperiled faunas in North America (Master 1990). During this same period, 5% of the native North American fish fauna disappeared. An additional 364 species are considered endangered, threatened, or of special concern (Williams et al. 1989). Because these two faunas are inexorably linked, it seems reasonable to assume that the

disappearance of the host fish may also cause the extirpation of unionids from the same river reaches or entire river systems. Alternatively, the same environmental stresses (e.g., pollution, habitat alteration) may influence the abundance and distribution of fish and mussels independently but along the same environmental gradients. The purpose of this study was to evaluate the relative importance of fish and abiotic characteristics on mussel abundance and diversity.

Although freshwater mussels are a conspicuous component of many North American streams, and may exceed by an order of magnitude the biomass of other invertebrate taxa (Negus 1966), the biotic and abiotic attributes that define suitable habitats for individual mussel species are poorly understood. Ecosystem-level studies of freshwater mussels are few, and it is unclear what factors should be measured, and at what spatial and temporal scales, to elucidate meaningful relationships between mussels, suitable habitat, and community structure. It has been suggested that freshwater mussel communities are structured primarily by three types of environmental factors: 1) the distribution and availability of their host fish (Haag and Warren 1998, Watters 1995), 2) drainage-level characteristics (e.g., stream area) (Strayer 1983), and 3) micro-habitat variables (e.g., flow, depth, substrate composition) (Harman 1972, Leff et al. 1990, Layzer and Madison 1995). Much ambiguity remains over the role of these three groups in structuring freshwater mussel communities, and results are often contradictory concerning their usefulness in predicting the occurrence or density of unionids in streams (Holland-Bartels 1990, Bauer et al. 1991, Strayer and Ralley 1993, Di Maio and Corkum 1995).

To evaluate the usefulness of these three sets of environmental factors in explaining mussel community structure, quantitative samples of mussels, fish, and sediments were collected from 30 sites in the Apalachicola, Chattahoochee, and Flint (ACF) basin of Alabama, Florida, and Georgia. These rivers form one of the largest drainages in the eastern Gulf of Mexico and are known for their high level of endemism (Butler 1989). Although historically these rivers were known for their rich unionid mussel (Clench and Turner 1956) and fish (Yerger 1977) faunas, we know of no studies that have examined relationships between fish and mussel community structure in the basin. It also is not clear if mussel or fish community composition can be tied to physical habitat descriptors, such as streambed sediment composition, although in other river systems substrate composition was important in delineating suitable habitat for fish (Peters 1967, Berkman and Rabeni 1987) and other invertebrate taxa (Hynes 1960, Chutter 1969, Minshall 1984). The objective of this study was to correlate mussel and fish assemblage structures to each other and to macro- and micro-habitat descriptors.

Methods

Mussels, fish, and sediments were collected from 30 sites in the Coastal Plain Physiographic Province of the ACF basin (Fig. 3-1). These 30 sites represent a subset of 150 ACF tributary streams originally surveyed for mussels from 1991 to 1992 (Brim Box and Williams, in press). Measurements of species diversity at each of the original 150 sites indicated a wide range of mussel richness. Therefore, each of the original 150 sites was assigned to one of six species richness categories (very low = 1-2 species; low = 3-4 species; medium = 5-6 species; medium high = 7-8 species; high = 9-10 species; very

high = 11-12 species). Sites that were not in the coastal plain or where no mussels were found were excluded from further consideration. From the remaining pool of 62 sites, five sites were randomly selected from each of the six species richness categories to be the 30 sites used in this study.

At each of the 30 sites, a 100-m reach was delineated and stratified for sampling into bank, slope, and channel habitats. These habitats were defined by a combination of physical and geomorphologic attributes of the channel morphology. The bank habitat extended from the shoreline to the point in the channel where the depth began to increase, indicating the beginning of the slope habitat. The slope habitat ended where the gradient leveled out, indicating the beginning of the channel habitat. Visible changes in substrate (e.g., mud to sand) also were used to demarcate these habitats and generally coincided with changes in gradient. Previous sampling in the New River, Florida, a Suwannee River tributary that also drains into the Apalachicola Region, indicated that mussel species composition and density differed significantly among these three habitats (J. Brim Box and L. Arvanitis, unpublished data).

At each of the 30 sites, mussels, fish, and sediments were collected from the same 100-m reach. Upstream and downstream sections were blocked off using nets. Fish were collected using DC backpack electroshocking, one of the least selective of all active fishing gears (Reynolds 1983). This technique is especially effective in coastal plain streams that typically have high turbidity and multiple debris dams. Larger fish that could be identified to species were measured and released. Any fish that could not be identified in the field was preserved and identified in the laboratory. The total shock time

(sec) was recorded and used to calculate fish density per site, defined as the total number of fish captured per total shock time. Fish richness, abundance, and diversity (H') of each of the 30 sites were determined from these data. Some fish species were classified as obligate benthic species, based on either feeding or reproductive guilds, following Burkhead et al. (1997). Fish considered obligate benthic species based on feeding guild were benthic insectivores, whereas fish considered obligate benthic species based on spawning guild included buriers, attachers, and cavity nesters. These fish were subsequently referred to as obligate benthic feeders or obligate benthic breeders.

Quadrats were used to collect samples of mussels and sediments from the bank, slope, and channel habitats. In each habitat, 32 quadrats (0.25 m^2) were selected randomly from a grid for collecting mussels. This number was based on an estimate from Downing and Downing (1992), given a 95% level of confidence and a precision of 20% of the true mean number of mussels/ m^2 . All mussels falling within or touching the sides of the quadrats were placed into dive bags (noting quadrat number and habitat type), identified to species, and returned to the substrate. These data were used to determine mussel species richness, abundance, diversity (H'), and evenness (J') per site. Historical mussel richness for each site was also determined using museum records and prior survey data (Brim Box and Williams, in press). The percentage of rare mussels, those that had previously been considered endangered, threatened, or of special concern in any part of their range (Williams et al. 1993, Williams and Butler 1994, USFWS 1998), was also determined. The percent stream area sampled was calculated as the total

area sampled by the quadrats (24 m^2) divided by the stream area (width*length) and multiplied by 100.

At each site and quadrat a 4.7- cm-diameter core was collected from the top 8.5 cm of sediment for determination of bulk density, porosity, and sediment particle size composition. Bulk density is the ratio of mass to volume (g/cm^3) of the bed material and varies with composition and compaction of the sediments (Gordon et. al. 1992). Porosity is inversely related to bulk density and is the ratio, in percent, of the volume of void space to the total volume of the sample (Friedman 1992). We were unable to collect sediment cores from 195 quadrats that contained predominantly rock; therefore our total sample size was limited to 2685 quadrats.

There are no standard methods for characterizing sediments in freshwater streams in ecological studies (Bovee 1982, Gordon et al. 1992), but samples typically are divided into a set of particle-size categories, and the relative proportion (by weight) in each of these categories is measured. In this study, each quadrat sample was divided into 19 sediment particle-size categories that corresponded to 0.5 phi intervals of the Wentworth scale (Wentworth 1922, and included pebble to clay-sized particles. The choice of particle-size categories was guided by standard methods of fluvial geomorphology (Mudroch and Azcue 1995) and by the desire to avoid the lack of resolution that can occur with fewer size categories. The composition of sediment particle sizes larger than silt was determined using a series of nested sieves (Folk 1980). The amount of silt and clay (i.e., fine sediments $< 0.063 \text{ mm}$) in each sample was determined by pipette analysis (Folk 1980).

Statistical parameters of grain size are typically derived from a cumulative frequency plot or measures of moments calculated from the weight of sediment in each size class (Lindholm 1987, Gordon et al. 1992). In this study, we back-calculated the number of particles present in each of the 19 size classes by assuming the density of each particle was approximately 2.65 g/cm^3 (the approximate density of quartz and sandy, siliceous particles with little organic matter), and that each particle was spherical. These estimates were then used to determine the average particle size, standard deviation, sorting, skewness, and kurtosis of each sediment core sample, by using a method of moments derived for grain-size calculation (Lindholm 1987). Sorting, defined as the standard deviation of each core divided by the mean particle size (Lindholm 1987), is a measure of the spread of particle sizes in the substrate. Sorting classes usually range from very well sorted to very poorly sorted (Gordon et al. 1992). Skewness measures the asymmetry of the substrate distribution, ranging from strongly fine-skewed (positive skewness) to strongly coarse-skewed (negative skewness). Kurtosis measures the ratio between the sorting in the tails of the distribution and sorting in the central portion of the distribution (Lindholm 1987). The resulting distributions ranged from very platykurtic (flat peaked) to extremely leptokurtic (central portion is better sorted than the tails of the distribution).

Spearman's rank correlation coefficient (ρ) was used to determine whether substrate composition (as described by the above measures) and/or fish and mussel assemblage structure were correlated at the site level. An alternative form of Spearman's rank correlation coefficient, the Hotelling-Pabst test (Conover 1971), was used to test the null hypothesis that attributes of the fish and mussel communities (e.g., species richness and

species abundance) and substrate composition were mutually independent. The alternative hypothesis of this two-tailed test is that there is a tendency for an attribute of the fish community to be either positively (or negatively) correlated with an attribute of the mussel community, or for attributes of the fish and/or mussel community to be either positively or negatively correlated with attributes of the substrate.

To examine whether mussel or fish assemblage structure varied with stream size or subbasin, each stream was assigned a stream order (Shreve 1966), link magnitude (Knighton 1984), and hydrologic unit (USGS 1975a, b and c). Stream order was determined by designating each finger-tip tributary as first order (magnitude one), and each subsequent stream link as a magnitude equal to the sum of all the first-order segments that were tributary to it (Shreve 1966). Link magnitude measures the number of first-order segments above a specific point on a stream and is more sensitive than stream order for describing hydrological variability (Osborne and Wiley 1992, Haag and Warren 1998). Hydrologic units correspond to cataloging units shown on USGS hydrologic unit maps and are differentiated by physiography, climate, and hydrological characteristics (Frick et al. 1996). The eight units encompassed in this study were Chipola, Spring, Ichawaynochaway, Lower Flint, Kinchafoonee-Muckalee, Middle Flint, Lower Chattahoochee, and Middle Chattahoochee-Walter F. George Reservoir (USGS 1975a, b, and c).

Morisita's Index of Similarity (I_m) was used to measure the similarity of mussel community composition within stream order (Strahler 1957) and hydrologic unit. The index varies from 0 (no similarity) to 1.0 (complete similarity). Of the approximately

two dozen similarity indices available, Morisita's Index is the best overall measure of similarity for ecological use (Krebs 1989). Coefficients of variation were calculated to assess the variability of total mussel and fish abundance and richness in each stream order and hydrologic unit. First- and second-order streams were pooled for these analyses, because only two streams of each order were included in this study.

At least one species of rare mussel was found at 20 of the 30 study sites. A t-test was used to assess if the 10 sites where no rare mussels occurred differed in habitat quality from the other 20 sites, based on the percentage of fine sediments in the bank, slope, and middle habitats. Relationships between mussel and fish assemblage structure and macro- and micro-habitat variables, as described previously, were also examined for these 20 sites.

A sub-set of the data was also used to determine whether the abundance of a mussel species was related to the density of its host fish. Mussel-host fish relationships were examined if two criteria were met: 1) if the host fish for a mussel species had been reported in the literature and verified through laboratory experimentation and 2) if a mussel species accounted for > 2% of the total mussel abundance in this study. Fish density per site was defined as the number of fish of a particular species captured per total shock time. The hypothesis that mussel abundance increased with increasing host-fish density (a one-tailed test for positive correlation) was examined using Spearman's rank correlation analysis. The following mussel/host-fish relationships were examined: Elliptio icterina/Micropterus salmoides, Lepomis macrochirus (Keller and Ruessler 1997); Utterbackia imbecillis/M. salmoides, L. macrochirus (Keller and

Ruessler 1997); Villosa lienosa/M. salmoides, L. macrochirus (Keller and Ruessler 1997); Villosa vibex/M. salmoides, M. punctulatus, L. cyaneus (Haag and Warren 1997); Villosa villosa/M. salmoides (Keller and Ruessler 1997); Pleurobema pyriforme /Pteronotropis hypselopterus (O'Brien 1997).

Results

A total of 2, 662 mussels (Table 4-1) and 7, 665 fish (Table 4-2) were collected from the 30 sites. Of the 25 species of mussels collected, the majority were Elliptio (70%) or Villosa (16%). Nine mussel species, Elliptio complanata, E. crassidens, E. icterina, Toxolasma paulus, Unio merus carolinianus, Utterbackia imbecillis, Villosa lienosa, V. vibex, and V. villosa were found in at least one percent of the 2685 quadrats. Of the 54 species of fish collected, the majority were cyprinids (51%), centrarchids (18%), or percids (13%). Twenty species accounted for at least one percent of the fish surveyed (Table 4-2).

Significant relationships were detected between mussel assemblage structure and macro- and micro-habitat descriptors, fish assemblage structure and macro- and micro-habitat descriptors, but not between mussel and fish assemblage structures (Table 4-3). The percentage of rare mussels was positively correlated with link magnitude ($p = 0.463$, $p = 0.01$) and stream order ($p = 0.436$, $p = 0.016$). Fish richness also increased with increasing stream size. No trend was obvious, however, between mussel richness and stream size. The highest mussel and fish abundance occurred in the smallest streams. To determine if fish and mussel abundance

Table 4-1. Total number of each species of mussel collected from quadrats at 30 sites in the ACF basin from 1994 to 1995.

Species	Common Name	Total Number
<u>Anodonta sp.</u>		1
<u>Anodontoides radiatus</u>	Rayed creekshell	3
<u>Elliptio arctata</u>	Delicate spike	8
<u>Elliptio complanata</u>	Eastern elliptio	1,542
<u>Elliptio crassidens</u>	Elephant ear	70
<u>Elliptio icterina</u>	Variable spike	211
<u>Elliptio purpurella</u>	Inflated spike	21
<u>Elliptio sp.</u>		21
<u>Lampsilis claibornensis</u>	Southern fatmucket	6
<u>Lampsilis subangulata</u>	Shinyrayed pocketbook	7
<u>Medionidus penicillatus</u>	Gulf moccasinshell	12
<u>Megaloniaias nervosa</u>	Washboard	1
<u>Pleurobema pyriforme</u>	Oval pigtoe	18
<u>Pyganodon grandis</u>	Giant floater	1
<u>Quincuncina infucata</u>	Sculptured pigtoe	17
<u>Strophitus subvexus</u>	Southern creek mussel	4
<u>Toxolasma paulus</u>	Iridescent lilliput	99
<u>Unio merus carolinianus</u>	Florida pondhorn	53
<u>Utterbackia imbecillis</u>	Paper pondshell	83
<u>Utterbackia peggyae</u>	Florida floater	41
<u>Villosa lienosa</u>	Little spectaclecase	282
<u>Villosa vibex</u>	Southern rainbow	94
<u>Villosa villosa</u>	Downy rainbow	60
<u>Villosa sp.</u>		3
Unidentified		4
Total		2,662

Table 4-2. Total number of each species of fish collected from 30 ACF basin sites from 1994 to 1995.

Family	Species	Common name	Total number
Anguillidae	<u>Anguilla rostrata</u>	American eel	1
Aphredoderidae	<u>Aphredoderus sayanus</u>	pirate perch	231
Atherinidae	<u>Labidesthes sicculus</u>	brook silverside	409
Catostomidae	<u>Erimyzon sucetta</u>	lake chubsucker	7
Catostomidae	<u>Hypentelium etowanum</u>	Alabama hog sucker	6
Catostomidae	<u>Minytrema melanops</u>	spotted sucker	36
Catostomidae	<u>Moxostoma sp.</u>		9
Centrarchidae	<u>Ambloplites ariommus</u>	shadow bass	1
Centrarchidae	<u>Elassoma okefenokee</u>	Okefenokee pygmy sunfish	2
Centrarchidae	<u>Elassoma zonatum</u>	banded pygmy sunfish	17
Centrarchidae	<u>Lepomis auritus</u>	redbreast sunfish	305
Centrarchidae	<u>Lepomis cyanellus</u>	green sunfish	91
Centrarchidae	<u>Lepomis gulosus</u>	warmouth	41
Centrarchidae	<u>Lepomis macrochirus</u>	bulegill	353
Centrarchidae	<u>Lepomis marginatus</u>	dollar sunfish	21
Centrarchidae	<u>Lepomis megalotis</u>	longear sunfish	10
Centrarchidae	<u>Lepomis microlophus</u>	redear sunfish	30
Centrarchidae	<u>Lepomis punctatus</u>	spotted sunfish	474
Centrarchidae	<u>Micropterus punctulatus</u>	spotted bass	15
Centrarchidae	<u>Micropterus salmoides</u>	largemouth bass	26
Centrarchidae	<u>Pomoxis nigromaculatus</u>	black crappie	1
Cyprinidae	<u>Campostoma oligolepis</u>	largescale stoneroller	23
Cyprinidae	<u>Cyprinella venusta</u>	blacktail shiner	353
Cyprinidae	<u>Hybopsis winchelli</u>	clear chub	65
Cyprinidae	<u>Luxilus zonistius</u>	bandfin shiner	2
Cyprinidae	<u>Notemigonus crysoleucas</u>	golden shiner	40
Cyprinidae	<u>Notropis buccatus</u>	silverjaw minnow	232
Cyprinidae	<u>Notropis chalybaeus</u>	ironcolor shiner	10
Cyprinidae	<u>Notropis cummingsae</u>	dusky shiner	48
Cyprinidae	<u>Notropis harperi</u>	redeye chub	641
Cyprinidae	<u>Notropis longirostris</u>	longnose shiner	182
Cyprinidae	<u>Notropis petersoni</u>	coastal shiner	296

Table 4-2,continued

Family	Species	Common name	Total number
Cyprinidae	<u>Notropis texanus</u>	weed shiner	673
Cyprinidae	<u>Notropis winchelli</u>	clear chub	17
Cyprinidae	<u>Opsopoeodus emiliae</u>	pugnose shiner	76
Cyprinidae	<u>Pteronotropis euryzonus</u>	broadstripe shiner	109
Cyprinidae	<u>Pteronotropis hypselopterus</u>	sailfin shiner	1146
Cyprinidae	<u>Semotilus thoreauianus</u>	Dixie chub	6
Esocidae	<u>Esox americanus americanus</u>	redfin pickerel	43
Esocidae	<u>Esox niger</u>	chain pickerel	2
Fundulidae	<u>Fundulus lineolatus</u>	lined topminnow	2
Fundulidae	<u>Fundulus olivaceus</u>	blackspotted topminnow	18
Ictaluridae	<u>Ameiurus brunneus</u>	snail bullhead	46
Ictaluridae	<u>Ameiurus natalis</u>	yellow bullhead	13
Ictaluridae	<u>Ameiurus nebulosus</u>	brown bullhead	1
Ictaluridae	<u>Ameiurus serracanthus</u>	spotted bullhead	8
Ictaluridae	<u>Ictalurus punctatus</u>	channel catfish	1
Ictaluridae	<u>Noturus leptacanthus</u>	speckled madtom	93
Pecidae	<u>Percina nigrofasciata</u>	blackbanded darter	720
Percidae	<u>Etheostoma edwini</u>	brown darter	141
Percidae	<u>Etheostoma swaini</u>	gulf darter	106
Petromyzontidae	<u>Ichthyomyzon gagei</u>	southern brook lamprey	30
Poeciliidae	<u>Gambusia hobrooki</u>	eastern mosquitofish	212
Soleidae	<u>Trinectes maculatus</u>	hogchoker	3
Total			7,665

Table 4-3. Spearman rank values (ρ) for correlations of mussel assemblage structure with environmental factors representing three spatial scales (* denotes significance at $\alpha = 0.05$ level). Aspects of fish assemblage structure were also correlated with macro- and micro-habitat descriptors. Micro-habitat descriptors are average values per site.

Mussel assemblage					Fish assemblage				
	richness	abundance	diversity	percent rare	richness	abundance	diversity	percent feeders	percent breeders
Fish assemblage									
fish richness	0.05	-0.07	-0.05	0.02					
abundance	0.09	-0.07	0.04	-0.33					
diversity	-0.22	-0.23	0.04	-0.19					
percent feeders	0.04	0.2	0.03	0					
percent breeders	-0.07	-0.15	-0.26	0.21					
Macrohabitat									
link magnitude	0.04	-0.17	0.18	0.4631*	0.17	-0.33	0	0.14	0.29
stream order	-0.12	-0.31	0.07	0.4357*	0.02	-0.31	-0.06	0.06	0.27
Microhabitat									
percent fines	-0.6829*	-0.5193*	-0.34	-0.3713*	0.03	0.02	0.19	-0.03	0.05
mean particle size	0.4520*	0.34	0.12	0.23	0.09	-0.25	0.08	0	0.18
kurtosis	0.04	0.1	0.02	0.11	-0.05	0.33	-0.31	-0.13	0.12
skewness	0.04	-0.03	-0.06	-0.06	0.03	0.3	-0.15	-0.03	0.1
percent porosity	0.24	0.32	0.4018*	-0.03	-0.12	0.04	-0.14	0.4091*	-0.11
sorting	-0.24	-0.31	-0.29	0.07	0.33	-0.02	0.17	-0.5546*	0.26
bulk density	-0.24	-0.28	-0.4122*	-0.02	0.06	0.06	0.01	-0.3926*	0.13

decreased with stream size because of sampling effort (e.g., because 96 quadrats were sampled per site, larger streams had proportionally less area surveyed), correlation coefficients were calculated between mussel and fish abundance and either the percentage of stream area surveyed per site or shock time. These correlations were not significant, suggesting that the number of mussels and fish collected in this study were independent of area or time sampled.

The smallest streams were the least variable in fish abundance and richness, whereas the largest streams were the least variable in overall mussel richness and abundance (Table 4-4). Small (first and second order) and medium-sized (third order) streams were dominated by a single species, Elliptio complanata. This species accounted for 71% of the individuals collected in first/second order streams and 60% of the mussels collected in third-order streams. Species evenness (J') decreased from large to small streams. Larger streams (fourth and fifth order) were more diverse ($H' = 2.69$ for fifth order, 2.83 for fourth order) and even ($J' = 0.69$ for fourth order and 0.71 for fifth order) than third ($H' = 2.08$, $J' = 0.55$) or first/second ($H' = 1.74$, $J' = 0.43$) order streams. Fifth-order streams were the least similar to one another in mussel composition, which was very similar for all other stream orders (Table 4-5). Mussel assemblage structure within hydrologic units ranged from very similar in Chipola ($I_m = 0.91$) to dissimilar in Ichawaynachaway ($I_m = 0.25$).

Fish and mussel assemblage structure were correlated with several substrate properties (Table 4-3). Mussel diversity was positively correlated with porosity ($\rho =$

Table 4-4. Coefficients of variation used to assess mussel and fish richness and abundance. Variation per stream order was interpreted as $cv < 25\%$ = unvariable; $26\% < 50\%$ = slightly variable; $51\% < cv < 75\%$ = moderately variable; $cv > 76\%$ = highly variable.

Stream Order	Coefficient of Variation (%)			
	Mussel abundance	Mussel richness	Fish abundance	Fish richness
1-2	95	43	63	13
3	153	59	90	49
4	111	40	75	24
5	78	26	104	35

Table 4-5. Similarity of mussel assemblage structure, based on Morisita's Index (I_m) values, within each stream order and hydrological unit. The index ranges from 0 (no similarity) to 1.0 (complete similarity).

Stream Order	Morisita's Index (I_m)
1-2	0.71
3	0.83
4	0.76
5	0.11
Hydrologic Unit	Morisita's Index (I_m)
Chipola	0.91
Ichawaynachaway	0.25
Kinchafoonee	0.59
Lower Chattahoochee	0.86
Middle Chattahoochee	0.31
Middle Flint	0.60
Spring	0.60
Upper Flint	0.00

0.4018, $p = 0.0277$). Mussel richness was negatively correlated with the percentage of fine sediments ($\rho = -.6829$, $p = 0.0434$), and positively correlated with mean particle size ($\rho = 0.4520$, $p = 0.0122$). Mussel abundance was negatively correlated with the percentage of fine sediments ($\rho = -0.5193$, $p = 0.0033$). The percentage of obligate benthic feeders (but not breeders) was negatively correlated with sediment sorting ($\rho = -0.5546$, $p = 0.0015$) and bulk density ($\rho = -0.3926$, $p = 0.0319$), and positively correlated with porosity ($\rho = 0.4091$, $p = 0.0248$).

At the 20 sites where at least one species of rare mussel occurred, a significant positive correlation ($\rho = 0.5521$, $p = 0.0116$) was found between the presence of rare mussels and obligate benthic breeders. Fish richness was positively correlated with mussel richness ($\rho = 0.5933$, $p = 0.0058$) and sediment sorting ($\rho = 0.4502$, $p = 0.0464$). Mussel diversity was negatively correlated with bulk density ($\rho = -0.5027$, $p = 0.0239$). These 20 sites also had significantly less fine sediments present (t-test, $p < 0.05$) in all three habitats (bank, slope, middle) than at the other 10 sites.

Mussel species used in this study to test host fish/mussel relationships employed one of three reproductive strategies to attract potential host fish. Villosa lienosa, V. vibex and V. villosa were considered displaying host specialists. Elliptio icterina and Pleurobema pyrifforme were considered nondisplaying host specialists, and Utterbackia imbecillis was considered a host generalist. The abundance of only U. imbecillis was positively correlated to the density of its host fish (Table 4-6).

Table 4-6. Correlations of mussel abundance with fish density (* significant correlation at $\alpha = 0.05$).

Mussel species	Fish species	ρ	p
Displaying host specialists			
<u>Villosa lienosa</u>	<u>Micropterus salmoides</u> , <u>Lepomis macrochirus</u>	0.14	0.62
<u>Villosa vibex</u>	<u>Micropterus salmoides</u> , <u>M. punctulatus</u> , <u>Lepomis cyanellus</u>	0.31	0.33
<u>Villosa villosa</u>	<u>Micropterus salmoides</u>	0.34	0.45
Nondisplaying host specialists			
<u>Elliptio icterina</u>	<u>Micropterus salmoides</u> , <u>Lepomis macrochirus</u>	0.33	0.24
<u>Pleurobema pyriforme</u>	<u>Pteronotropis hypselopterus</u>	0.22	0.6
Host generalists			
<u>Utterbackia imbecillis</u>	<u>Micropterus salmoides</u> , <u>Lepomis macrochirus</u> , <u>Notemigonus crysoleucas</u>	0.82	0.0254*

Discussion

Stream Size

Small and medium-sized streams were dominated by a single species, Elliptio complanata. This species accounted for 71% of the individuals collected in first/second order streams and 60% of the mussels collected in third-order streams. Not surprisingly, species evenness also decreased from large to small streams. Larger streams (fourth and fifth order) were more diverse and even than third or first/second order streams. Therefore, the high level of similarity between small and medium-sized streams in this study can partially be explained by the influence of a single, abundant species. These results differ from what has been reported from other studies. In northwestern Alabama, the mussel faunas of large stream sites were similar whereas the faunal composition of headwater sites was variable, especially for sites in different drainages (Haag and Warren 1998). The variability could not be explained merely by host-fish availability or habitat. Differences in mussel community structure in southern Michigan streams were attributed to underlying geological differences that caused variability in channel geomorphology among similar-sized streams (Strayer 1983).

The percentage of rare mussels increased with link magnitude and stream order and was attributed to species replacement rather than addition, because no significant relationship was found between mussel richness and stream size. Freshwater mussels probably evolved from marine ancestors and moved upstream, and thus species richness is thought to increase from the headwater to the mouth (Vannote et al. 1980). Mussel richness increased downstream in other studies due to species addition (van der Schalie

1938b, Cvancara 1970, Haag and Warren 1998). It is not clear why species replacement rather than addition occurred downstream in this study. Fish richness in this study did increase with stream size, an observation consistent with other studies in which increased species richness was due to a combination of species replacement and addition (Sheldon 1968, Edds 1993, Paller 1994).

Substrate

Mussel community structure, including diversity, richness, and abundance, was correlated with aspects of substrate composition. For instance, mussel diversity was positively correlated with porosity. Although the effects of deposited sediment on lotic habitats have been well documented for other faunal groups, especially fish (Peters 1967, Muncy et al. 1979, Berkman and Rabeni 1987), porosity has seldom been used to describe the impacts of sedimentation on stream faunas. This is surprising, in that much of the impact of deposited sediments on aquatic faunas relates to the filling of interstitial spaces by fine sediments, and porosity is a measure of inter-particle space (Friedman et al. 1992). Porosity was also negatively correlated with sediment sorting ($\rho = -0.5898$, $p = 0.0006$). This is not surprising, because sorting measures the spread of particle sizes in the substrate (Gordon et al. 1992), and substrates with low porosity and high sorting may indicate that interstitial pore spaces are filled with fine sediments. This hypothesis is supported, albeit indirectly, by the observation that mussel richness and abundance decreased as the percentage of fine sediments increased per site. Although there has been much anecdotal information linking increased fine sediment production to changes in freshwater mussel populations (Ellis 1931, van der Schalie 1938a, Clench 1955, Stein

1972, Bogan 1993, Williams and Neves 1995), definitive studies linking the two are lacking (Brim Box and Mossa in press). However, it is possible that habitat suitability for mussels is partly defined by the quality of the interstitial space, as it is for speleophilic fish (Balon 1975) and their fry (Bustard and Narver 1975, Hillman et al. 1987).

Fish and mussel community structure in this study were closely related to streambed substrate composition. Substrate properties, including grain size, provided little predictive information about mussel assemblages in other studies (Layzer and Madison 1995, DiMaio and Corkum 1995, Haag and Warren 1998). The lack of association between mussel community structure and micro-habitat variables in previous studies may be related to difficulties associated with identifying and quantifying sediment loads, both natural or human-induced, and quantifying the subsequent impacts on unionid mussels. It is often not clear what physical properties of the streambed are important to measure, and as a result, the same mussel species have been judged tolerant or intolerant in different studies (e.g., Stein 1972, Houpp 1993). In addition, conventional measurements of water velocity, depth, substrate composition, and other micro-habitat variables have not always provided the information needed to predict the occurrence or density of unionids in streams (Holland-Bartels 1990, Strayer and Ralley 1993, Strayer et al. 1994). Part of the problem relates to the sampling designs used to survey mussel populations and their habitats. It is often difficult to devise a sampling scheme that accounts for differences in the spatial heterogeneity of mussels and habitat-related variables. In addition, although much of the literature on freshwater mussels, sediment transport, and channel change is based on qualitative or anecdotal information, rigorous and sophisticated sampling

methods must be adopted to clarify relationships between these elements. Our ability to correlate mussel assemblage structure in this study to aspects of substrate composition may be related to both the number of samples collected ($> 2,500$) and sediment size fractions analyzed (19). Dividing substrate samples into too few particle categories can obscure relationships between aquatic biota and substrate composition, and collecting too few samples inhibits the ability to draw meaningful inference between mussels and micro-habitat variables (Brim Box and Mossa 1999).

Fish

Freshwater mussel assemblage structure in this study was closely related to both macro- and micro-habitat descriptors, but was poorly correlated to fish assemblage structure. These results differ from several other studies that found aspects of the fish and mussel assemblage to be closely linked (Watters 1992, Haag and Warren 1998). In Ohio River tributaries mussel distribution and diversity were closely related to the distribution and diversity of fish (Watters 1992). Aspects of the fish and mussel faunas were correlated in two Black Warrior River tributaries, because the streams were relatively unmodified by humans (Haag and Warren 1998). Similarly, in this study, when the 10 sites that contained no rare mussels were removed from analyses, significant relationships were found between the percentage of rare mussels at the remaining 20 sites, the percentage of obligate benthic breeders, and fish richness. These relationships were not significant when all 30 sites were included. Because freshwater mussels are sensitive to water quality and/or habitat degradation (Keller and Zam 1991, Goudreau et al. 1993, Jacobson et al 1993), the lack of rare mussels at these sites suggests that significant

habitat degradation has occurred. This is supported by the fact that the 10 sites with no rare mussels also contained a significantly higher percentage of fine sediments than the other 20 sites. However, there was no attempt made in this study to score water or habitat quality quantitatively at each site, other than in respect to substrate composition. Further studies are needed to test the hypothesis that the lack of rare mussels at sites where they historically occurred can be used as a quantitative tool for assessing habitat degradation.

The percentage of benthic obligate feeders was positively correlated with sediment porosity and negatively correlated with sediment sorting. The results of this study suggest that the distribution of obligate benthic fish species in the ACF basin may be partially limited by substrate quality, as measured by porosity, sediment sorting, and the percentage of fine sediments present. In northeast Missouri, the abundance of fish classified as benthic insectivores decreased as the percentage of fine sediments increased (Berkman and Rabeni 1987). In the Etowah River drainage of northern Georgia, 80% of the imperiled fish fauna was comprised of obligate benthic species (i.e., species that spawn, feed, or shelter on the stream bottom), and elevated sedimentation was considered the primary source of degradation to benthic habitats (Burkhead et al. 1997). The tricolor shiner, Cyprinella caerulea, a crevice spawner, suffered reduced number of spawns and number of propagules spawned when exposed to increased levels of suspended sediments (Burkhead and Jelks 1998).

Five of the 30 sites surveyed are directly below small dams. At three of these sites a large number of mussels (> 350) and fish (> 400) were collected. At the fourth site, 5 mussels and 433 fish were collected, whereas at the fifth site, a moderate number of

mussels (197) and fish (120) were found. One site sits on the fall line between the Coastal Plain and Piedmont physiographic provinces and is in the Upper Flint hydrologic unit, one site is in the Chipola hydrologic unit, and the other three sites are in the Middle Flint hydrologic unit. These streams range in size from first to fourth order. Because of the disparity in size and location of these streams within the ACF basin, the large number of mussels and/or fish found at these sites is probably a result of their proximity to these small dams. These results are unexpected, in that dams, both large (Williams et al. 1992) and small (Watters 1996), often reduce mussel diversity and abundance through fluctuating flow regimes, scour, dissolved oxygen sags, water temperature changes, and changes in the fish fauna (Neves et al. 1997). Numerous detrimental effects on fish downstream from dams have also been documented (Petts 1984, Ligon et al. 1995). For example, in the Etowah River in northern Georgia, only five species of fish, including one nonindigenous to the river, were found below Allatoona Reservoir, and the ichthyofauna did not fully recover for 64 river km below the dam (Burkhead et al. 1997). The exact factors controlling the local faunal structures at these sites are unclear, including whether the large number of potential host fish present enhanced the reproductive success of unionid mussels. Alternatively, mussels and fish were simply responding similarly to the same local, environmental factors.

Mussel/Host-Fish Relationships

It has often been stated that freshwater mussels owe their distributional patterns to the superimposed range, abundance, or density of their host fish. Significant relationships between the abundance of host fish and mussels were found for two of six

mussel/fish pairs tested by Haag and Warren (1998). Both mussel species whose abundance was correlated to the density of their host fish were nondisplaying host-specialists found only in larger streams. Haag and Warren (1998) speculated that the density-dependent relationship between these mussel species and their host fish provided a mechanism to increase chances of glochidia infestation in large streams where host-fish abundances were stable, but was a disadvantage for persistence in variable headwater stream environments. Similarly, no correlation was found in headwater streams in Ohio and Texas between fish and mussel richness, although in larger Texas streams mussel diversity was correlated with fish diversity and not drainage area, and the relationship between fish and mussels determined the number of unionid species (Watters 1992). In southern Michigan streams, correlations found between freshwater mussel diversity, distribution, and drainage area were related to the strong correlations that existed between fish distributions and drainage area, and between unionid mussels and fish (Strayer 1983).

In this study, the two mussel species considered nondisplaying host-specialists were found in first- to fifth-order streams, and so it is doubtful that there is some longitudinal pattern to their distribution and abundance that is linked to the availability of their host fish. Also, it is curious that the only positive correlation found in this study between a mussel species and its host fish was for Utterbackia imbecillis, a non-displaying host generalist. Over a dozen host fish have been identified for U. imbecillis (Trdan and Hoeh 1982, Watters 1994), and glochidial parasitism in this species may be facultative rather than obligate (Fuller 1974). In addition, only a few field studies have linked the extirpation of unionids with the extirpation of their host fish, and most of that evidence is

anecdotal (Davenport and Warmuth 1965, Sickel 1982, Arter 1989). Other factors can often be implicated in the disappearance of individual mussel populations. For instance, the extirpation of many of the mussel species from the Caney Fork River system in Tennessee was not correlated with the disappearance of fish hosts as supposed, but rather was caused by the release of cold water from a dam in the study area (Layzer et al. 1993). The lack of correlation in this study between the abundance of mussel species and their host fish may indicate that other factors, such as suitable habitat, are more important in delineating freshwater mussel distributions than host fish availability. Suitable host fish may be available in sufficient numbers that relationships between the two faunal elements appear to be density independent. In addition, factors that control the current distribution of both mussels and fish in the basin may include stream size and habitat suitability. However, because mussels are, in most cases, obligate parasites on fish, it cannot be ignored that host fish must be available at suitable times in sufficient numbers to complete the unionid reproductive cycle. In addition, the lack of sufficient suitable host fish may explain the paucity of recent recruitment for many mussel species in the basin (Brim Box and Williams 1999, O'Brien and Brim Box 1999) and should be explored.

CHAPTER 5 RESPONSE TO CATASTROPHIC BURIAL

Introduction

The greatest freshwater mussel diversity in the world is found in North America and comprises approximately 300 species within two families, Unionidae and Margaritiferidae (Turgeon et al. 1988). Currently 21 taxa (7% of the fauna) are presumed to be extinct, and an additional 120 taxa (40% of the fauna) are considered to be threatened (Williams and Neves 1995). Causes of the decline in unionid populations are not fully known, but the following factors have been implicated: impoundments, excessive sedimentation, overharvesting, commercial dredging, industrial and municipal pollution, in-channel and floodplain gravel or sand mining, channelization, and introduction of nonindigenous mollusks such as the Asian clam, Corbicula fluminea, and the zebra mussel, Dreissena polymorpha (Bogan 1993, Williams et al. 1993).

Perhaps one of the most ubiquitous factors that may adversely affect mussel populations is excessive sedimentation caused, in part, by poor land use practices. Excessive sedimentation has been suspected as a causal factor in the decline of unionid mussels since the late 1800s (Kunz 1898). The Environmental Protection Agency cited sediments as the number one pollutant of rivers in the United States, impairing over 40% of the nation's river miles (U.S. Environmental Protection Agency 1990). This estimate is nearly 50% higher than the estimate for the next factor.

Most sediments in fluvial systems originate within the river channel or from erosion in the accompanying watershed. Studies of the effects of sedimentation on riverine biota have focused primarily on sediments supplied from the watershed, which is not surprising because it is estimated that 60% of the approximately 9058×10^6 tonnes of soils lost each year from cropland in the United States is deposited in rivers, streams and reservoirs (USDA 1989). Although crop farming is considered to be the most widespread human activity that has increased sediment loads in North American rivers (Meade et al. 1990), other significant sources of waterborne sediments include erosion from upland gullies, roads, highway ditches, construction sites, and surface mined areas.

Increased sediment loads produce conspicuous changes in the physical character of many rivers (Waters 1995). However, the effects of increased sedimentation on unionid mussels are not well understood, although anecdotal evidence suggests that changes in sedimentation rates and patterns may alter the composition and abundance of mussel faunas. In the Mississippi, Tennessee, and Ohio rivers, erosional silt may have destroyed a large portion of the mussel population by directly smothering the animals (Ellis 1931). In the North Fork of the Red River, Kentucky, the mussel fauna changed during an 11-year period from species that were intolerant of chronic sedimentation to species that, because of their morphology and behavior, were considered to be highly tolerant of sedimentation (Houp 1993). The sources of sedimentation in this river included coal mining in the headwaters of the river, disturbances from a stream relocation project, and logging practices in the watershed. In the Olentangy River, Ohio, increased sedimentation may have led to the extirpation of 14 unionid species (Stein 1972).

The southeastern region of the United States contains more freshwater mussel species (about 270) than any other region in North America (Williams and Neves 1995). The majority of imperiled mussel species are found in southeastern rivers (Master 1990). In the Apalachicola, Chattahoochee and Flint (ACF) River basin in Alabama, Florida, and Georgia, unionid mussel diversity is greatly reduced from historical levels (Brim Box and Williams 1999). Six species of ACF mussels were recently listed as endangered or threatened by the U. S. Fish and Wildlife Service (USFWS 1998), and two additional species are presumed to be extinct (USFWS 1994). The decline in freshwater mussel populations in the basin has been attributed, in part, to land use modifications that cause changes in sediment regimes and, correspondingly, increase sediment transport in streams (Williams and Butler 1994, USFWS 1998, Brim Box and Williams in press). The specific associations between unionid mussels and stream sediments, however, are poorly understood, making it difficult to assess the impacts of changes in sedimentation rates. Previous experimental studies (Ellis 1936, Vannote and Minshall 1982) have shown that high mortality rates can occur when mussels are intentionally buried by even small amounts of sediments. The effects of catastrophic burial on ACF mussels are not known, although historical changes in sediment production in the basin (Glenn 1911, van der Schalie 1938a, Clench 1955, Faye et al. 1980) suggest that mussel beds have periodically been covered by erosional sediments. The objective of this study was to evaluate the responses of four species of unionid mussels from the ACF basin to catastrophic burial by both fine sediments and sand.

Methods

Four species of mussels, Quincuncina infucata, Elliptio complanata, E. crassidens and Villosa lianosa, were used to assess the effects of catastrophic burial by sand and fine sediments. Quincuncina infucata were collected from the Ochlockonee River, Grady County, Florida, on 29 October 1996. Elliptio complanata were collected from Spring Creek, a tributary of the Chipola River, Jackson County, Florida, on 30 January 1997. Villosa lianosa were collected from Kinchafoonee Creek, a tributary of the Flint River, Webster County, Georgia, on 29 August 1997. Elliptio crassidens were collected from the Chipola River, Calhoun County, Florida, on 7 September 1997. Adult mussels were collected by hand and transported in coolers with ambient temperature river water to flow-through current tanks at the USGS/BRD laboratory, Gainesville, Florida. Mussels were held for a week before each experiment in order to acclimate them and to assess if any mortality resulted from transport.

All experiments were conducted in 33-liter, aerated aquaria, with about 4 inches of sand that served as a base sediment for the mussels. All aquaria were maintained at 20 C with a 12-hour photoperiod throughout the experiments. In each of 16 aquaria, 20 mussels of a single species were placed with their anterior end in the sediment. After 24 hours, mussels were checked to make sure they were partially buried in the base sediment and were actively filtering.

To assess the response to catastrophic burial, mussels were buried in either sand or fine (diatomaceous earth) sediments. The sand was collected from the Suwannee River, and a subsample was run through a series of 13 sieves. The sediment used in the

experiments consisted of approximately 99% sand-sized particles, 1% silt-sized particles, and less than one percent granule gravel-sized particles. The fine sediments were purchased commercially to avoid possible contamination with heavy metals that may adhere to river-borne fine sediments. Four amounts of sedimentation (1 cm, 4 cm, 7 cm and 14 cm) for each treatment were based on field observations of sediment transport in the ACF basin. Two replicates of 20 mussels each were used in each trial (i.e., sediment type/sediment amount combination). Thus, 320 mussels of each species were tested.

Mussels were checked for emergence daily over a ten day period. Mussels that emerged from burial and were visibly filtering on the sediment surface were considered successful migrants and were removed from the treatment aquaria. Any mussel that emerged but was dead was also removed, but was not counted as a success. At the end of ten days, all remaining mussels were removed from the aquaria and recorded as buried alive or dead.

Statistical Methods

Logistic regression models were used to evaluate the effects of sedimentation amount and sediment type on migration success. Logistic regression models differ from linear regression models in that the conditional distribution of the outcome variable follows a binomial distribution with the probability given by the conditional mean, $\pi(x)$ (Hosmer and Lemeshow, 1989). This model was defined as

$$\pi(x) = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}}$$

The logit transformation, $g(x)$, was used in place of $\pi(x)$, because it transforms the relationship to one that is linear in its parameters. It is also continuous and ranges from

negative infinity to infinity (Hosmer and Lemeshow, 1989). The logit transformation was defined as

$$g(x) = \ln \left[\frac{\pi(x)}{1-\pi(x)} \right] = \text{logit}(x)$$

In logistic regression, the log likelihood function, $L(B)$, is minimized as a function of the unknown parameters, $B = (\beta_0, \beta_1)$. The log likelihood function is defined as

$$L(B) = \ln(l(B)) = \sum \{y_i \ln [\pi(x_i)] + (1 - y_i) \ln [1 - \pi(x_i)]\}$$

The deviance, D , was used to assess the significance of sediment type and amount on migration success and was defined as

$$D = -2 \sum \left[y_i \ln \left(\frac{\pi_i}{y_i} \right) + (1 - y_i) \ln \left(\frac{1 - \pi_i}{1 - y_i} \right) \right]$$

The change in D (referred to as the residual deviance) with and without the independent variable was evaluated as $G = D(\text{model without variable}) - D(\text{model with variable})$. The likelihood ratio test statistic, G , will follow a chi-square distribution under the hypothesis that β_1 is equal to zero ($H_0: \beta_1 = 0$).

Odds ratios were used to quantify the impact of both sediment type (sand, fine sediment) and sediment amount (1, 4, 7 or 14 cm) on the probability of migration success. The odds ratio, ψ , was defined as the ratio of the odds for $x=1$ to the odds of $x=0$, or

$$\psi = \frac{\pi(1)/[1-\pi(1)]}{\pi(0)/[1-\pi(0)]}$$

The odds ratio approximates how much more likely (or unlikely) it is for the outcome to be present among those with $X=1$ than among those with $X=0$ (Hosmer and Lemeshow 1989).

For each of the four species, overdispersion first was assessed. This occurs when a linear logistic model is considered adequate, but the residual mean deviance exceeds unity, thus invalidating the assumption of binomial variability (Collett, 1991). If overdispersion was not detected, the main effects of sediment type and amount on migration success, as well as any interactions between these two variables, were evaluated using goodness of fit and analysis of maximum likelihood estimates (Stokes et al., 1995). If interactions between the independent variables were not significant, sediment amount was modeled as a continuous variable, and odds ratios were used to quantify the relative significance of sediment type and amount on migration success.

Results

Of the 320 Elliptio complanata buried, 258 migrated successfully through overlying sediments while 62 failed to migrate. One hundred percent of the E. complanata buried in 1 and 4 cm of fine sediments or sand migrated (Fig. 5-1a). In comparison, 48% of the E. complanata buried in 14 cm of sand migrated, while 28% successfully migrated in 14 cm of mud.

The residual deviance for the model that included the main effects of sediment type and amount, as well as their interactions, was not significant ($5.51 < \chi^2_{8,95}$), indicating that overdispersion was not present. In addition, the change in deviance on adding the interaction term in the model was 1.17 on 3 df, which also was not significant ($\chi^2_{3,95} = 7.81$), and the interaction terms were dropped from the model. Based on the likelihood ratio test statistic, G, both sediment type ($G_1 = 9.03$) and sedimentation amount ($G_1 = 145$) had a significant effect ($\chi^2_{1,95} = 3.84$) on migration success.

Figure 5-1. Average number of mussels that migrated per sediment treatment for each of the four species.

Preliminary analysis suggested that both sediment type and amount had a significant effect on migration success, amount was modeled as a continuous variable. The residual chi-square (χ^2_{res}), or score goodness of fit statistic was 0.4821, suggesting that the main effects model adequately fit the data. In addition, analysis of the maximum likelihood estimates indicated that both sediment type and amount were significant at the 0.05 level. The following model was produced from these data:

$$g(x) = 4.84 + 1.21(\text{sediment type}) - 0.4347 (\text{sedimentation amount})$$

The migration success of Elliptio complanata was negatively associated with burial amount. The odds ratio for sediment type, 3.35, indicated that E. complanata were three times more likely to migrate vertically in sand than in mud, adjusted for sediment amount. The odds ratio for amount, 0.65, suggests that the odds of migrating decreased per level increase in amount. Based on this ratio, it was estimated that E. complanata were 440 times more likely to migrate in 1 cm of sediment than in 14 cm of sediment, adjusted for sediment type.

Of the 320 Elliptio crassidens buried, 219 migrated successfully through overlying sediments while 101 failed to migrate. Migration success was over 90% for E. crassidens buried in 1 or 4 cm of mud or sand (Fig. 5-1b). In comparison, only 5% of the individuals buried in 14 cm of mud successfully migrated, while 15% successfully migrated through 14 cm of sand.

The residual deviance for the main effects model of sediment type and amount, as well as their interactions, was not significant ($10.9 < \chi^2_{8,95}$), indicating that overdispersion was not present. In addition, the change in deviance on adding the

interaction term in the model was 7.0, which also was not significant ($\chi^2_{3,95} = 7.81$), and the interaction terms were dropped from the model.

Preliminary analysis indicated that sediment amount ($G_1 = 206$), but not type ($G_1 = 1.71$) had a significant effect on migration success, and therefore sediment amount was modeled as a continuous variable. Although sediment type did not have a significant effect on migration success, it was retained in the model (Stokes et al., 1995). The residual chi-square, $\chi^2_{15,1}$, was 2.60, indicating that the main effects model adequately fit the data. Analysis of the maximum likelihood estimates also indicated that sedimentation amount, but not type, had a significant effect on migration success. The following model was produced from these data:

$$g(x) = 4.24 + 0.49(\text{sediment type}) - 0.48 (\text{sedimentation amount})$$

The migration success of Elliptio crassidens was negatively associated with burial amount. The odds ratio for amount, 0.61, is the extent that migration success decreased per each cm increase in amount, adjusted for sediment type. Based on this odds ratio, it was estimated that E. crassidens were over 900 times more likely to migrate in 1 cm of sediment than 14 cm of sediment. The odds ratio for sediment type, 0.65, indicated that E. crassidens were 1.5 times more likely to migrate vertically in sand than mud, adjusted for amount.

Of the 320 Quincuncina infucata buried, 187 migrated successfully through overlying sediments while 133 failed to migrate. For this species, migration success varied considerable among sedimentation amounts (Fig. 5-1c).

The residual deviance for the model that included the main effects of sediment type and amount, as well as their interactions, was not significant ($8.6 < \chi^2_{8,95}$), indicating that overdispersion was not present. However, the change in deviance on adding the interaction term in the model was 20.94 ($\chi^2_{3,95} = 7.81$), and the interaction terms were retained in the model. The following model was produced from these data:

$$g(x) = -2.51 + 0.31(\text{mud}) + 3.36(\text{one}) + 4.06(\text{four}) + 3.48(\text{seven}) + 1.35(\text{one}*\text{mud}) \\ - 0.31(\text{four}*\text{mud}) - 2.13 (\text{seven}*\text{mud})$$

where mud = 1, sand = 0, and sediment amounts were either 0 or 1. Based on this model, mussels buried in 14 cm of mud were over 100 times less likely to migrate than mussels buried in 1 cm of mud, and 28 times less likely to migrate in 7 cm of mud than 1 cm of mud (Table 5-1). Mussels buried in 14 cm of sand also had low odds of migrating, about 30 times less than in 1 cm of sand, but mussels buried in 7 cm of sand were just as likely to migrate as those buried in 1 cm of sand. At 7 cm, Quincuncina infucata were six times more likely to migrate through sand than mud.

Table 5-1. Odds ratios and parameter estimates, based on maximum likelihood estimates, for *Quincuncina infucata*, for all sediment amounts and types.

Sediment Type	Sediment Amount (cm)	Logit	Odds of Migrating
Sand	14	-3	0
Sand	7	1	3
Sand	4	2	5
Sand	1	1	2
Mud	14	-2	0.11
Mud	7	-1	0
Mud	4	2	5
Mud	1	3	12

Of the 320 *Villosa lienosa* buried, 251 migrated successfully through overlying sediments while 69 failed to migrate. One hundred percent of the *V. lienosa* buried in 4 and 7 cm of mud migrated, as did those buried in 1 or 4 cm of sand (Fig. 5-1d). In comparison, 30% of the *V. lienosa* buried in 14 cm of sand migrated, while 12.5% migrated in 14 cm of mud.

The residual deviance for the model that included the main effects of sediment type and amount, as well as their interactions, was not significant ($7.72 < \chi^2_{8,95}$), indicating that overdispersion was not present. However, the change in deviance on adding the interaction term in the model was 11.9, which was significant ($\chi^2_{3,95} = 7.81$), and therefore the interaction terms were retained in the model. The following model was produced by these data:

$$g(x) = -0.85 - 1.10(\text{mud}) + 15.53(\text{one}) + 15.53(\text{four}) + 2.80(\text{seven}) + \\ 1.10(\text{mud}*\text{four}) + 13.84(\text{mud}*\text{seven}) - 9.92(\text{mud}*\text{one})$$

where mud = 1, sand = 0, and sediment amounts were either 0 or 1. In general, the estimated probabilities for migrating in either sediment type were high for 1, 4 or 7 cm of sediment, and decrease significantly in 14 cm of sediment (Table 5-2). The estimated odds ratios suggest that *Villosa lienosa* were about a million times less likely to migrate in 14 cm of sand or mud than 4 or 7 cm of mud, or 1 or 4 cm of sand. Mussels were 3 times more likely to migrate successfully in 14 cm of sand than 14 cm of mud.

Table 5-2. Odds ratios and parameter estimates, based on maximum likelihood estimates, for *Villosa lienosa*, for all sediment amounts and types.

Sediment Type	Sediment Amount (cm)	Logit	Odds of Migrating
Sand	14	-1	0
Sand	7	2	7
Sand	4	15	> 1,000,000
Sand	1	15	> 1,000,000
Mud	14	-2	0.14
Mud	7	15	>1,000,000
Mud	4	15	> 1,000,000
Mud	1	4	39

Discussion

Covering mussels with as little as 14 cm of sediments significantly decreases their chances of extricating themselves from burial. Increased sediment loading, because it is so ubiquitous, may therefore be an important cause of freshwater mussel declines.

More Elliptio complanata migrated in this study than any other species. This was not surprising, given that this species is often both widespread and abundant (Taylor 1985, Strayer and Ralley 1991, Downing et al. 1993) and has been reported from a variety of habitats, from small creeks to large rivers, as well as from ponds, lakes and reservoirs (Counts et al, 1991). It was the most common species encountered in a recent survey of the ACF Basin and occurred at 32% of 324 sites surveyed (Brim Box and Williams 1999). Elliptio complanata is often the most abundant unionid at a particular site outside of the ACF Basin, and sometimes can be the only species present at a location (Clarke and Berg 1959, Counts et al. 1991).

Elliptio complanata was the only species of the four tested for which migration was significantly affected by sediment type. Elliptio complanata was three times more likely to migrate through sand than mud, adjusted for rate. Although this species is found in a wide variety of habitat types, it may grow faster (Kat, 1982), occur in higher densities (Leff et al. 1990), and burrow more efficiently in sandy substrates (Lewis and Riebel 1984). In the ACF Basin, Brim Box and Williams (in press) found 93% of 2,524 specimens at sites that contained predominantly sand, sand and limestone rocks, or sand and fine sediments (silts and clays). The results of this study suggest that E. complanata is adept at moving through sandy sediments, as only 23 of the 160 mussels buried in sand

failed to migrate successfully. In addition, although migration success in sand was significantly higher than in mud, the success rate in mud was also relatively high: 75% of all animals buried in mud successfully migrated.

There is some evidence to suggest that Elliptio crassidens is more common in sandy habitats than fine sediments, although sediment type did not have a significant effect in this study. In Florida, Elliptio crassidens was reported from muddy sand, sand, and rock substrates in moderate currents (Heard 1979), and in southeastern Georgia, it occurs in strong currents in the sandbars of large rivers and creeks (Johnson 1970). In the ACF Basin this species is known primarily from sites with sand and limestone rock substrates (Brim Box and Williams 1999). Alternatively, Hamilton et al. (1997) suggested E. crassidens may be a habitat generalist, in that it has been found in a range of substrate types. This is consistent with this study, in that sediment amount but not type had a significant effect on migration success.

Successful migration was recorded for only 5% of the Elliptio crassidens that were buried in 14 cm of mud and 15% buried in 14 cm of sand. In comparison, 28% of the E. complanata buried in mud and 48% buried in sand successfully migrated. This experiment was not designed to compare species (e.g., mussels of multiple species were not buried in the same aquaria at the same time). These results do suggest, however, that because both of these species are in the same genus, the effects of catastrophic burial are species-specific.

Migration success for Villosa lienosa in this study was high in both mud and sand at all sediment amounts except 14 cm. In 14 cm of sediment, this species was three times

more likely to migrate through sand than mud. High migration success (over 85%) in both sediment types except at 14 cm may help to explain why this species, like Elliptio complanata, is widespread and abundant in the ACF Basin (Brim Box and Williams 1999). Villosa lienosa was able to extricate itself from burial in both sand and mud, and there is some evidence to suggest that it may be a habitat generalist, as it has been reported from a wide variety of habitat types, from soft mud to underneath rocks in fast current (Jenkinson 1973), to sandy substrates in slight to moderate current (Heard 1979), to muddy substrates in detritus-rich areas (Clench and Turner 1956).

Quincuncina infucata was the least likely to successfully migrate of the four species tested. About 59% of all Q. infucata buried successfully migrated. Migration success for this species was low for mussels buried in 14 cm of mud (10%) or sand (8%). In contrast, over 70% of the mussels buried in 7 cm of sand migrated, as compared to 30% in mud. Observations of Q. infucata in the ACF Basin suggest that this species is usually found in sand-bottomed pools and in rocky areas with swift currents (Jenkinson 1973), to sand, muddy sand and fine gravel substrates in small to large streams with moderate current (Heard 1975, 1979). The inability of Q. infucata to migrate through overlying sediments may partly explain why this species has disappeared from the entire main channel of the Chattahoochee River, several Chattahoochee River tributaries, and portions of the Apalachicola River, and why it was recently considered a species of special concern in the basin (Brim Box and Williams 1999).

The mussel fauna of the ACF basin is in decline. Although specific causal factors have been poorly documented, sediment erosion associated with basin and riparian land

use changes has numerous potential effects on benthic invertebrates and their habitats (Chutter 1969, Waters 1995). Changes in sediment production have been particularly well documented in the Chattahoochee River system since early this century, and of the four major rivers of the basin, the Chattahoochee River has suffered the most serious decline in mussel populations. For instance, 30 species were historically known from the Chattahoochee system, but only about half of those species persist there today (Brim Box and Williams 1999). Of the eight species that were recently listed as federally threatened or endangered (USFWS 1998) or extinct (USFWS 1994), six historically occurred in the Chattahoochee basin, but only two of these species persist there, and only in a few tributary streams. None of the six species has been collected from the main stem of the Chattahoochee River in over 20 years. All four of the species that were used in this study were historically found in the Chattahoochee River system. Elliptio complanata and Villosa lienosa are still found in large numbers in several Chattahoochee River tributaries, while Elliptio crassidens and Quincuncina infucata are rare there (Brim Box and Williams 1999). None of these species was found in the main channel of that river.

Reductions in the mussel fauna of the ACF Basin during the past 150 years may have been caused by species-level responses to changes in substrate composition that resulted from changes in sedimentation patterns. Soil erosion in the Piedmont and Coastal Plain physiographic regions was noted early (Glenn 1911), and intensive land clearing for cotton and row-crops in the 19th century led to extensive erosion and gully formation in this region (Bennett 1939). In the counties that border the Chattahoochee River, settlement began in the 1750s, land was converted to cotton plantations, and by the

Civil War severe soil erosion was evident (Trimble 1974). Tenant farming with corresponding poor farming practices after the Civil War exacerbated the problem, and erosive land uses continued until about the 1930s. During this period, erosional sediments filled streams and covered floodplains (Trimble 1974), and by the late 1930s it was estimated that 44 percent of the land in Georgia had reached the gully stage, and 22 percent of the land had been abandoned due to erosion, although these high figures were latter disputed (Magilligan and Beach 1993). Correspondingly, as early as 1915 the historically diverse mussel fauna of the Chattahoochee River at Columbus, Georgia, was in decline, and by 1929 it was apparently extirpated (Clench and Turner 1956). Erosional sediment was implicated early on for mussel declines in the ACF basin (van der Schalie 1938a), especially in the Chattahoochee River system (Clench 1955, Clench and Turner, 1956). Clench (1955) also noted that while the Flint River also suffered from silting, a series of large springs mitigated the negative impacts of sedimentation. However, it is cautioned that further experiments and field studies are needed to draw inference between historical changes in sediment deposition within the Chattahoochee River and mussel extirpations.

Several mechanisms for the intolerance of some unionid species to increased levels of sediment deposition seem possible and are likely to differ among species. Sediment deposition may impact freshwater mussels by interfering with feeding and/or respiration, as it does for other invertebrates, particularly Odonata, Trichoptera, and other families of Bivalvia (Hynes 1960, Minshall 1984, Robinson et al. 1984). Inorganic silt in suspension reduced the amount of food available to the common mussel, Mytilus

edulis, through dilution, rather than by affecting the amount of material filtered by the mussel (Widdows et al. 1979). Hard clams, Mercenaria mercenaria, had significantly lower clearance rates and algal ingestion rates with increasing sediment loads (Bricelj and Malouf 1984), and juvenile hard clams had significantly lower growth rates at suspended fine sediment concentrations of 44 mg/L (Bricelj et al. 1984). Suspended clays and fine silts can also settle out of the water column, even in turbulent streams, and stick to benthic invertebrates, which can be damaged by the accumulation of these particles on their body surfaces (Davies-Colley et al. 1992). The main impacts of excess sedimentation on unionids are often sublethal, and detrimental effects may not be immediately apparent. Elliptio complanata had significantly lower growth rates in muddy substrates than in a sand/gravel/clay mix, possibly because the fine sediments in suspension in the muddy substrates clogged gill filaments and reduced feeding efficiencies, which was especially apparent at higher population densities (Kat 1982).

Migration rates varied considerably for the four mussel species used in these experiments, suggesting the ability to migrate vertically through overlying sediments is species-specific. These results are consistent with other laboratory studies that have examined the impacts of gradual or catastrophic burial on unionid mussels. When Fusconaia flava were intentionally buried with silt and sand in an Upper Mississippi River experiment, 55% of the individuals died when buried under 10 cm of material (Marking and Bills 1980). In this same experiment, two other species, Lampsilis siliquoidea and L. cardium, were more adept at moving vertically through the deposited material and suffered lower mortality rates. In laboratory trials Gonidea angulata were

able to move vertically under varying rates of sedimentation, while Margaritifera falcata remained buried until they died (Vannote and Minshall 1982). This may partially explain why, in the Salmon River Canyon in Idaho, populations of M. falcata were buried alive in canyon reaches that were aggrading with sand and gravel caused by mining, logging, irrigation diversion, and massive slope failure of a tributary stream caused by hydraulic mining activities (Vannote and Minshall 1982). The dead, buried populations of M. falcata were found intact in beds that were inundated by sand and gravel bars, and G. angulata replaced M. falcata in reaches aggrading or inundated with sand. In the ACF Basin, the ability of V. lienosa and E. complanata to migrate through both mud and sand may help to explain why these two species are widespread and common in the basin, and 20 other species are either extinct, extirpated, endangered, threatened or of special concern.

CHAPTER 6 CONCLUSIONS

Whereas other authors have suggested that habitat is only of secondary importance when describing fish and mussel distributions, the results of this study suggest that fish and mussel community structure is closely related to stream size and suitable habitat. This is not surprising, in that lotic fish faunas are often closely tied to landscape-level processes (Schlosser 1991) and in the ACF basin, fish and mussel community structure is regulated, in part, by interactions at the stream-floodplain interface (Michener et al. 1998). In addition, in streams that were historically degraded, some fish species may have recovered, whereas mussels have not. For example, Pteronotropis hypselopterus, the only known host fish in the basin for Pleurobema pyriforme, occurred at 16 sites, whereas P. pyriforme were found at only six. Thus, because fish are vagile and mussels are not, it is possible that fish can recolonize stream reaches much more quickly than mussels. This notion could be tested in the Chattahoochee River drainage, where historical levels of sedimentation were much higher than present levels (Kundell and Rasmussen 1995), fish populations can be diverse and locally abundant, and mussel communities are depauperate.

The causes for the decline of freshwater mussels in North America are not well understood, although possible causes were summarized by van der Schalie (1938a), Fuller (1974), Williams et al. (1993), and Bogan (1993). These include habitat

degradation, the introduction of exotic bivalves including the Asian clam, Corbicula fluminea, and the zebra mussel, Dreissena polymorpha, pollution and impoundments, although in most cases, the information implicating these factors is qualitative and/or anecdotal. Overharvesting, commercial dredging, in-channel gravel or sand mining, channelization, and excess sedimentation caused, in part, by poor land use practices, are also thought to impact unionids. van der Schalie (1938a) speculated the following factors had contributed to the decline of the North American mussel fauna in the previous decade: silting, pollution by sewage, mine and industrial wastes, power-dam developments, and unrestricted mussel gathering for the pearl button industry. Bogan (1993) suggested that the causes of unionid mussel declines are poorly known due to the cumulative lack of knowledge of unionid life history, ecology, distribution, fish hosts, and systematics.

Sedimentation processes have changed within the ACF basin over the past 200 years, and these changes may have impacted unionid mussel populations early on, especially in the Chattahoochee River drainage. In 1826, Richard Blount, a surveyor of the Georgia-Alabama state line, wrote that he counted 36 trout (probably bass, genus Micropterus) in the Chattahoochee River, near present day Lanett, Alabama, while standing on the bank of the river, and that this was possible because the water was so clear (Trimble 1974). Soil erosion in the Piedmont and Coastal Plain physiographic provinces was noted early on, and intensive land clearing for cotton and row crops in the 19th century led to extensive gully formation in this region (Bennett 1939). In the counties that border the Chattahoochee and Flint rivers, settlement began in about the

1750s, land was converted to cotton plantations, and by the Civil War severe soil erosion was evident (Trimble 1974). The most striking example of soil erosion in the basin is Providence Canyon, Georgia's "Little Grand Canyon," where a group of seven gullycanyons with up to 100 m of relief started forming in the mid-1800s (Magilligan and Beach 1993). Tenant farming with corresponding poor farming practices after the Civil War exacerbated the problem, and erosive land uses continued until about the 1930s. During this period, erosional sediments filled streams and covered floodplains (Trimble 1974). Beginning in the 1930s, erosion had decreased due to a combination of improved soil conservation practices, the transition of farmland to pasture and forest, and an overall decrease in agriculture. The average annual concentration of total suspended sediment in the Chattahoochee River near Atlanta was about 400 ppm in the mid-1930s (when records are first available), compared to 1960s levels of less than 50 ppm (Hewlett and Nutter 1969). This decrease in sediment yields had one potentially negative effect on unionid mussels, however, in that lower stream order tributaries have incised into their aggraded floodplains, and this headward incision produced new sources of high sediment yield and led to continued valley aggradation (Trimble 1974).

By the mid-1970s, in the upper Chattahoochee River, the estimated average annual erosion ranged from approximately 900 to 6,000 tons per square mile per year (Faye et al. 1980). Erosion yields were highest in watersheds with high percentages of agricultural and transitional land uses, and lowest in urbanized watersheds. Conversely, estimated average suspended sediment yields were highest in predominantly urban watersheds (800 tons per year) as compared to mostly forested watersheds (300 tons per year). A large

part of the sediment discharged from urban streams was probably due to channel erosion (Faye et al. 1980). Increased sediment loads, especially fine sediment, can negatively affect unionid mussels through several mechanisms. Fine silt and clay particles can clog the gills of mussels (Ellis 1936), interfere with filter feeding (Kat 1982, Aldridge et al. 1987), or limit burrowing activity (Marking and Bills 1980, Vannote and Minshall 1982). Fine sediments also may affect mussels indirectly by reducing the light available for photosynthesis and thus reducing the availability of unionid food items (Kanehl and Lyons 1992).

Difficulties in identifying and quantifying sediment loads, whether natural or human-induced, have made it hard to assess the impacts of sedimentation on unionid mussels. The same species have been judged tolerant or intolerant in different studies. In addition, it is not clear what physical properties of the streambed are important to measure. Conventional measurements of water velocity, depth, substrate composition, and other microhabitat variables have not always provided the information needed to predict the occurrence or density of unionids in streams (Holland-Bartels 1990, Strayer and Ralley 1993). Part of the problem relates to the sampling designs used to survey mussel populations and their habitats. It is often difficult to devise a sampling scheme that accounts for differences in the spatial heterogeneity of mussels and the spatial heterogeneity of habitat-related variables.

Some researchers considered substrate particle size to be an important microhabitat descriptor when assessing associations between mussels and their physical habitats (Bronmark and Malmqvist 1982, Salmon and Green 1983, Leff et al. 1990), whereas

others have failed to find meaningful relationships between unionid mussels and substrate composition (Lewis and Riebel 1984, Strayer and Ralley 1993, Di Maio and Corkum 1995, Layzer and Madison 1995). For example, Strayer and Ralley (1993) concluded that microhabitat-mussel associations, as estimated from discriminant analysis, were weak, and that larger spatial scales might be more useful in predicting mussel occurrence. They also suggested that descriptions of habitat based on fluvial geomorphology might be more informative. Others have suggested that substrate stability, not composition, is important in predicting mussel occurrence. In the Holston River, Virginia, the greatest species densities were associated with stable mixed sand, gravel, and pebble substrates (Neves and Widlak 1987). Freshwater mussels of the lower Cumberland River, Kentucky, were abundant only in stable habitats composed of gravel in firm sandy clay (Sickel 1982). Kat (1982) suggested that streambeds can be divided into high- and low-quality microhabitats. High-quality microhabitats are characterized by stable substrates, uncrowded conditions, and protection from scour; low-quality microhabitats are characterized by unstable substrates and a significant reduction of energy input available for growth and reproduction. Some authors have suggested that hydrological variables such as the type of stream flow or shear stress, or macrohabitat descriptors such as stream size may be more useful than substrate composition in predicting mussel occurrence.

The lack of correlation between substrate particle size and mussel distributions in some studies may be a result of inadequate sampling effort and improper substrate particle size analysis. Associations between substrate composition and the aquatic fauna are often evaluated based on a limited number of samples (e.g., 30) or particle-size

classes (e.g., 6). One hundred to 300 samples may be necessary to adequately characterize the substrate at a particular site in rivers with spatially heterogeneous beds (Wolcott and Church 1991).

In the Apalachicola River basin, substrate composition was clearly important in determining where some species of mussels occurred. However, substrate composition was not the only factor that determined the distribution and abundance of mussels in the basin. There are several possible reasons for the lack of an apparent association between substrate properties and some species of freshwater mussels. First, some species may be generalists with respect to substrate composition, surviving equally well in many types of substrates. Second, factors other than substrate composition may be important in defining the physical habitat of some mussel species. This finding is consistent with other studies where, for example, water velocity was a better predictor of mussel distribution than substrate type (Huehner 1987). Third, although 2,713 quadrats were sampled for mussels and sediments, rare unionids were not found in enough quadrats to draw inferences between their presence and substrate composition. More quadrat samples may have resulted in statistically significant mussel-substrate associations for some of the less common mussel species encountered in this study.

In conclusion, these results indicate that some mussel species are habitat specialists whose distributions are closely tied to aspects of streambed substrate composition. However, there remains considerable debate and uncertainty regarding the associations between anthropogenic erosional sediments and freshwater mussels. The relative significance of human activities to sediment production, and their subsequent effects on

freshwater mussels, is difficult to evaluate. Some of the apparent associations between increased sediment loads and unionid mussels may involve long lag times, and/or may include potential impacts on host fishes and juvenile mussels. Quantitative work is needed to determine the mechanisms through which human-induced sedimentation affect freshwater mussels, as well as to determine the sediment properties important to measure. In addition, numerous studies have documented the adverse effects of human-induced sedimentation on fish communities, but few studies have examined how these effects influence the availability of suitable host fish for freshwater mussels. More quantitative work is needed to document the specific effects that changes in sediment regimes have on host fish-mussel interactions, including how increased turbidity affects the reproductive success of mussels that use visual lures to attract hosts.

Marine bivalves are life-history generalists known for their high degree of habitat specificity (Stanley 1973, Vermeij 1989, Hurlbut 1991, Morton 1992). Freshwater mussels, in contrast, have highly specialized life histories but are frequently referred to as habitat generalists (Holland-Bartels 1990, Strayer and Ralley 1993, Strayer 1994, Haag and Warren 1998). This study suggests that in the ACF basin, freshwater mussels are habitat specialists, whose distributions are tied to suitable habitat defined by a combination of macro- and micro-habitat variables. In addition, this study suggests that meaningful relationships between mussels, fish, and their suitable habitat, defined at both macro- and micro-spatial scales, can be obscured if past habitat alterations and corresponding faunal shifts are not accounted for at the community level.

APPENDIX
LIST OF STUDY SITES

Chattahoochee River Drainage. **ALABAMA: Barbour County:** North Fork Cowikee Creek at unnamed/unnumbered dirt road ca. 7.5 air mi E of Spring Hill ca. 14 air mi NNW of Eufaula. **Lee County:** Little Uchee Creek below CR 77 below Meadows Mill Pond ca. 7 air mi NW of Crawford ca. 11 air mi SE of Opelika. **Russell County:** 1) Hatchechubee Creek at U.S. Rt 431/Alabama Rt 1 ca. 8 air mi WNW of Jakin; 2) Uchee Creek at Alabama Rt 169 ca. 5.5 air mi N of Seale. **GEORGIA: Clay County:** Hog Creek at Georgia Rt 266 ca. 5.5 air mi ENE of Fort Gaines. **Early County:** 1) Kirkland Creek at U.S. Rt 84/Georgia Rt 38, 1.75 air mi WNW of Jakin; 2) Sawhatchee Creek at U.S. Rt 84/Georgia Rt 38, ca. 5 air mi. WNW of Jakin. **Randolph County:** Pumpkin Creek at CR 27 ca. 6.5 air mi WSW of Benevolence ca. 7.5 air mi NW of Cuthbert. **Stewart County:** Lime Spring Branch at CR 148 ca. 6.25 air mi SE of Westville ca. 7 air mi SE of Lumpkin.

Chipola River Drainage. **FLORIDA: Jackson County:** 1) Spring Creek 200 m below Merritts' Mill Pond dam; 2) Baker Creek on unnamed dirt road near Jenkins Pond ca. 7 air mi NNW of Marianna.

Flint River Drainage: Baker County: 1) Coolewahee Creek at Georgia Rt 91, 2.0 road mi NW of junction Georgia Rt 37/ Georgia Rt 91 in Newton; 2) Ichawaynachaway Creek at Georgia Rt 216, 4.8 road mi WNW of junction Georgia Rt 37/Georgia Rt 216 ca. 13.25 air mi WNW of Newton. **Crisp County:** 1) Swift Creek at CR 33 ca. 9 air mi SW of Cordele; 2) Cedar Creek at CR 20 (Byrds Mill Rd) ca. 4.75 air mi SW of Cordele.

Decatur County: Spring Creek at U.S. Rt 84/Georgia Rt 38 ca. 0.75 air mi SW of Brinson. **Dooley County:** Hogcrawl Creek at Georgia Rt 329 ca. 4.7 air mi E of Montezuma. **Dougherty County:** Kiokee Creek ca. 1 air mi N of Georgia Rt 253 ca. 5.6 air mi W of Albany. **Lee County:** Muckalee Creek at Georgia Rt 195 ca. 3.5 air mi NE of Leesburg. **Miller County:** Aycocks Creek at CR 190 ca. 3.25 air mi WSW of Boykin ca. 5.75 air mi S of Colquitt. **Sumter County:** 1) Chokee Creek at U.S. Rt 280/Georgia Rt 30 ca. 2.25 air mi E of Leslie; 2) Lime Creek at CR 53 (Spring Creek Church Rd/Joe Stewart Rd) ca. 14.25 air mi ESE of Americus; 3) Muckalee Creek at U.S. Rt. 19/Georgia Rt 3 in Americus. **Taylor County:** Patsiliga Creek at junction Georgia Rt. 208/Georgia Rt 137 ca. 7.5 air mi NNE of Butler. **Terrell County:** Chickasawhatchee Creek at Cr 130 ca. 4.5 air mi SW of Chickasawhatchee ca. 8.5 air mi S of Dawson.

Webster County: Kinchafoonee Creek at CR 123 ca. 5.25 air mi NW of Preston.

Worth County: 1) Abrams Creek at Georgia Rt 300 ca. 4.25 air mi SSW of Oakfield; 2) Jones Creek at Georgia Rt 300 ca. 1.25 air mi SSW of Oakfield; 3) Abrams Creek tributary (unnamed) at CR 123 below an impoundment ca. 6.25 air mi SSE of Oakfield; 4) Mill Creek tributary (unnamed) at CR 12 below Mercer Mill Pond ca. 7.25 air mi SSW of Oakfield.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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