To the Graduate Council:

I am submitting herewith a dissertation by Brenda Rashleigh entitled "Multi-scale Analysis of Unionid Freshwater Mussel Community Structure in the Upper Tennessee River Basin." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

James Drake, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of the Graduate School

MULTI-SCALE ANALYSIS OF UNIONID FRESHWATER MUSSEL COMMUNITY STRUCTURE IN THE UPPER TENNESSEE RIVER BASIN

A Dissertation
Presented for the Doctor of Philosophy Degree
The University of Tennessee, Knoxville

Brenda Rashleigh
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DEDICATION

This work is dedicated to my family, John, Louise, and Jon Rashleigh, Charles Reynolds, and Nellie Napoli. Thank you for your encouragement and support, which I found in both your words and your silence; thank you for your love and kindness, which were my greatest sources of joy during my work; and most importantly, thank you for your unwavering faith in me, which has carried me though these difficult years.

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ABSTRACT

Populations of freshwater mussels of the family Unionidae are experiencing a decline in the upper Tennessee River basin. An understanding of the processes by which mussel community structure is created and sustained may aid conservation efforts. Here, modelling was used to explore the patterns that developed in local, mesoscale, and regional communities when particular biotic or abiotic processes were specified, and to generate predictions to which upper Tennessee River mussel data were compared.

Locally competing mussel species can coexist at equilibrium only when each is sufficiently more successful on a different resource in terms of resource use, life history characteristics, or a combination of the two. Temporal variability in fecundity promotes coexistence of a poorer competitor, particularly when variability is high and uncorrelated between species. Neither resource partitioning nor the influence of temporal variability explained coexistence of two similar mussel species: coexistence may be influenced by past competition or processes at different scales.

At the mesoscale, competition can reduce species number and lead to nested species composition among sites, whereas long-distance dispersal consistent with metapopulation dynamics has the opposite effect. Patterns in three mussel communities were most consistent with structuring by competition, however, at the low species number per patch exhibited in real communities, differences between scenarios with and without competition were relatively minor.

Highest regional-scale species richness occurred at lowest critical fitness values for colonization and extinction, not at intermediate colonization levels as would be expected if environmental heterogeneity generated pattern. High-richness communities exhibited low variability among replicate scenarios and high resource specialization among species, consistent with classical competition theory. Field data were consistent with the range of model results where competition appeared to structure communities.

Different processes appear to structure freshwater mussel communities at different spatial scales: communities appear increasingly structured by biotic processes with increasing spatial scale. Biotic processes generate simple rules that guide a system's development, while abiotic processes control expression of pattern at particular sites. Results of this study can be used to develop predictive models, and to interpret observed patterns of decline in the upper Tennessee River basin.

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INTRODUCTION

Populations of freshwater mussel species of the family Unionidae are in decline in the upper Tennessee River basin. Over half of the freshwater mussel species known from this basin are federally protected, and seven are presumed extinct (Williams et al. 1992). Mussels serve as food for predators, mutualists with fish, and the basis of the pearl industry. Thus, their conservation is important for economic as well as ecological reasons. Efforts to preserve the diversity of mussel species include identification of populations and species in peril, relocation and reintroduction of organisms, and development of mussel sanctuaries. Success of conservation efforts depends on the ability to understand how community patterns are created and sustained (Lawton 1997). The most appropriate explanation for a particular type of community will depend on characteristics of the constituent species and the specific environmental setting (Rahel et al. 1984, Huston 1994). The goal of this dissertation is to understand the structure of unionid freshwater mussel communities in the upper Tennessee River basin.

DESCRIPTION OF THE UPPER TENNESSEE RIVER BASIN

The upper Tennessee River basin encompasses an area of 21,390 mi^2 of the Tennessee River watershed upstream of Chattanooga, Tennessee, and includes parts of 4 states: Tennessee (11,500 mi^2), North Carolina (5,480 mi^2), Virginia (3,130 mi^2), and Georgia (1,280 mi^2) (Hampson 1995) (Figure 1.1). In 1990, about 2.4 million people

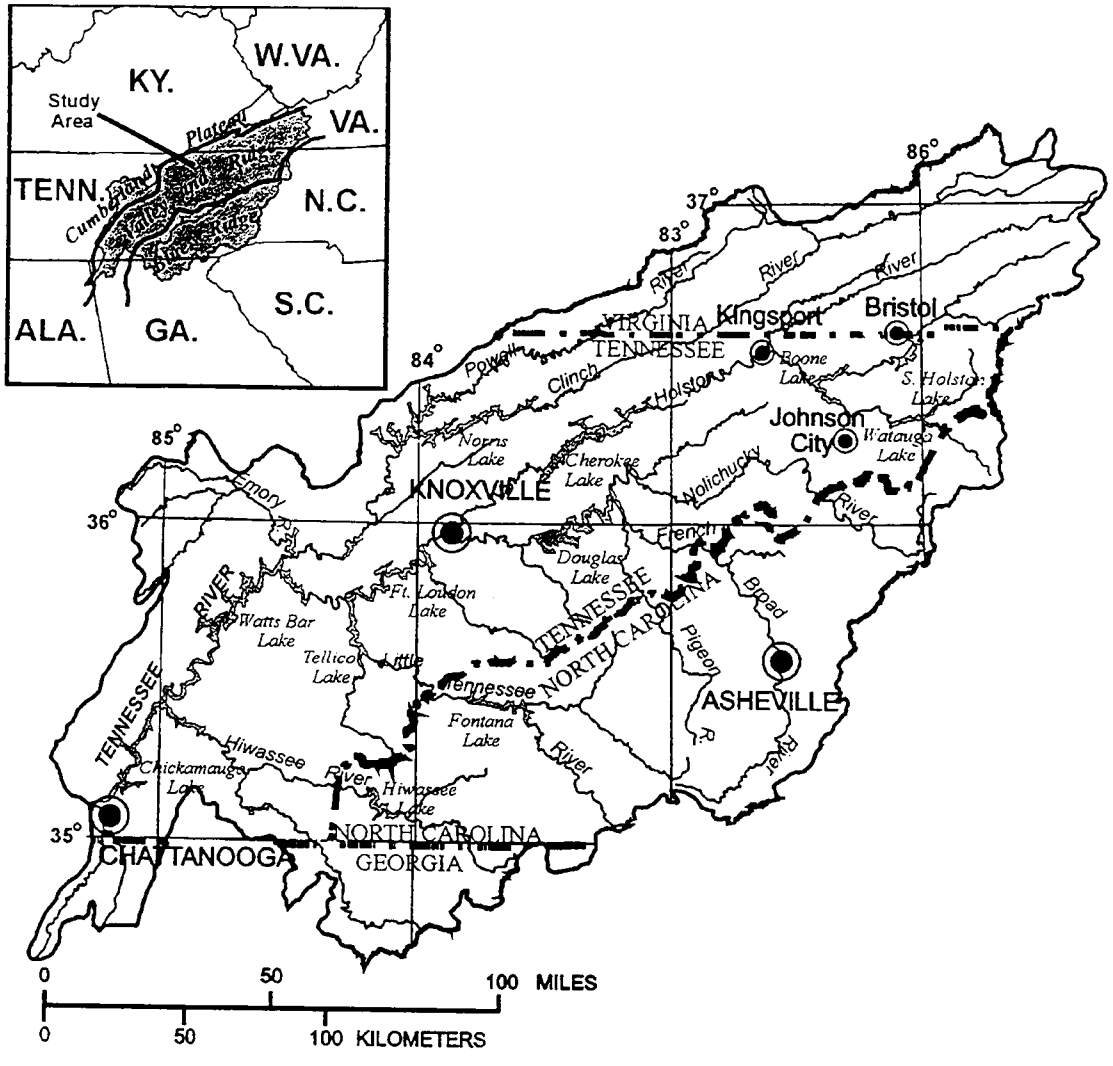


Figure 1.1. Location of the upper Tennessee River basin and map of physiographic provinces (inset). Source: U.S. Geological Survey National Water Quality Assessment Program, Knoxville, Tennessee.

resided in the basin, more than 70% of whom lived within the metropolitan statistical areas of Chattanooga and Knoxville, Tennessee; the tri-cities of Johnson City-Kingsport-Bristol in Tennessee and Virginia; and Asheville, North Carolina (Hampson 1995). Elevations in the basin range from 620 to 6,684 feet above sea level. At Knoxville, which has an elevation of approximately 1,000 feet above sea level, the average annual temperature is 59 degrees Fahrenheit: annual temperatures generally decrease by about 3 degrees for every 1,000 foot increase in elevation (Hampson 1995). Most areas in the basin receive rainfall averaging 50-60 inches (Carriker 1981).

Physiography, geology, hydrology

The upper Tennessee River basin spans three physiographic provinces: the Blue Ridge, the Ridge and Valley, and the Cumberland Plateau (Figure 1.1). Approximately 35% of the basin falls into the Blue Ridge physiographic province, the most easterly province, which is characterized by high-elevation peaks and igneous/metamorphic geology (J. Connell, U.S. Geological Survey, pers. comm.). A small portion (7%) of land along the west edge of the basin falls in the Cumberland Plateau physiographic province (J. Connell, U.S. Geological Survey, pers. comm.). The Cumberland Plateau is at an elevation intermediate between that of the Ridge and Valley and that of the Blue Ridge. The geology of the Plateau is dominated by sandstone. The majority of the basin falls in the Ridge and Valley province, located between the Blue Ridge and the Cumberland Plateau, which is characterized by parallel ridges and valleys running northeast to southwest. The geology is dominated by shale, limestone, and dolomite.

The six major tributaries to the upper Tennessee River are the Holston, French Broad, Little Tennessee, Clinch-Powell, Hiwassee, and Emory rivers (Figure 1.1). The headwaters of the French Broad, Little Tennessee, and Hiwassee rivers drain the Blue Ridge physiographic province. These streams are relatively cool, clear, and steep, and the substrate consists of boulders and bedrock. The Emory River drains the Cumberland Plateau, flowing in a pool-drop pattern over sand and bedrock substrate. The Ridge and Valley physiographic province contains the Clinch, Powell, and Holston rivers, and lower reaches of the French Broad and Little Tennessee rivers. These rivers are moderately shallow and productive with alternating riffle, shoal, and pool areas. The Ridge and Valley province also contains the mainstem Tennessee River, which is formed by the confluence of the Holston and French Broad rivers in Knoxville. Below Chattanooga, the Tennessee River drains west and then north into the Ohio River.

Land use and water quality

There is a long history of human activity in the upper Tennessee River basin. Native Americans inhabited the basin from as early as 12,000 B.C. European contact began in the 1700s. As the population increased through the 1800s, the land was used for more intensive farming and industry, such as iron works, salt mining, and lumbering. As of 1992, over 67% of the basin was forested (SAMAB 1996). Agriculture, dominated by corn, soybeans, and tobacco, utilizes approximately 26% of the basin (Carriker 1981, SAMAB 1996). Agricultural areas are predominantly located in the Ridge and Valley physiographic province. Although the Blue Ridge and Cumberland Plateau

physiographic provinces are more forested than the Ridge and Valley, they are impacted by logging, mining, and tourism and recreation.

Human activity in the basin has impacted hydrology and water quality. Early in the 1900s, the Tennessee Valley Authority began to impound some of the larger rivers in order to control flooding and encourage economic development. Presently, thirty-seven impoundments are located in the upper Tennessee River basin (Etnier and Starnes 1993). Impoundments affect a river's flow regime by slowing water above the dam, regulating the outflow, trapping sediment, and altering the thermal regime and water chemistry (Yeager 1993). Water quality threats facing the remaining free-flowing waters of the upper Tennessee River basin include agricultural and livestock activities; municipal discharges, including wastewater pollution and urban runoff; industrial discharges and catastrophic spills; and mining, logging, and land development (Carriker 1981). These activities have resulted in sediment, chemical, and bacterial problems (e.g., Sagona and Carroll 1991, Treece and Johnson 1997) and pose a threat to biological resources.

UNIONID FRESHWATER MUSSELS

Freshwater mussels in the family Unionidae (Phylum Mollusca, Class Bivalvia, Order Unionoidea, superfamily Unionacea) descended from salt water mollusks approximately 400 million years ago (Oesch 1984). Unionids originated in Southeast Asia and dispersed west across Eurasia to Europe, and east across the Bering land bridge to North America (Banarescu 1971). Ancestors of many recent forms of Unionidae diversified in western North America during the Cretaceous, and the few that survived

the extinction at the end of the Cretaceous moved eastward when the intracontinental seaway closed (Watters 1994a). The southeastern United States has become a secondary dispersal center for Unionidae (Banarescu 1971). Davis and Fuller (1981) recognize three subfamilies of Unionidae (Margaritiferinae, Anodontinae, and Ambleminae) and four tribes in Ambleminae (Gonideini, Pleurobemini, Lampsilini, Amblemini).

Biology

Diet and Habitat

Unionids are filter feeders that primarily consume detritus (Coker et al. 1921, Fuller 1974, James 1987). Coker et al. (1921) described the work of Franz Schrader who demonstrated with four representative species that there was no apparent discrimination in feeding (stomach contents corresponded to water content) and there were no discernible feeding differences among species. Food has not been found to be limiting to freshwater mussels in Bavarian trout streams (Bauer et al. 1991). Similarly, Bronmark and Malmqvist (1982) found little evidence of trophic competition among unionids.

Freshwater mussels appear to be tolerant of a range of habitat types between the intolerable limits of shifting sand or bare rock (Coker et al. 1921, Cvancara 1970). Kelner and Balding (1995) report that riverine mussels in Wisconsin were distributed evenly across mussel beds, regardless of depth or substrate type. Brim-Box (1995) found few differences in mussel species density or diversity among habitat types (bank, slope, middle of channel) in a survey of the Apalachicola, Chattahoochee, and Flint rivers. However, certain habitat types may be preferred by unionids as a whole. Way et al.

(1989) found higher mussel density and diversity at inshore vs. offshore sites in the lower Tennessee River, and noted that inshore sites had lower current velocity.

There is little evidence of species-specific habitat differences among unionids (Fuller 1980). Strayer (1981) found that 21 of 22 species in small Michigan streams occupied a wide range of microhabitats in terms of current speed, proximity to shore, substrate, depth, and presence of vegetation. Holland-Bartels (1990) found broad habitat tolerances among 30 species in the upper Mississippi River, and concluded that few interspecific differences in habitat preference exist. Layzer and Madison (1995) found no species-specific patterns with respect to depth among 17 species in Horse Lick Creek, Kentucky. Salmon and Green (1983) found that most mussel species in the Middle Thames River, Ontario, occurred in shallow water with slow flow and coarse substrate, but there were few species specific differences among unionids.

Unionids are fairly tolerant of natural environmental stresses and variability. Mussels can survive at low levels of dissolved oxygen and can tolerate periods of anoxia (Imlay 1971). Although low temperature may stunt growth or limit distributions, mussels are tolerant of temperature fluctuations (Fuller 1974). However, they are fairly susceptible to human-induced stress. High levels of sedimentation are known to adversely affect freshwater mussels (Ellis 1933). There is some indication that ammonia can be toxic to freshwater mussels (Horne and McIntosh 1979). Bauer (1983) found a positive relationship between freshwater mussel mortality and phosphate, calcium, and pH, in five streams of North Bavaria, which he interpreted as the negative effect of eutrophication on mussel survival.

Life cycle

Breeding among unionids takes place once a year, when sperm is shed by the male and drawn into a downstream female on inhalant current. Age at first reproduction for most species is in the range of 4-6 years (Yokley 1972, Zale and Neves 1982, Weaver et al. 1991). Unionid species use one of two breeding strategies: long-term breeders breed from mid-summer through fall and release larvae in the following spring (Anodontinae and Lampsilini), while short-term breeders breed in the spring and release larvae by late summer of the same year (Pleurobemini and Amblemini) (Ortmann 1911, Fuller 1974).

All North American unionacean larvae, known as glochidia, have an obligate parasitic stage on freshwater fish, with the exception of *Simpsonichoncha ambigua*, which parasitizes the mud puppy, *Necturus maculosa* (Figure 1.2) (McMahon 1991).

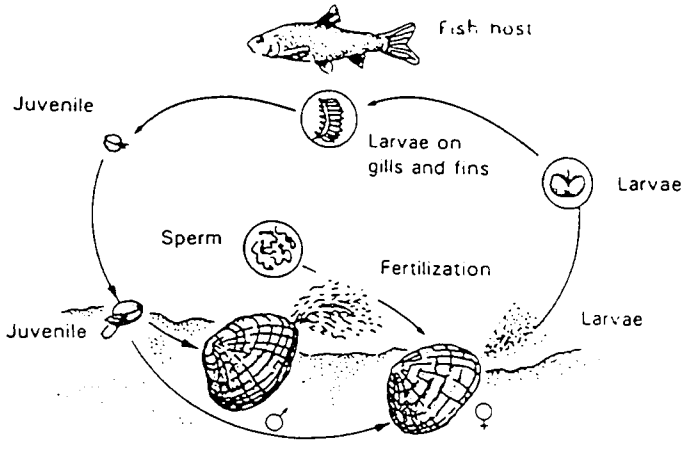


Figure 1.2. Diagram of mussel life cycle.

Hosts provide nourishment, dispersal, and protection for glochidia. Glochidial release corresponds with either the spawning or migration of host fish species (McMahon 1991). Davenport and Warmuth (1965) and Anders and Wiese (1993) have shown that

glochidial release in two species of *Anodonta* is timed so that glochidia infect anadromous hosts during their upstream migration. Glochidial release takes place over a period of weeks to months (Wiles 1975, Trdan 1981, Widlak 1982, Yeager and Neves 1986, Weaver et al. 1991). Through gradual glochidial release, mussel species avoid massive infection of individual fish and increase chances for survival (Tudorancea 1972).

Upon release from the parent, unionid glochidia may attach to a fish and encyst within 2-36 hours of attachment. Attachment site depends of the form of the glochidia. Hooked glochidia, possessed by the Anodontinae (Stein 1971), attach to tougher parts of the fish such as fins or scales (Fuller 1974, Coker et al. 1921). Hookless glochidia, possessed by Margaritiferinae, all Amblemini, and most Lampsilini, attach to gills (Stein 1971). Axe-head glochidia, found in only three species of the Lampsilini genus *Potamilus* (Fuller 1974, Coker et al. 1921), have a rounded ventral margin that resembles an axe-head. Their attachment site is unknown (Stein 1971). Glochidia do not appear to be host-specific in attachment (Davenport and Warmuth 1965): Wood (1974) has found that glochidia will readily attach to paper tissue. However, glochidia of a particular mussel species can only encyst and develop successfully on a subset of fish species. Once attached to an appropriate host, glochidia remain encysted from 6-160 days (McMahon 1991), depending on temperature (Stein 1971, Jirka 1986).

The larval phase of the mussel life cycle is characterized by low survival and unpredictable recruitment, while the adult phase is characterized by high survival and stability. Although mussels release from 75,000 to 3,000,000 glochidia per adult, the vast majority of glochidia fail to attach to a suitable host (Coker et al. 1921, Fuller 1974).

Mortality during attachment has been estimated at 99.9996% (Young and Williams 1984). Freshwater mussel communities exhibit high annual variation in recruitment (Payne and Miller 1989). Mortality of juveniles is also high between the steps of excystment and establishment on appropriate substrate (Neves and Widlak 1987). Adult survivorship of freshwater unionids is at or about 80% per year (Negus 1966). Life span for most species is in the range of 10-15 years (Tudorancea 1972, Lewandowski and Stanczykowska 1975) but can range up to nearly 100 years (Zale 1980). Species composition appears relatively stable on ecological (Norelius 1967, Dennis 1984), historical (Fuller 1980), and archaeological (Bogan 1990) time scales.

Ecology

The relationship between mussels and host fish

An increase in glochidial infection has a negative effect on the condition of juvenile fishes (Cunjak and McGladdery 1991). Laboratory infections have demonstrated that there is a limit to the level of infection that an individual fish can sustain (Wiles 1975, Meyers and Milleman 1977). However, natural glochidial infection rates are fairly light, and not physically limited by space (Stern and Felder 1978, Trdan and Hoeh 1982, Neves and Widlak 1988). Carrying capacity may be determined by the host immune response: a series of 2-3 infections of a host fish by glochidia has been shown to increase the resistance of that fish to future infections (Fuller 1974, Bauer et al. 1991). The immune response may also determine host specificity (Isom and Hudson 1984, Waller and Mitchell 1989). Kirk (1995) found that *Venustaconcha sima* glochidia

developed on the non-host fish species *Etheostoma spectabile* after cortisol-induced suppression of the fish species' immune response, suggesting that the immune response precluded successful attachment of *V. sima* glochidia. A successful long-term infection may reflect the ability of glochidia to block host fish antibodies (O'Connell 1991).

Freshwater mussels have evolved varying strategies for attracting fish hosts. Anodontinae commonly discharge glochidia within a mucous secretion that helps to keep them suspended (Stein 1971). Wood (1974) notes that *Anodonta cygnea* glochidia possess a mucosal thread that increases time afloat and contact with fish hosts. In many species, glochidia are ejected as a unit that resembles a worm or an insect larvae (food items commonly taken by fish) (Stein 1971, Kat 1984, Hartfield 1996). *Epioblasma capsaeformis* females (unlike other *Epioblasma* species) possess a blue mantle that they display during glochidial release (Hill 1986). In some species of the *Lampsilis* genus, females have a modified mantle edge that mimics the motions of a small fish, so that larger fish are attracted and potentially infected (Stein 1971). A strategy recently confirmed for two mussel species involves the suspension of a glochidial unit resembling a small fish on a thread up to 4 feet long (Haag et al. 1995, O'Brien et al. 1995).

Mussels may have a mutualistic relationship with fish. Ziuganov and Zotin (1995) have suggested that the interaction between the pearl mussel *Margaritifera margaritifera* and its host the Atlantic salmon *Salmo salar* is mutually beneficial, where the mussels filter river water and improve habitat for salmon spawning, and the salmon are infected by glochidia while spawning over mussel beds. Moy (1991) has found in laboratory studies that mussels beds may attract fish by providing firm substrate for colonizing

invertebrates, which serve as food for the fish. Watters (1992) found that for 37 sub-basins of the Ohio River (including the Tennessee River), mussel species number was positively related to number of fish species (r^2=0.92).

Role in ecosystem

Mussels are both ecologically and economically important in aquatic ecosystems. Predators of freshwater mussels include otters, mink, muskrats, hogs, raccoons, fishes, turtles, birds, and humans (Fuller 1974). Muskrats are the dominant predator of unionids (Convey et al. 1989), but effects of predation on mussel populations in the Clinch River (Tennessee/Virginia) were observed to be slight (Dennis 1984). Freshwater mussels were used by native North Americans for food, jewelry, tools, and temper for pottery (Bogan 1990). In the late 1800s through the 1950s, mussel shells were used in the pearl button industry. Recently, mussels have been used in the cultured pearl industry. Their shells are cut into beads that serve as nuclei for cultured pearls in oysters (Cummings and Mayer 1992). Mussels are also important as biological monitors of pollution.

Diversity and status

The family Unionidae is very speciose, with 292 species found in North America (Williams et al. 1992). The highest diversity in North America occurs in the Southeast. The regions of the Southeast supporting the highest diversity include the Cumberland River in Kentucky/Tennessee, with 94 species (Gordon and Layzer 1989), the Coosa River in Alabama/North Carolina/Tennessee, with 65 species (Hurd 1974), and the upper Tennessee River, with 93 species (Ahlstedt and Rashleigh, in review).

Currently, taxa of the family Unionidae are experiencing a reduction in population

size, as well as a loss of species diversity. At present, 213 North American freshwater mussel species and sub-species have federally protected status, and 21 are presumed extinct (Williams et al. 1992). Current extinctions are considered in the "kilo-death" range (Nott et al. 1995). In the last 100 years the fauna, especially members typically found in silt-free riffle areas, has declined (Ahlstedt 1984, Hill 1986). The major causes are habitat loss, pollution, and sedimentation (Neves 1993). Conservation efforts, based on an understanding of the mussel ecology, will be crucial to the protection of this fauna.

COMMUNITY STRUCTURE

Community structure refers to the number, identities, and abundances and distributions of species in an ecological community. The number of species (sometimes termed species richness), identities, and abundance and distribution are typically measured by field survey. Field data must be considered estimates of true community parameters, due to the variability introduced by sampling methods, duration, timing, and effort, and the difficulty of collecting rare organisms. Measurement of these parameters is further complicated by taxonomic difficulties in the identification of distinct species, and the uncertainty of community boundaries, in terms of time, space, and taxa (Drake 1990). Despite these difficulties, studies of community structure have received much attention in ecology.

There are two main schools of thought regarding how communities are structured, one that emphasizes biotic processes and the other that believes abiotic processes are more important. Proponents of the "biotic school" believe that competition, which is

defined as an interaction between two species that is detrimental to both, is responsible for most of the patterns in communities. The presence of competition in natural communities has been documented in two major review papers: Schoener (1983) summarized 164 studies where approximately 90% showed competition; and Connell (1983) summarized 72 studies, where competition was demonstrated in more than half of the studies. Early studies of plant species (Tansley 1917) and flour beetles (Park 1948) showed that the environment can affect the outcome of species interactions. The "abiotic school" of thought would argue that disturbances, stresses, and extreme conditions are the primary limits on community structure and diversity patterns. Abiotic processes and conditions may control and limit populations enough that they do not experience strong competition (Andrewartha and Birch 1954, Hairston et al. 1960). Although both biotic and abiotic processes occur in all communities, it is likely that a specific community will be more strongly structured by one or the other (Grossman et al. 1982).

Biotic control of community structure

The "biotic school" of community structure is based on the idea that organisms that are complete competitors cannot coexist at competitive equilibrium. This idea, which is called the Competitive Exclusion Principle (CEP) (Hardin 1960), was supported by the mathematical work of Lotka (1925) and Volterra (1926), who demonstrated that exclusion would occur if interspecific effects were greater than intraspecific effects. The CEP was also supported by the experimental work of Gause (1932, 1934) and Park (1948), who demonstrated exclusion of a poorer competitor in the laboratory. According

to classical competition theory, similar species can coexist under stable equilibrium conditions because they differ from each other in at least one ecological characteristic, which allows them to utilize different portions of the limiting resources (Schoener 1974). This resource partitioning can involve food, habitat, or reproductive resources, and may occur in either time or space (Schoener 1986). Theoretical work by MacArthur and Levins (1967) and May (1974) suggested that there is a limiting similarity between species. However, Abrams (1983) found that models with competition in different dimensions and with alternate utilization curves lead to alternate limits to similarity.

The classic view of multi-species communities in ecology is that they are structured by competition. Models have demonstrated that including competition among species in a system of patches reduced the number of species that could coexist locally under equilibrium conditions (Hanksi 1983, Caswell and Cohen 1993). Diamond (1975) proposed that some pairs of species that compete can never coexist, which will lead to negatively associated distributions of species across a collection of sites. Classical competition theory considers species richness patterns across a region as predictably structured by local competition for limiting resources (Schluter and Ricklefs 1993). Regional species richness at competitive equilibrium is determined by the limiting similarity between species and the total niche space available (MacArthur 1965).

Abiotic control of community structure

The "abiotic school" of community ecology focuses on the role of the environment in determining pattern, and assumes that competitive equilibrium, and therefore

competitive exclusion, is prevented or delayed by environmental conditions and variability (Hutchinson 1961). These dynamics have been explored by Chesson and Warner (1981), who have proposed that temporal variability in birth rates allows persistence of species with overlapping habitat requirements. Coexistence among competitors is maintained by temporal variability because the better competitor is at a high enough density that it is limited by its own density, but a poorer competitor is less limited by intraspecific competition and therefore able to increase at a rate near its intrinsic rate of increase when it is favored (Chesson 1986, 1994).

Patterns across patches that are connected by local dispersal may be structured by abiotic processes and conditions, such as the stochasticity of immigration and the spatial configuration of patches. A set of models developed by Levins (1969) and Hanski (1982) describe changes in patch occupancy frequency as the result of differences between the immigration and emigration rates between patches, where immigration and extinction may be dependent on the total number of sites occupied. Hanski's model incorporates the "rescue effect" (Brown and Kodric-Brown 1977) where dispersal among patches can supplement local populations and may homogenize sites. Regional community patterns may also be predominantly structured by the spatial and temporal heterogeneity of the environment. Hubbell and Foster (1986) hypothesize that the unpredictability introduced into competition by the environment may lead to similarity and generalization among species. If communities are influenced by environmental heterogeneity, history and chance may determine patterns at a particular site (Shmida and Ellner 1984, Hubbell and Foster 1986, Cornell 1993).

DISSERTATION OVERVIEW

This study endeavors to explain the structure of freshwater mussel communities in the upper Tennessee River system. This study focuses on a single tribe of freshwater mussels, the Lampsilini, because species of this taxa use similar fish host resources and may potentially compete. This dissertation focuses on the alternative hypotheses that communities are structured by competition for hosts or by abiotic processes. Experimentation is not feasible in freshwater mussel communities, due to their longevity and protected status. Here, modelling is used to explore the patterns that are generated when different processes are specified, to delineate conditions under which different processes will be important, and to generate predictions to which field data are compared.

A multi-scale approach is used in this dissertation because communities at different scales may appear to be structured by different processes (Rahel et al. 1984, Levin 1992, Holling 1992, Ricklefs and Schluter 1993). Structure is considered at local, meso, and regional scales, which correspond to chapters 2, 3, and 4, respectively. Chapter 2 considers coexistence of similar species in an area where they are potentially competing for the same resources on an ecological time scale. Chapter 3 considers species number and composition in a collection of local communities connected by dispersal in historical time. Chapter 4 considers species richness in a region, a collection of mesoscale communities connected by colonization in evolutionary time. Chapter 5 synthesizes findings at each scale to develop a general explanation for freshwater mussel community structure in the upper Tennessee River basin.

CHAPTER II. CONDITIONS FOR LOCAL COEXISTENCE OF FRESHWATER MUSSEL SPECIES

INTRODUCTION

Local communities of freshwater mussels of the family Unionidae in the upper Tennessee River support coexisting populations of species that are similar in terms of their use of food and habitat resources (Coker et al. 1921, Fuller 1980, Strayer 1981). To some extent, they are also similar in their use of fish hosts, on which virtually all North American freshwater mussel larvae (glochidia) are obligate parasites for a period of weeks. This pattern of coexistence seems inconsistent with ecological theory, which argues that similar species should experience competition. Because it is infinitely unlikely that two similar species will be perfectly balanced in their abilities to use resources, the stronger competitor is expected to outcompete the poorer competitor and force its exclusion in ecological time. The mechanism by which similar species coexist, despite their use of similar resources, has received much attention in ecology.

According to classical competition theory, similar species coexist because they differ from each other in at least one ecological characteristic, which allows them to utilize different portions of the resource spectrum (Schoener 1974). This resource partitioning can involve food, habitat, or reproductive resources, and may occur in either time or space (Schoener 1986). Differences in species' use of resources has been recognized in several studies: Schoener (1974) found complementary differentiation among lizard species along dimensions of habitat, vertical space, and food; Cody (1968) noted complementary differentiation among bird species in terms of habitat, vertical

space, and food; and Emmons (1980) reported differentiation of African tree squirrel species along habitat and food dimensions. Early theoretical work by MacArthur and Levins (1967) and May (1974) suggested that possibility that there is a limiting similarity between species. However, Abrams (1983) found that models with competition in different dimensions and with alternate utilization curves lead to alternate limits to similarity. Recent work in resource partitioning has focused on trade-offs between two species that allow coexistence when each species is more successful on a different resource (Tilman 1982, Abrams 1987) or combination of resources and physical factors (Tilman and Pacala 1993), or if species have different encounter efficiencies with each resource (Vincent et al. 1996).

More recently, ecologists have recognized that the time to competitive exclusion can be long, and competitive outcome may be slowed or altered by temporal variability (Hutchinson 1961). Chesson and Warner (1981) have proposed that temporal variability in birth rates allows persistence of species with overlapping habitat requirements for coral reef fish in a space-limited environment, if the mean advantage of one species over another does not override the effects of variability. Coexistence is maintained by temporal variability because the better competitor is at a high enough density that it is limited by its own density, and cannot respond to periods when it is favored, but a poorer competitor is less limited by intra-specific competition and therefore able to increase at a rate near its intrinsic rate of increase when it is favored (Chesson 1986, 1994). Warner and Chesson (1985) note that this mechanism is effective when both reproductive and adult survival rates are high, and reproductive success is determined by lottery.

Either resource partitioning or temporal variability could promote coexistence of freshwater mussel species. These species do not appear to partition either food or habitat resources (Bronmark and Malmqvist 1982, Strayer 1993). Larvae of a given species of mussel can only develop successfully on a subset of the fish species available in a given area (Hill 1986, Bauer and Vogel 1987, Waller and Holland-Bartels 1988), so species that do not overlap in host use could be expected to coexist. However, species that overlap on hosts may compete. Species known to overlap on hosts have been shown to use different attraction strategies (Moy 1991, Luo 1993), and may coexist through resource partitioning (Fuller 1980, Dennis 1984). There is a high level of variability in mussel recruitment (Payne and Miller 1989, Whitney et al. 1996), and Townsend (1989) has noted that temporal variation in physical conditions is significant in stream communities; it is possible that species coexistence is related to temporal variation.

Here, a modelling approach was used to derive the conditions for coexistence of two species in competition for space as adults, and discrete, substitutable resources during recruitment. A series of models was developed and solved analytically for the cases of recruitment limitation and overlap on resources during recruitment. Invasibility analysis (Turelli 1981) was used to test for coexistence. This approach assumes that a particular species has been introduced to the system at very low density after the other species has had sufficient time to reach its maximum population size. A successful invasion occurs under the condition that low-density growth rate for an invading species is greater than one. A simulation approach was used to determine whether uniformly distributed variability introduced into the fecundity parameter promotes coexistence.

Two model predictions were examined for two species known to overlap on hosts, *Lampsilis fasciola*, the wavy-rayed lampmussel, and *Villosa iris*, the rainbow shell.

THE MODELS

Relative importance of reproductive resource limitation

First, a model of competition between two species for one resource, such as space or food, that is required by all species, is developed. The equation describing number density of an arbitrary species at a given time step is written as

$$N_j(t+1) = \frac{N_j(t) \cdot (S_j)}{1 + \left[\sum_{m=1}^{M} \alpha_{mj} N_m(t)\right]} + \frac{N_j(t) \cdot (f_j s_j)}{1 + \left[\sum_{m=1}^{M} \gamma_{mj} N_m(t)\right]}. \qquad (2.1)$$

Separate terms are used to describe adult and larval dynamics. Adult survival rate in the absence of competitive effects is represented as S, and density dependence of adult survival is represented as the sum of each species' density multiplied by the competitive effect of each species on the species in question. Here α_{mj} represents the competitive effect of adults of species m on adults of species j (see Appendix A for a full listing of parameters). The rate of larval production of species j is represented as the product of the parameter f_j, which represents fecundity, and s_j, the survival of larvae in the absence of competitive effects. Larval production rate is assumed to be density dependent, and γ_{mj} represents the competitive effect of adults of species m on larvae of species j. Separate terms are used to represent the competitive effects of adults on other adults and the effects of adults on larvae, because it is assumed that the former will generally be

stronger. Additionally, this model assumes that all yearlings and adults are reproducing, adult and post-larval survival have the same form, and there is a negligible effect of larvae on adults and on each other for space and food.

The conditions for invasibility for species *i* can be established by first assuming that species *i* is removed and all other species reach their maximum densities. In a two-species case (*i* and *j*), the equation for the number density of species *j* would be

$$N_j(t+1) = \frac{N_j(t) \cdot (S_j)}{1+\alpha_{jj}N_j(t)} + \frac{N_j(t) \cdot (f_j s_j)}{1+\gamma_{jj}N_j(t)} , \tag{2.2}$$

so that for large values of N_j the equilibrium value would be

$$N_j^* \approx \frac{(S_j)}{\alpha_{jj}} + \frac{(f_j s_j)}{\gamma_{jj}} . \tag{2.3}$$

Species *i* will be able to invade the system if its low-density growth rate is positive, that is, if $N_i(t+1)/N_i(t) > 1$. The condition for invasibility of species *i* is then

$$1 < \frac{(S_i)}{1+\alpha_{ji}N_j^*} + \frac{(f_i s_i)}{1+\gamma_{ji}N_j^*} . \tag{2.4}$$

Equation (2.3) can be substituted into equation (2.4). If it is assumed that N_j^* is large, the substitution of equation (2.3) into equation (2.4) becomes

$$1 < \frac{(f_i s_i \alpha_{ji} + S_i \gamma_{ji}) \cdot \alpha_{jj} \cdot \gamma_{jj}}{\alpha_{ji}\gamma_{ji}[(S_j)\gamma_{jj} + (f_j s_j)\alpha_{jj}]} . \tag{2.5}$$

If it is specified that $\alpha_{jj} = \alpha_{ji} = \gamma_{jj} = \gamma_{ji}$, equation (2.5) reduces to

$$(S_i) + (f_i s_i) > (S_j) + (f_j s_j) . \tag{2.6}$$

Similarly, the condition for the invasibility of species j to a system of species i is

$$(S_i) + (f_i s_i) < (S_j) + (f_j s_j) . \tag{2.7}$$

Clearly, equations (2.6) and (2.7) cannot be satisfied simultaneously. The species with the highest survival and fecundity parameters exclude the poorer competitor.

If resources used by larvae differ from resources needed by adults, and each species uses different reproductive resources, equation (2.1) can be rewritten as

$$N_j(t+1) = \frac{N_j(t) \cdot (S_j)}{1 + \left[\sum_{m=1}^{M} \alpha_{mj} N_m(t) \right]} + \frac{N_j(t) \cdot c_j (f_j s_j) \cdot K_j F}{1 + c_j N_j(t) f_j}, \tag{2.8}$$

where K_j represents the average capacity of glochidia of species j on a host fish, F represents the density of hosts or habitat available, and c_j represents the success of the larvae of species j in obtaining reproductive resources. The number of new recruits is limited by the density of larvae in competition for reproductive resources. When N_j is large, the upper limit of new recruits is set by equation (2.8) at approximately $s_j K_j F$.

In a two-species case, the maximum population size that species j can obtain is

$$N_j^* \approx \frac{S_j}{\alpha_{jj}} + s_j K_j F , \tag{2.9}$$

assuming that species i is not present. The invasibility condition for species i is given by

$$1 < \frac{(S_i)}{1 + \alpha_{ji} N_j^*} + c_i (f_i s_i) \cdot K_i F . \tag{2.10}$$

If the expression for N_j^* given by equation (2.9) is substituted into equation (2.10), the

invasibility condition becomes

$$1 < \frac{(S_i)}{1 + \alpha_{ji}\left(\frac{S_j}{\alpha_{jj}} + s_j K_j F\right)} + c_i (f_i s_i) \cdot K_i F . \qquad (2.11)$$

Species i can increase if enough reproductive resource space is available. If fish host densities are too low, species i will go to extinction.

To compare the relative importance of recruitment limitation to adult limitation, the N_j^* calculated from recruitment limitation (equation (2.9)) is used in the invasibility condition for species i where adults and larvae used the same resources (equation (2.4)):

$$1 < \frac{(S_i)}{1 + \alpha_{ji}\left(\frac{S_j}{\alpha_{jj}} + s_j K_j F\right)} + \frac{(f_i s_i)}{1 + \gamma_{ji}\left(\frac{S_j}{\alpha_{jj}} + s_j K_j F\right)} . \qquad (2.12)$$

If it is assumed that N_j^* is large, and $\alpha_{jj} = \alpha_{ji} = \gamma_{jj} = \gamma_{ji}$, equation (2.13) reduces to

$$1 < \frac{(S_i) + (f_i s_i)}{(S_j) + \alpha_{ji} s_j K_j F} , \qquad (2.13)$$

and if it is further assumed that $S_i = S_j$, equation (2.12) reduces to $\alpha_{ji} s_j K_j F < f_i s_i$.

Here, decreases in K_j or F promote coexistence. Under conditions of complete reproductive resource partitioning, mussels can not competitively eliminate each other when reproductive resources are limiting. However, if fish densities are too high, i.e.,

$$F > (f_i s_i) / (\alpha_{ji} s_j K_j) , \qquad (2.14)$$

adult interactions will dominate, and the best competitor will exclude the other species.

Coexistence under overlap conditions

If mussel species that overlap in their use of reproductive resources experience competition for these resources, different conditions for coexistence may apply. Here it is assumed that hosts or habitat used by larvae can be represented as either a single resource or a number of resources, each of which a species obtains equally. The equation describing the number density of a particular mussel species *j* at a given time becomes

$$N_j(t+1) = \frac{N_j(t)\cdot(S_j)}{1+\left[\sum_{m=1}^{M}\alpha_{mj}N_m(t)\right]} + \frac{N_j(t)\cdot c_j(f_j s_j)\cdot K_j F}{1+c_j\sum_{m=1}^{M}C_{mj}N_m(t)f_m}. \qquad (2.15)$$

Equation (2.15) maintains the adult survival term and the density-dependent limit on the number of larvae using a resource used in equation (2.8), but additionally incorporates competition from species with overlapping resource requirements as the competitor's larval density multiplied by the effect of competition on the species in question. The term C_{mj} is used to represent the effect of a larvae of species *m* on one of species *j*. In a two-species case (*i* and *j*), the invasibility condition for species *i* is given by

$$1 < \frac{(S_i)}{1+\alpha_{ji}N_j^*} + \frac{c_i(f_i s_i)\cdot K_i F}{1+c_i C_{ji}N_j^* f_j}. \qquad (2.16)$$

If N_j^* is assumed to be large, equation (2.16) reduces to

$$1 < [S_i C_{ji} f_j + f_i s_i \alpha_{ji}(K_i F)] \Big/ \left(\alpha_{ji} C_{ji} f_j N_j^*\right). \qquad (2.17)$$

The maximum population size that species *j* can obtain, assuming that species *i* is not present, is still given by equation (2.9). When this expression is substituted into equation

(2.17), and it is assumed that $\alpha_{jj} = \alpha_{ji}$ and $S_i = S_j$, equation (2.17) reduces to

$$C_{ji} f_j s_i (K_j F) < C_{jj} f_i s_i (K_i F) . \tag{2.18}$$

If it is assumed that $s_i = s_j$, $f_j = f_i$, and $K_j = K_i$, equation (2.18) reduces to $C_{ji} < C_{jj}$. Similarly, the condition for species j invading a system of species i is $C_{ij} < C_{ii}$. These are the coexistence conditions for traditional Lotka-Volterra systems: intraspecific competition must be greater than interspecific competition (Lotka 1925, Volterra 1926). If the C parameter is defined as

$$C_{mi} = c_m / c_i \tag{2.19}$$

where c_i represents the reproductive ability of species i (therefore $C_{ii} = 1$), the coexistence conditions become $c_j / c_i < 1$ and $c_i / c_j < 1$. Since these cannot simultaneously be true, the stronger competitor will exclude the other.

For the case of separate, substitutable resources, recruitment dynamics can be described by a generalization to two resource pools for the Beverton-Holt equation:

$$N_j(t+1) = \frac{N_j(t) \cdot \left(S_j\right)}{1 + \sum_{m=1}^{M} \alpha_{mj} N_m(t)} + \frac{N_j(t) \cdot \left(f_j s_j\right) \cdot r_j}{1 + r_j \left(1 / \left\{ \sum_{h=1}^{H} \left[\left(K_{jh} \cdot F_h\right) \div \left(\sum_{m=1}^{M} C_{mjh} N_m(t) f_m \right) \right] \right\} \right)}, \tag{2.20}$$

where the parameter r is defined as

$$r_j = \sum_{h=1}^{H} (F_h \cdot c_{jh}) . \tag{2.21}$$

The term C_{mjh} represents the competitive effect of species m on species j for resource h:

$$C_{mjh} = c_{mh}/c_{jh}. \tag{2.22}$$

The net competition experienced by an individual is calculated as the harmonic mean of the competition experienced for each resource pool. This formulation is used because this assumes that the entire resource pool is available to both species simultaneously.

The invasibility condition for species *i* derived from equation (2.20) is

$$1 < \frac{(S_i)}{1+\alpha_{ji}N_j^*} + \frac{(f_i s_i)\cdot r_i}{1+r_i\left(1/\left\{\sum_{h=1}^{H}\left[(K_{ih}\cdot F_h)/\left(C_{jih}N_j^* f_j\right)\right]\right\}\right)}. \tag{2.23}$$

for the two-species case (*i* and *j*). Assuming N_j^* is large, this can be rearranged to

$$\frac{C_{ji1}C_{ji2}f_j}{K_{i1}F_1C_{ji2}+K_{i2}F_2C_{ji1}} < \frac{(f_i s_i)}{N_j^* - (S_i)/\alpha_{ji}}. \tag{2.24}$$

Assuming that species *i* is absent, the maximum population size species *j* can obtain is

$$N_j^* \approx \frac{(S_j)}{\alpha_{jj}} + (s_j)\left(\frac{K_{j1}F_1}{C_{jj1}} + \frac{K_{j2}F_2}{C_{jj2}}\right). \tag{2.25}$$

If equation (2.25) is substituted in equation (2.24), and it is assumed that $S_i = S_j$, $C_{jj1} = C_{jj2} = 1$, and $\alpha_{jj} = \alpha_{ji}$, equation (2.24) reduces to:

$$K_{j1}F_1 + K_{j2}F_2 < \left(\frac{K_{i1}F_1}{C_{ji1}} + \frac{K_{i2}F_2}{C_{ji2}}\right)\cdot\left(\frac{f_i s_i}{f_j s_j}\right). \tag{2.26}$$

Similarly, the condition for species *j* invading a system of species *i* is given by

$$K_{i1}F_1 + K_{i2}F_2 < \left(\frac{K_{j1}F_1}{C_{ij1}} + \frac{K_{j2}F_2}{C_{ij2}}\right)\cdot\left(\frac{f_j s_j}{f_i s_i}\right). \tag{2.27}$$

Coexistence is determined by the parameters K, F, C, f, and s. Clearly, an increase in a species' fecundity (f) or larval survival (s) will increase its ability to coexist.

To illustrate the effects of resource use (C parameter) on coexistence, it is further assumed that $f_i s_i = f_j s_j$, $K_{i1} = K_{j1}$, $K_{i2} = K_{j2}$, $C_{ji1} = c_{j1}/c_{i1}$, $C_{ji2} = c_{j2}/c_{i2}$, and $F_1 = F_2$, in which case equations (2.26) and (2.27) reduce to

$$(c_{i1}/c_{j1} + c_{i2}/c_{j2}) > 2 \text{ and } (c_{j1}/c_{i1} + c_{j2}/c_{i2}) > 2, \tag{2.28}$$

respectively. The conditions given in equation (2.28) are shown in Figure 2.1, assuming $c_{j1} = c_{j2} = 0.5$. According to Figure 2.1, coexistence occurs in a wide range of parameter space when species are sufficiently different in their resource use, such that one species is more successful in using one resource and the other species is more successful with the other resource. As the strategies of the species become more similar, the range of coexistence narrows, including only those species whose overall attraction abilities are approximately evenly matched. When the strategies of both species are very similar, there is an exceedingly small range of parameter space which allows coexistence, however, points in this space would be structurally unstable.

The effect of resource density on coexistence can be illustrated by the rearrangement of equations (2.26) and (2.27) to solutions for limits to coexistence and zero-net growth isoclines, under the following assumptions: $f_i s_i = f_j s_j$, $K_{i1} = K_{j1}$, $K_{i2} = K_{j2}$, $C_{ji1} = c_{j1}/c_{i1}$, $C_{ji2} = c_{j2}/c_{i2}$. Limits to coexistence describe levels of resource densities for which coexistence is possible:

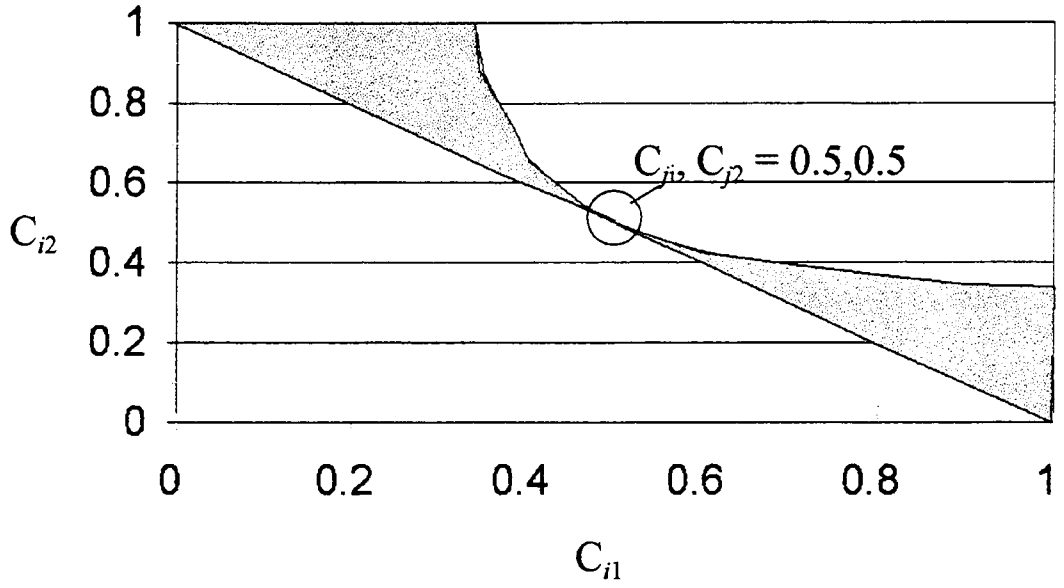


Figure 2.1. Conditions for coexistence in competitive-ability state space. The parameters c_{i1} and c_{i2} represent the success of mussel species i in attracting host fish species 1 and 2, respectively. This figure shows the range of c_{i1} and c_{i2} parameters that allow coexistence when the strategy of species j is given by $c_{j1} = 0.5$ and $c_{j2} = 0.5$ (coexistence occurs in the shaded area). As the two species become more similar in terms of attraction success parameters, the range of parameter space promoting coexistence narrows.

$$(F_2)_i > \left(\frac{F_1}{C_{ji1}} - F_1\right) \Big/ \left(1 - \frac{1}{C_{ji2}}\right) \tag{2.29}$$

$$(F_2)_j > \left(\frac{F_1}{C_{ij1}} - F_1\right) \Big/ \left(1 - \frac{1}{C_{ij2}}\right). \tag{2.30}$$

Zero net growth isoclines (Tilman 1982), resource levels below which species cannot survive, are calculated from equation (2.20) for small populations of species i and j as:

$$(F_2)_i = \frac{(1 - S_i)}{f_i s_i c_{i2}} - \frac{c_{i1}}{c_{i2}} F_1 \tag{2.31}$$

$$(F_2)_j = \frac{(1 - S_j)}{f_j s_j c_{j2}} - \frac{c_{j1}}{c_{j2}} F_1. \tag{2.32}$$

The conditions in equations (2.29-2.32) are shown in Figure 2.2 when c_{i1}, c_{i2}=(0.7, 0.3), c_{j1}, c_{j2}=(0.4, 0.6), and $f_i s_i = f_j s_j$. Limits of the ratios of F_2/F_1 which allow stable coexistence of the two mussel species appeared as straight lines in the F_1,F_2 plane such that any ratio in the region bounded by these lines allows coexistence. As the magnitude of both fish host density parameters (F_1,F_2) increases, the distance between the two limits increases. Conversely, the field of coexistence narrows as the magnitudes of F_1 and F_2 decrease. At low values of F_1 and F_2, neither species could survive.

A simulation approach to equation (2.20) was used to perform a sensitivity analysis of this model for a two-species system. The percent change in low-density and average growth rates of an invading species in response to a 10% increase in each of the 17 parameters was determined sequentially. For each simulation, the resident species (j) was allowed to exist alone for 50 time steps, during which it reached an equilibrium

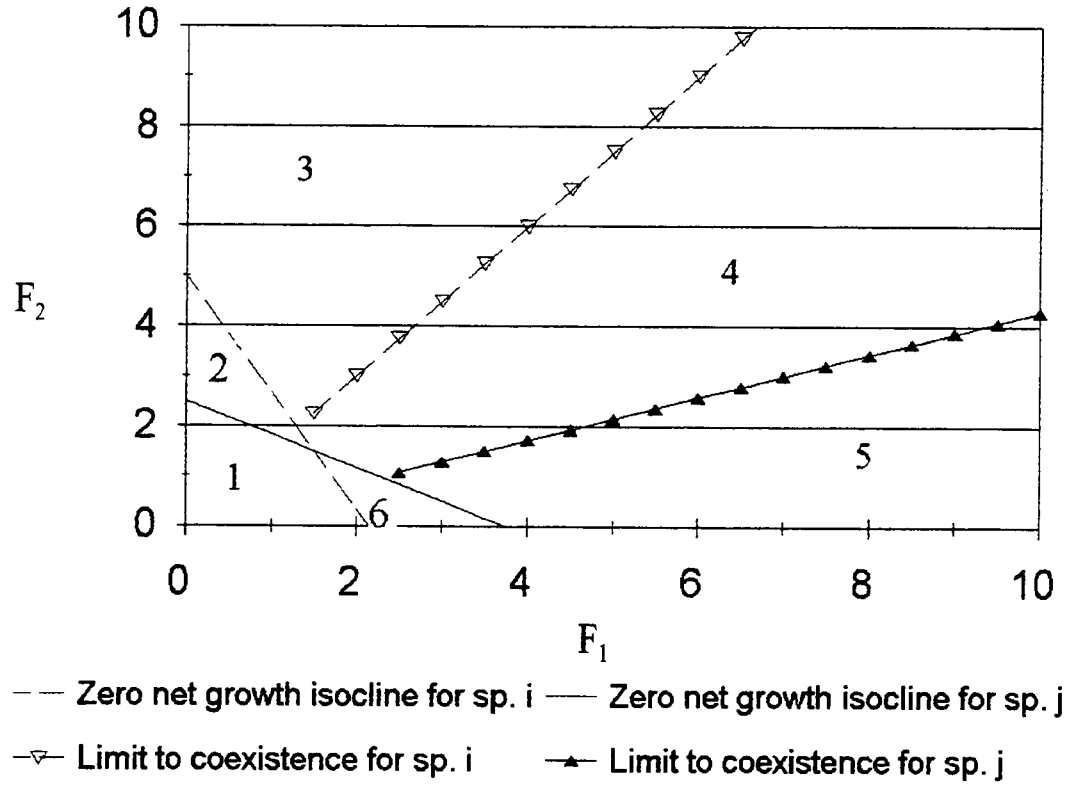


Figure 2.2. Effect of fish host densities on competitive coexistence of two mussel species. Fish host densities are given as F_1 and F_2. Figures shows Zero net growth isoclines for two competing species i and j (taken from equations (2.31) and (2.32)), as well as limits to coexistence for these two species (taken from equation 2.29 and 2.30 for species i and j, respectively). Limits of the ratios of F_2/F_1 which allow stable coexistence of the two mussel species appeared to be straight lines in the F_1,F_2 plane such that any ratio between these two straight lines allowed coexistence when c_{i1}, c_{i2}=(.7,.3) and c_{j1}, c_{j2}=(.4,.6). In region 1, neither species can survive. In region 2, only species i can survive, and in region 6 only species j can survive. In region 3, species i outcompetes species j, in region 5 species j outcompetes species i, and in region 4, the two species coexist.

population size. Then species i was introduced at a density of N=5. Low-density growth rate for species i was calculated as its growth rate between its introduction and the time at which it reached a density of N=50. Average growth rate for species i was calculated as its growth rate over a period of 100 time steps after its introduction.

Sensitivity of low-density and average growth rates of the invading species to changes in parameters is given in Table 2.1. Low-density and average growth rates responded similarly in the sensitivity analysis, although low-density growth rate was more sensitive to change in parameters. The growth rate of the invading species was most sensitive to fecundity and survival parameters, followed by infection success parameters, fish host densities, carrying capacities, and the adult interaction parameter.

Effects of variability

The simulation approach described above was used in determining whether temporal variability in fecundity increases the long-term low-density growth rate of an invading species that is a poorer competitor (under non-variable conditions, the poorer competitor could not coexist). A poorer competitor is defined in terms of its life history and competition parameters, as given by $(f_i s_i) \cdot r_i$. Normally distributed variability at seven standard deviation levels (0, 0.5, 1.0, 1.5, 2.0, 2.5, 3) was introduced into the fecundity parameter f for a two-species case (i and j). A set of 1000 simulations was run for each of the four combination of parameters in Table 2.2 at each variability level: for each set of simulations, the geometric mean of low-density growth rate and number of extinctions for species i were calculated and graphed against standard deviation.

Table 2.1. Sensitivity of low-density and average growth rates of an invading species i to model parameters. Sensitivity is calculated as the percent change in growth rates in response to a relatively small (10%) change sequentially specified in each of the parameters of the model described in equation (2.20).

Parameter	Default parameter value	Percent change	Low-density growth rate (between 5 and 50)	Sensitivity ranking for low-density growth rate (1=most sensitive)	Average growth rate	Sensitivity ranking for average growth rate (1=most sensitive)
α	0.002	+10%	-0.05%	17	-0.04%	17
c_{j1}	0.4	+10%	-1.36%	9	-0.75%	8
c_{j2}	0.6	+10%	-1.50%	8	-0.78%	6
c_{i1}	0.7	+10%	+1.07%	10	+0.42%	10
c_{i2}	0.3	+10%	+2.26%	7	+0.53%	9
F_1	4	+10%	-0.66%	14	-0.32%	14
F_2	4	+10%	+0.10%	16	+0.39%	11
S_j	0.8	+10%	-4.57%	2	-3.50%	1
S_i	0.8	+10%	+5.18%	1	+0.98%	4
s_j	0.4	+10%	-3.10%	6	-2.09%	2
s_i	0.4	+10%	+3.90%	3	+0.83%	5
f_j	0.5	+10%	-3.10%	5	-2.01%	3
f_i	0.5	+10%	+3.72%	4	+0.76%	7
K_{j1}	50	+10%	-0.72%	12	-0.37%	12
K_{j2}	50	+10%	-0.66%	13	-0.29%	15
K_{i1}	50	+10%	+0.33%	15	+0.17%	16
K_{i2}	50	+10%	+0.95%	11	+0.35%	13

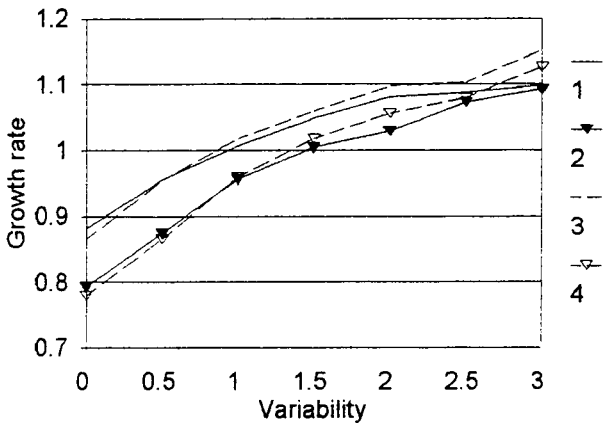
Table 2.2. Parameter combinations used for simulation runs.

Scenario number	Parameters			Assumptions about invader (species i) as compared to resident (species j)
	f_i,f_j	c_{j1},c_{j2}	c_{i1},c_{i2}	
1	(0.5,0.5)	(0.5,0.5)	(0.1,0.6)	Lower/different competitive ability, similar fecundity
2	(0.6,0.4)	(0.5,0.5)	(0.1,0.6)	Lower/different competitive ability, lower fecundity
3	(0.5,0.5)	(0.6,0.6)	(0.4,0.4)	Lower competitive ability, similar fecundity
4	(0.6,0.4)	(0.6,0.6)	(0.4,0.4)	Lower competitive ability, lower fecundity

Temporal variability did promote coexistence of a poorer competitor for the two-species case (Figure 2.3). A poorer competitor that had lower fecundity required a higher level of variability for coexistence. For example, in Figure 2.3a, the growth rate of the poorer competitor in scenario 1, where both species have similar fecundity, exceeds 1 in the range of 0.5 - 1.0 for standard deviation of variability, whereas the growth rate of the poorer competitor in scenario 2, where the poorer competitor also has lower fecundity, exceeds 1 in the range of 1 - 1.5 for variability of standard deviation. A difference in competitive ability had no apparent effect on competitive outcome. In Figure 2.3a, scenario 1, where the poorer competitor was different in terms of resource use, gave results that were very similar to scenario 3, where competing species used resources similarly (also compare 2 and 4). The number of extinctions decreased with increasing variability, and the pattern in extinctions mirrored that of growth rate (Figure 2.3b).

The effects of correlated variability were also examined. The simulation approach to equation (2.20) described above was parameterized in accordance with scenario 3 in Table 2.2 and run at two levels of variability (standard deviation 1 and 2) at correlation

A) Geometric mean of low density growth rate:



B) Number of extinctions per 1000 model runs:

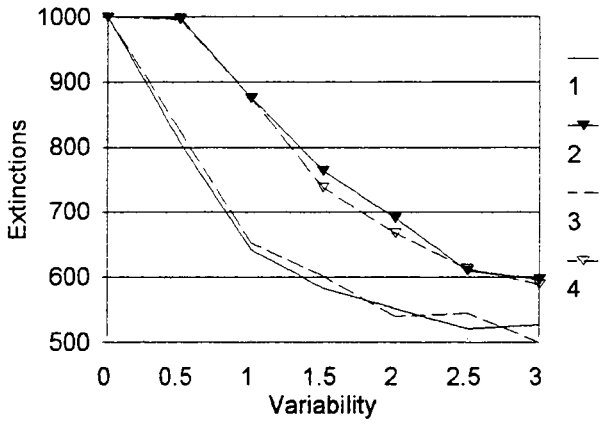


Figure 2.3. Effects of variability in a two-species competition model. This figure gives the A) geometric mean low-density growth rate and B) number of extinctions of a poorer competitor for 1000 simulations under different levels of variability (measured as the standard deviation of random noise introduced into fecundity parameter). In scenarios 1 and 2, the poorer competitor is significantly different from the stronger competitor in terms of resource use; in scenarios 3 and 4, the poorer competitor is not significantly different in terms of resources use. In scenarios 1 and 3, the poorer competitor has a fecundity level equal to that of the stronger competitor; in scenarios 2 and 4, the poorer competitor has lower fecundity (see Table 2.2 for parameters characterizing each scenario). Differences in fecundity affect how well variability promotes coexistence (compare 1 and 2, 3 and 4), but differences in resource use do not (compare 1 and 3, 2 and 4).

values between 0 and 1 (interval of 0.1). Results of these simulations are given in Figure 2.4. An increase in the correlation of the variability introduced to the fecundity parameter decreased the long-term low-density growth rate. Above a certain level of correlation, the growth rate becomes less than one, and the two species were unable to coexist. The exact level of correlation above which coexistence is not possible depended on the magnitude of the standard deviation of the variability: for a standard deviation of 1, a level of correlation above approximately 20-30% prohibited coexistence, while at a standard deviation of 2, a level of correlation above 60-70% prohibited coexistence. That is, species that experience correlated variability in fecundity are more likely to coexist with increasing standard deviation of variability.

COMPARISON OF MODEL PREDICTIONS TO FIELD DATA

The predictions that coexistence will be increasingly likely under higher ratios of host fish used by invader to host fish used by the stronger competitor, and that coexistence will be increasingly likely under higher variability, were tested for two species of freshwater mussel. If resource partitioning maintains coexistence, assuming that carrying capacities and fecundities of the two mussel species are equal, then coexistence should be a function of host fish ratio. If temporal variability in fecundity maintains coexistence, then coexistence should be more likely at higher levels of variability. For freshwater mussel species, the dominant source of temporal variability in fecundity is most likely hydrologic variability (Hynes 1970, Resh et al. 1988). Discharge rates affect fertilization rates (Haggerty et al. 1995) and survival of released propagules

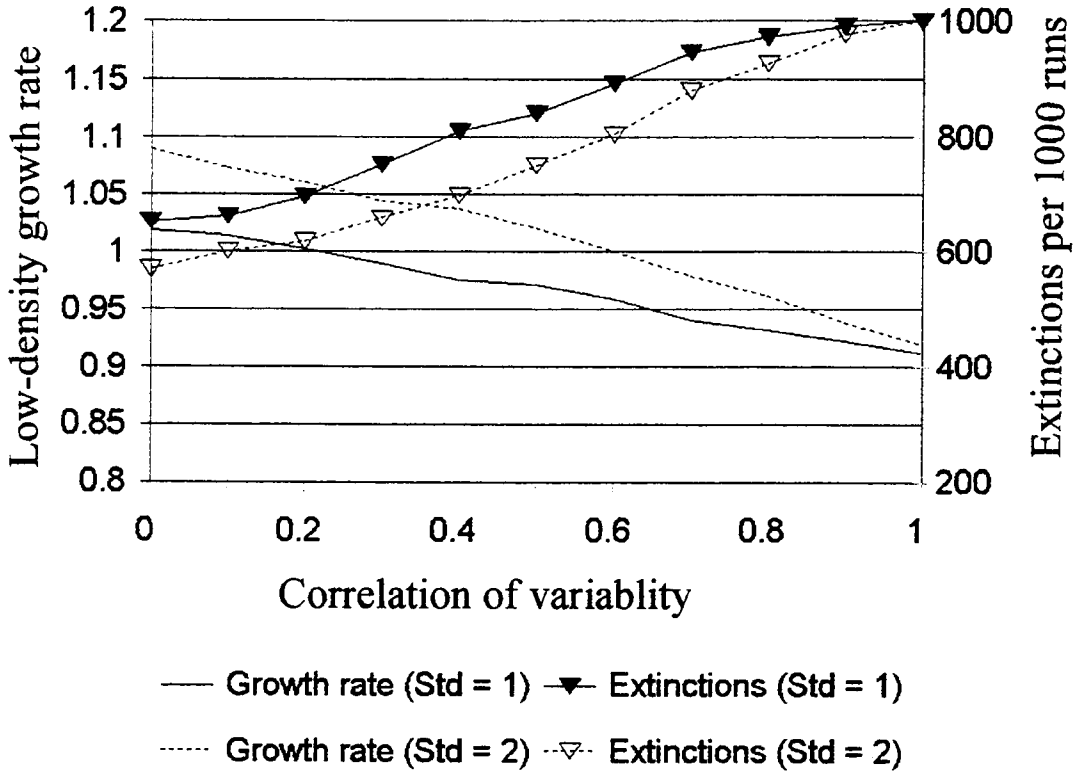


Figure 2.4. Effects of correlated variability in fecundity in a two-species competition model. Figure shows effects of correlated ability on geometric mean low-density growth rate and number of extinctions per 1000 simulations for the points c_{j1},c_{j2} =(0.6,0.6), c_{i1},c_{i2} =(0.4,0.4) for standard deviation levels of 1.0 and 2.0. The level of correlation above which coexistence is prohibited is dependent on the standard deviation of the variability.

(Widlak 1982), and can therefore affect fecundity.

These predictions are tested with two species known to overlap on hosts, *Lampsilis fasciola*, the wavy-rayed lampmussel, and *Villosa iris*, the rainbow. These species coexist in streams throughout the upper Tennessee River basin (Ahlstedt and Rashleigh, in review). These species possess similar life history characteristics: length of life of 12-15 years; onset of sexual maturity at age 3; and glochidial discharge periods during the spring (Zale 1980). *Villosa iris* parasitizes the fish species *Ambloplites rupestris* (rock bass) and *Micropterus dolomieu* (smallmouth bass), and *L. fasciola* parasitizes only *Micropterus dolomieu* (Zale 1980). In laboratory infections performed by Zale (1980), *L. fasciola* produced 666 propagules per fish from one *M. dolomieu* in one trial, whereas *V. iris* produced an average of 370 propagules per fish from 45 *A. rupestris* in 5 trials, and an average of 42 propagules per fish from 17 *M. dolomieu* in 2 trials. Additionally, *V. iris* is know to parasitize *Micropterus salmoides* (largemouth bass) (average of 304 propagules per fish from 4 fish in 1 trial) and slightly parasitize *Micropterus punctulatus* (spotted bass) (average of 7 propagules from 7 fish in 1 trial) (Neves et al. 1985).

As part of U.S. Geological Survey (USGS) National Water Quality Assessment program, 35 sites in the upper Tennessee River basin were sampled for mussels and fish in 1996 at a reach that contained two examples of each of three geomorphic channel types (riffle, run, and pool). Within the reach, mussels were sampled qualitatively in accordance with USGS protocol (Cuffney et al. 1993). All live and fresh-dead freshwater mussels encountered were collected and identified in the field (live specimens were returned to the stream). Quantitative fish sampling was conducted using the USGS

protocol of electrofishing and seining (Meador et al. 1993). Fish were identified and counted in the field (only voucher specimens were preserved). Specimens of either or both of the mussel species described above were found at 12 sites (Figure 2.5, Table 2.3).

Host fish ratios and hydrologic variability parameters were calculated for each site supporting one or both of the target species. The ratio of the combined abundance of *Ambloplites rupestris* and *Micropterus salmoides* to the abundance of *Micropterus dolomieu* (it is assumed that *Ambloplites rupestris* and *Micropterus salmoides* serve equally well as hosts for *V. iris*) was calculated for each site. Three surrogate variables for temporal hydrologic variability were recorded for each of these sites: flow variability, calculated as ratio of the 10th percentile of flow to the 90th percentile (Richards 1990); stream gradient, which is related to high flow and flood levels (Fitzpatrick and Giddings 1997); and soil porosity, which is related to hydrologic stability (McMahon 1991) (Table 2.3). Yearly flow variability was taken from U.S. Geological Survey 1996 records for sites at which a gage was located, and from the gage in closest proximity in the same drainage basin for sites without gages. Stream gradient was measured on 1:24,000-scale topographic maps for the segment (the stream section bounded by discontinuities or tributary junctions) that contained the sampling site (Frissel et al. 1986). Soil porosity for the drainage area above the site was calculated from the STATSGO data base as an area-weighted average of the top soil layer K-factor (U.S. Department of Agriculture 1991).

A series of G-tests was used to determine whether sites that contained either *Lampsilis fasciola* alone or together with *Villosa iris*, and those that contained only *Villosa iris*, could be distinguished based on host fish ratios or measures of hydrologic

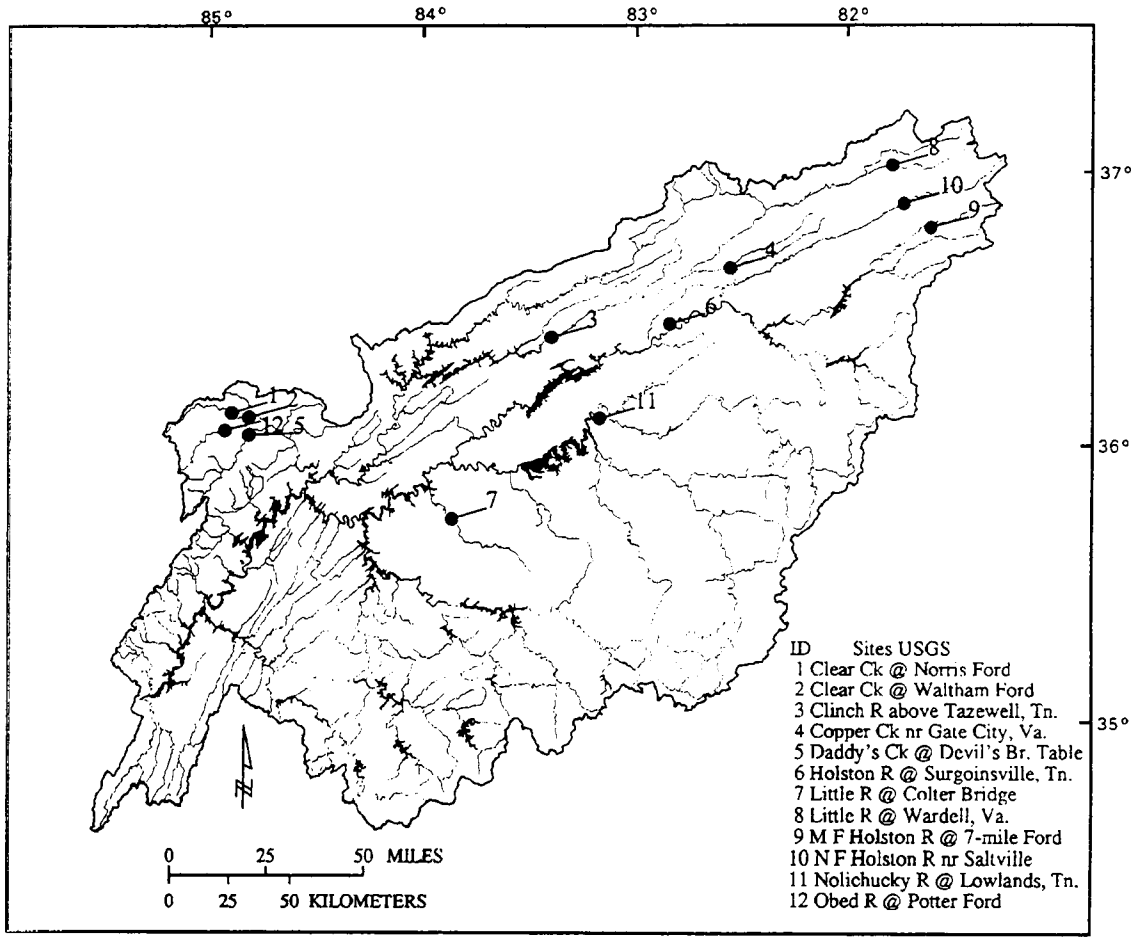


Figure 2.5. Sampling locations for freshwater mussel distribution survey.

Table 2.3. Description of sites at which target species were found. Species are *Vi* = *Villosa iris*, *Lf* = *Lampsilis fasciola*, *Ar* = *Ambloplites rupestris*, *Md* = *Micropterus dolomieu*, *Ms* = *Micropterus salmoides*. Further description of environmental characteristics given in text.

Site name	River mile	Date sampled	Mussel species		Fish species			Environmental characteristics		
			Lf	*Vi*	*Ar*	*Md*	*Ms*	Flow variability (10/90 perc)	Stream gradient (ft/mile)	Soil permeability (avg. K fact)
Clear Creek at Norris Ford	14.8	7/23/96	X	X	2	14	5	54.9	15.5	2
Clear Creek at Waltman Ford	7.8	7/22/96	X	X	14	4	0	54.9	13.8	2
Clinch River above Tazewell, Tn.	159.8	6/18/96		X	22	5	0	16.8	5.2	1.68
Copper Creek at Gate City, Va.	12.7	5/20/96		X	20	1	0	11.1	6.8	1.85
Daddy's Creek at Devil's Breakfast Table near Lancing, Tn.	2.4	7/24/96		X	32	23	0	54.9	45.5	2
Holston River at Surgoinsville, Tn.	118.3	6/17/96	X		49	24	1	5.7	5.2	1.64
Little River at Colter Bridge	20.0	7/9/96		X	39	16	12	5.4	22	2.72
Little River at Wardell, Va.	20.0	6/11/96		X	57	12	0	15.2	12.2	1.63
Middle Fork Holston at 7-mile Ford, Va	32.1	5/22/96		X	62	11	0	6.4	7.2	1.88
Nolichucky River at Lowlands, Tn.	10.7	7/15/96	X		2	3	1	4.7	2.1	1.54
North Fork Holston River at Saltville, Va.	85.0	6/13/96		X	134	7	1	14.3	6.6	1.76
Obed River at Potter Ford, Tn.	20.8	7/25/96	X	X	23	4	3	34.6	7.4	2

variability. G-tests, pairwise comparisons that test the hypotheses that means from two groups of independent observations are equal, were performed using SAS (SAS Institute 1989). The G-test is similar to a t-test, but is used when sample sizes are unequal. G-test results are given in Table 2.4: none of these were significant at $p<0.05$.

Table 2.4. G-test results of model predictions.

Variable	Number of sites	F value	Pr>F
Host abundance ratios	12	2.4	0.1523
Flow variability	12	1.21	0.2967
Stream gradient	12	0.82	0.3876
Soil permeability	12	0.26	0.6219

At the sites examined, coexistence of *Lampsilis fasciola* and *Villosa iris* was not explained by either resource partitioning or the effects of temporal variability.

DISCUSSION

Coexistence among freshwater mussel species that are functionally equivalent as adults may be facilitated by limitation of larvae by reproductive resources. That is, the coexistence of species that are functionally equivalent during one phase of their life cycle may be promoted by interactions at the other phase (Grosberg and Levitan 1992). This finding is similar to that of Roughgarden et al. (1988), who explained adult barnacle coexistence as a function of juvenile transport by tides. This scenario is often found in systems where a high number of propagules is produced, but their survival is low and tends to be more variable and environmentally determined (Doherty and Fowler 1994).

Among species in different functional groups, increase in resource density promotes coexistence up to a break point (Yodzis 1989), beyond which any increase in resource density promotes competitive exclusion. The break point coincides with a switch in control from the juvenile to the adult phase. The alternative control in different communities under different conditions may be able to explain the differences in diversity among them (Roughgarden et al. 1988).

A general result from this analysis is that the highest diversity of species with complex life cycles may not occur at the highest levels of resource diversity and density. If resource levels are high enough, adult competition becomes more important than larval competition, and the community becomes dominated by the strongest competitor. The model implies that as reproductive resources decline, although marginal species may be lost, coexistence may be facilitated in some communities. Conversely, if reproductive resources are augmented, coexistence may be reduced. The promotion of diversity by moderate resource densities agrees with the decline in diversity with enrichment observed in the field (Rosenzweig 1971). Huston (1994) notes that scarcity, but not absence of critical resources, can lead to high diversity, because of a lower growth rate of competing species. This mechanism would result in an increase in coexistence with increasing resource diversity and decreasing resource density: these patterns could be examined in future field studies of freshwater mussels.

Functionally analogous species required an interspecific trade-off in resource use in order to coexist. This coincides with the conclusion of Leon and Tumpson (1975) and Tilman (1982) for substitutable resources that in order to coexist, each species must

remove at a higher rate that resource which contributes more to its own growth rate. In cases where carrying capacities are equal, it is difficult to say which resource more limits a competitor. Therefore, it is concluded that for the case of substitutable resources, species must be significantly different in their resource use. There was a limit to species similarity in this model, similar to the spatial model of Tilman (1994), although the exact nature of the limit is system-specific (Abrams 1983). The limit does not preclude more than n species coexisting on n resources, although it makes coexistence increasingly difficult. A trade-off between competitive ability and mussel species' carrying capacity on fish hosts, life history parameters, or a combination of the two, promoted coexistence. This conclusion is similar to that of Vincent et al. (1996) for resource-consumer systems, that trade-offs in species' encounter-efficiencies promote coexistence.

These results agree with those of Chesson and Warner (1981), Warner and Chesson (1985) and Chesson (1983, 1994), that variable fecundity promotes coexistence, that the highest growth rate is found at the highest level of variability, and that non-equilibrium coexistence is easier if species are similar in average reproductive rates and competitive abilities. Variability became less effective at promoting coexistence as the variation in the fecundity parameters became increasingly correlated, which is consistent with the theoretical results of Abrams (1984). Temporal variability becomes less effective in promoting coexistence as the number of similar species increases (Chesson 1994).

The occurrence patterns at selected sites could not be explained by fish host ratios, as would be expected under classical competition theory. It is possible that the model assumptions regarding fish biology were not accurate. For example, the interactions of

hosts have not been considered here: it is assumed that fish species use similar resources, but do not interact strongly. The fish species *Ambloplites rupestris* (rock bass) and *Micropterus dolomieu* (smallmouth bass) show some differences in habitat use, and exhibit similarities in food and depth (George and Hadley 1979, Probst et al. 1984). However, there is no evidence that they interact with each other strongly (Covington et al. 1983). It is also possible that the fish host abundances measured are not good representations of host densities generally. However, fish host abundances at many of these sites are highly concordant across years (Tennessee Valley Authority, unpublished).

Patterns of mussel species occurrences at selected sites in the upper Tennessee River basin did not support the hypothesis that coexistence was promoted by temporal variability, measured as hydrologic variability, stream gradient, and soil porosity. Strayer (1983, 1993) found that mussel diversity was related positively to hydrologic stability in streams in Michigan, Pennsylvania, and New York. Strayer (1993) also found that stream gradient was a poor predictor of mussel distributions. The finding that gradient was not significant to coexistence status differed from that of Richardson (1989), who found that gradient was a significant predictor of sites with mussels in the Big South Fork of the Cumberland River, Kentucky/Tennessee. However, breaks in gradient form barriers for mussels (Ahlstedt 1984) and high gradient changes may reduce diversity (Richardson 1989). Hurd (1974) noted that Blue Ridge physiographic province sites in the Coosa drainage (Georgia/Alabama/Tennessee) were limiting to freshwater mussels due to habitat conditions including swift, turbulent current. DiMaio and Corkum (1995) found that different types of communities were associated with three hydrologically stable, as

opposed to three variable streams in southwest Ontario and southeast Michigan.

The additional constraint of uncorrelated variability, derived in the model, may limit the ability of temporal variability to promote coexistence in mussel communities. Miller et al. (1992) found a similarity in size structure in *Amblema plicata* and *Fusconaia ebena*, two similar species that overlap on hosts (Watters 1994b), in the lower Tennessee River, which suggested interspecific similarity in recruitment. At five locations in a south Swedish stream, the freshwater mussel species *Anodonta piscinalus* and *Unio pictorium* (species known to overlap on hosts (Watters 1994b)) exhibited correlated life histories (Norelius 1967). Age structures of *Anodonta piscinalus* and *Unio tumidus* in Mikolajskie Lake, Poland (species known to overlap on hosts (Watters 1994b)) reported by Lewandowski and Stanczykowska (1975) also appear moderately to highly correlated. The hypothesis that temporal variability promotes coexistence could be more rigorously tested through population studies that measure the variability within and the correlation among different mussel species' age classes, which are a good measurement of recruitment success (Payne and Miller 1989).

The lack of support for either of the mechanisms examined here suggest that other mechanisms may need to be considered. It is possible that species do not compete strongly, due to past competitive effects (Connell 1980). This idea is supported by the large difference in the way these two species use resources (Zale 1980). It is possible that species absences from some of the communities examined may reflect mortality unrelated to competition. The physical and chemical characteristics of a site could lead to mortality, either due to natural tolerances (Meyer et al. 1988, Tate and Heiny 1995) or

the effects of pollution (Bauer 1983, Strayer 1993). It is also possible that coexistence in local communities is influenced by processes at larger scales. Strayer and Ralley (1993) found that they could not predict local mussel community structure in the Neversink River, New York, and suggested that other scales may be more appropriate.

SUMMARY AND CONCLUSIONS

A model of resource utilization by two species that overlap in adult resource requirements but use discrete, substitutable resources during recruitment was developed. The model was used to determine conditions for coexistence for scenarios of complete resource non-overlap among juveniles, partial resource overlap among juveniles, and partial overlap combined with temporal variability in fecundity. Conditions were tested for two freshwater mussel species that coexist in the upper Tennessee River basin.

When there is complete resource non-overlap among juveniles, species can coexist if fecundity exceeds carrying capacity on hosts. Species that overlap on resources can coexist only when each is sufficiently more successful on a different resource in terms of host attraction strategies, carrying capacities, or a combination of the two. Temporal variability in fecundity promotes coexistence of a poorer competitor. Coexistence is facilitated by increased standard deviation and decreased correlation of the variability between species.

Coexistence of two mussel species that overlap on hosts was not explained by host ratios or by three measures of environmental variability. Coexistence may be influenced by past competition, mortality unrelated to competition, or processes at other scales.

CHAPTER III. ROLES OF COMPETITION AND METAPOPULATION DYNAMICS IN MESOSCALE FRESHWATER MUSSEL COMMUNITIES

INTRODUCTION

Communities of freshwater mussels of the family Unionidae occur as series of multi-species patches in streams of the upper Tennessee River basin. Patches reflect the pool-riffle nature of the habitat, where good habitat (riffles) is interspersed with poorer habitat (pools). These patches are connected in ecological time by larval dispersal, which for mussels is accomplished through a parasitic stage on fish. Despite the connection by dispersal, similar habitat among patches, and similar evolutionary history, different patches in a stream support different numbers and compositions of species. The nature of differences among patches are of interest to community ecology, because they can provide clues to the processes that structure these communities. Systems of patches connected by dispersal have received much attention in ecology (Levins 1969, Slatkin 1974, Caswell 1978, Hanski 1982, Caswell and Cohen 1991).

The classic view of communities in ecology is that they are structured by competition among species. Models have demonstrated that including competition among species in a system of patches reduced the number of species that could coexist locally (Hanksi 1983, Caswell and Cohen 1993). This has been demonstrated experimentally by Bengtsson (1991), who found evidence of an increase in local extinction rates due to interspecific competition in *Daphnia* metapopulations in rock pools. Diamond (1975) proposed that some pairs of species that compete can never coexist, and that the stochasticity associated with competitive outcome will lead to negatively associated distributions of species across

a collection of sites. Case (1991) found that the inclusion of strong species interactions in a metapopulation model generated alternative stable states. Wilson (1992) found that when species interactions are incorporated in a collection of model communities, sensitivity to initial conditions creates enough variability that different species will be favored in different patches. Drake (1990, 1991) found that alternative states were driven by invasion sequence in both experimental and model systems.

Another view is that patterns across patches are determined by the stochasticity of immigration combined with the configuration of patches. Levins (1969) introduced a class of models called metapopulation models, in which changes in patch occupancy frequency were the result of differences between the stochastic processes of immigration and emigration rates between patches. Hanski (1982) developed a similar class of models assuming immigration and extinction to be dependent on the total number of sites occupied. Hanski's model incorporates the "rescue effect" (Brown and Kodric-Brown 1977) where continuous arrival of reinforcements from source populations supplement local populations that may not be self-sustaining. Hanski and Gyllenberg (1993) view the rescue effect as a decrease in the rate of extinction with increasing occupancy, due to both decreased risk of local extinction and increased probability of immigration. Long-distance dispersal associated with metapopulation dynamics promotes coexistence of species in the system (Horn and MacArthur 1972, Drake et al. 1993), and reduces the possibility of alternative states by homogenizing the system (Hanski et al. 1993).

Either competition, or metapopulation dynamics, or both, may be important in determining patterns in freshwater mussel communities. It is possible that competition for fish

hosts is a predominant force structuring freshwater mussel communities (Dennis 1984, Fuller 1980). It is also possible that metapopulation models are appropriate for application to freshwater mussel communities (Vaughn 1993). Lee (1996) has found some evidence that freshwater mussel distributions exhibit bimodality, a pattern associated with metapopulation dynamics. Here, a model was developed to compare the patterns generated under different assumptions about the processes structuring a set of local freshwater mussel species in the subfamily/tribe of Ambleminae/Lampsilini (Davis and Fuller 1981). The analysis involves a comparison of the average number of species per patch and the degree to which alternative states are generated when each of four scenarios -- neither competition nor long-distance dispersal associated with metapopulation dynamics, competition only, long-distance dispersal only, or both -- are sequentially specified. Results were then compared to data from three stream communities in the upper Tennessee River basin.

THE MODEL

Model configuration

A discrete-time model was developed for a series of X patches capable of supporting multiple species. At each time step t, each patch will be characterized by an assemblage of species, containing none, one, a subset, or all of the species in a collection of local communities. Each unique assemblage is said to be a community state. A set of communities with M species has $Y = 2^M$ different community states, where each adjacent state differs only by the presence/absence of one species. The array of possible states for a community can be represented by a matrix $\boldsymbol{Z}$, with dimensions MxY. The state of all patches at a par-

ticular time t can be represented by a matrix $\boldsymbol{B}(t)$ that has the dimensions YxX. Species' occurrence across the system of patches at time t can be represented by an MxX matrix $\boldsymbol{N}(t)$, which is calculated as $\boldsymbol{N}(t) = \boldsymbol{ZB}(t)$ (model parameters are defined in Appendix A).

The transition between a particular state y and another state y' for a given patch x at time t is determined by a transition probability $P(y,y')_x(t)$. The set of transition probabilities for all possible state transitions for a particular state y can be represented as a vector of length Y. To determine the actual state at the next time step, the unit interval is broken into a series of subintervals, each with a width corresponding to one of the transition probabilities in the vector. A random number over the range (0,1) is then generated, and the transition corresponding to the interval to which the random number falls is made. The matrix representing the state of all patches at time t is multiplied by the matrix of transitions probabilities to give the state of all patches at time t+1: $\boldsymbol{B}(t+1) = \boldsymbol{P}(y,y')_x(t)\boldsymbol{B}(t)$. This type of transition is similar to a Markov model (Acevedo 1981, McAuliffe 1988, Renshaw 1989).

Here, the transition probabilities for a particular state x are functions of the probabilities of gaining species (g) and losing species (l). It is assumed that two species cannot invade a patch at the same time, hence there are no two-state jumps. The probability of a particular species transition not occurring is 1 minus the probability that the species transition occurs. The probability that no species transitions occur is the product of the probabilities that each species transition does not occur. The species' transition probabilities are divided by the sum of all species' transitions to convert to state transition probabilities. An example of a transition matrix for two species is given in Table 3.1.

Table 3.1. Transition probabilities among states in a two-species system. Transition probabilities for a particular patch x are functions of the probabilities of gaining (g) and losing (l) species.

State y	State y' (Occupancy of species 1, species 2, for state y')			
	1 (0,0)	2 (1,0)	3 (0,1)	4 (1,1)
1	$\frac{[1-g_{1,x}(t)][1-g_{2,x}(t)]}{\{[1-g_{1,x}(t)][1-g_{2,x}(t)] + g_{1,x}(t) + g_{2,x}(t)\}}$	$\frac{[g_{1,x}(t)]}{\{[1-g_{1,x}(t)][1-g_{2,x}(t)] + g_{1,x}(t) + g_{2,x}(t)\}}$	$\frac{[g_{2,x}(t)]}{\{[1-g_{1,x}(t)][1-g_{2,x}(t)] + g_{1,x}(t) + g_{2,x}(t)\}}$	0
2	$\frac{[l_{1,x}(t)]}{\{[1-l_{1,x}(t)][1-g_{2,x}(t)] + l_{1,x}(t) + g_{2,x}(t)\}}$	$\frac{[1-l_{1,x}(t)][1-g_{2,x}(t)]}{\{[1-l_{1,x}(t)][1-g_{2,x}(t)] + l_{1,x}(t) + g_{2,x}(t)\}}$	0	$\frac{[g_{2,x}(t)]}{\{[1-l_{1,x}(t)][1-g_{2,x}(t)] + l_{1,x}(t) + g_{2,x}(t)\}}$
3	$\frac{[l_{2,x}(t)]}{\{[1-l_{2,x}(t)][1-g_{1,x}(t)] + l_{2,x}(t) + g_{1,x}(t)\}}$	0	$\frac{[1-l_{2,x}(t)][1-g_{1,x}(t)]}{\{[1-l_{2,x}(t)][1-g_{1,x}(t)] + l_{2,x}(t) + g_{1,x}(t)\}}$	$\frac{[g_{1,x}(t)]}{\{[1-l_{2,x}(t)][1-g_{1,x}(t)] + l_{2,x}(t) + g_{1,x}(t)\}}$
4	0	$\frac{[l_{1,x}(t)]}{\{[l-l_{1,x}(t)][1-l_{2,x}(t)] + l_{1,x}(t) + l_{2,x}(t)\}}$	$\frac{[l_{2,x}(t)]}{\{[l-l_{1,x}(t)][1-l_{2,x}(t)] + l_{1,x}(t) + l_{2,x}(t)\}}$	$\frac{[1-l_{1,x}(t)][1-l_{2,x}(t)]}{\{[l-l_{1,x}(t)][1-l_{2,x}(t)] + l_{1,x}(t) + l_{2,x}(t)\}}$

Local dispersal

To describe the probability (g) of gaining species m on patch x, a formulation similar to that of Maynard Smith (1974) is used:

$$g_{m,x}(t) = 1 - \prod_{q=-Q}^{Q} [1 - d_{m,q+x,x}(t)], \forall [(q+x) \leq X, (q+x) > 0] \qquad (3.1)$$

where $d_{m,q+x,x}(t)$ represents the probability of dispersal of species m from a patch $q+x$ to a target patch x, and the term $[1 - d_{m,q+x,x}(t)]$ is the probability that no dispersers reach the target patch x from patch $q+x$. The product of this probability over all contributing patches gives the probability that no dispersers arrive from any of the neighboring patches, and the subtraction of this product from one gives the probability that at least one disperser

arrives. The Q parameter is set at 3, that is, it is assumed that up to three patches on either side of the target patch potentially contribute propagules. This type of local dispersal is referred to as a stepping stone model (Hassell et al. 1991).

The probability (l) of losing species m from patch x is given by

$$l_{m,x}(t) = \left\{ \varepsilon_m \prod_{q=-Q}^{Q} [1 - d_{m,q+x,x}(t)] \right\}, \forall [q \neq 0,\ (q+x) \leq X,\ (q+x) > 0] . \quad (3.2)$$

The background extinction rate, ε_m, which represents natural mortality, is multiplied by the probability that no dispersers arrive from other patches. If this probability is 1, then the probability of losing a species is equal to the background extinction rate. If the probability that no outside propagules arrive is 0, then the probability of losing the species is 0.

The probability of dispersal d of species m from patch $q+x$ to patch x at time t is

$$d_{m,q+x,x}(t) = N_{m,q+x}(t)\, \rho_m D_{q+x}, \quad (3.3)$$

where $N_{m,q+x}(t)$ is a 1 or zero, representing the presence or absence, respectively, of species m on patch $(q+x)$ at time t; ρ_m is the probability that a population of species m successfully produces offspring during a time step; and D_{q+x} is the probability that an offspring successfully disperses from patch $q+x$. The parameter ρ_m is given by

$$\rho_m = \left(\sum_{h=1}^{H} c_{mh} \cdot F_h \right) \Big/ \left(\sum_{h=1}^{H} F_h \right), \quad (3.4)$$

where F_h is the density of host resource h in the system (all were assumed equal here), H is the number of available host fish species, and c_{mh} is the probability of success of species

m in using resource h to disperse larvae. The number of resources in the system, H, is set at 12, and c_{mh} is assigned randomly in the range (0,1), where each mussel species has a 25% chance of using each resource. These values are based on real mussel matrices (see below). The probability of propagules dispersing from a patch is given by

$$D_{q+x} = \Delta e^{(-|q|+2)}, \tag{3.5}$$

where Δ represents background dispersal, which is exponentially weighted by distance so that more distant patches contribute fewer propagules.

Competition

It is assumed that competition can occur for fish hosts. If competition occurs in a system with local dispersal, the probability of gaining a species becomes

$$g_{m,x}(t) = \left(1 - \left\{\prod_{q=-Q}^{Q} [1 - d_{m,q+x,x}(t)]\right\}\right) \cdot [1 - \lambda_{m,x}(t)],$$

$$\forall [q \neq 0,\ (q+x) \leq X,\ (q+x) > 0], \tag{3.6}$$

where a competition parameter, λ, decreases the probability that propagules will successfully disperse. The probability of losing a species from a patch with competition becomes

$$l_{m,x}(t) = \left(\left\{\prod_{q=-Q}^{Q} [1 - d_{m,q+x,x}(t)]\right\} \cdot \varepsilon_m^{[1-\lambda_{m,x}(t)]}\right),$$

$$\forall [q \neq 0,\ (q+x) \leq X,\ (q+x) > 0]. \tag{3.7}$$

A species' ability to produce larvae is also decreased when it experiences competition:

$$d_{m,q,x}(t) = N_{m,q+x}(t)\ \{\rho_m [1 - \lambda_{m,q+x}(t)]\}\ D_q. \tag{3.8}$$

The parameter representing competition, λ, can be interpreted as the relative decrease in recruitment due to larval competition. This parameter is derived from equation (2.20), which is given here as the change in population size species i on patch q:

$$N_{i,q}(t+1) = \frac{N_{i,q}(t)\cdot\left(S_i\right)}{1+\sum_{m=1}^{M}\alpha_{mi}N_{m,q}(t)} + \frac{N_{i,q}(t)\cdot\left(f_i s_i\right)\cdot r_i}{1+r_i\left(1/\left\{\sum_{h=1}^{H}\left[\left(K_{ih}\cdot F_h\right)\div\left(\sum_{m=1}^{M}C_{mih}N_{m,q}(t)f_m\right)\right]\right\}\right)}. \quad (3.9)$$

If it is assumed that competition occurs primarily among larvae, one can focus on the term for recruitment, which can be designated R:

$$R_i(t+1) = \frac{N_{i,q}(t)\cdot(f_i s_i)\cdot r_i}{1+r_i\left(1/\left\{\sum_{h=1}^{H}\left[(K_{ih}\cdot F_h)\div\left(\sum_{m=1}^{M}C_{mih}N_{m,q}(t)f_m\right)\right]\right\}\right)}. \quad (3.10)$$

When species i is unaffected by competition, equation (3.10) reduces to

$$R_i(t+1) = \frac{N_{i,q}(t)\cdot(f_i s_i)\cdot r_i}{1+\left(r_i/\left\{\sum_{h=1}^{H}\left[(K_{ih}\cdot F_h)\div(N_{i,j}(t)f_m)\right]\right\}\right)}. \quad (3.11)$$

The effect of competition is given by the difference between equation (3.10) and (3.11), divided by the term given in equation (3.10). That is,

$$\lambda_{i,q}(t) = 1-\frac{\left(\frac{N_{i,q}(t)\cdot\left(f_i s_i\right)\cdot r_i}{1+r_i\left(1/\left\{\sum_{h=1}^{H}\left[\left(K_{ih}\cdot F_h\right)\div\left(\sum_{m=1}^{M}C_{mih}N_{m,q}(t)f_m\right)\right]\right\}\right)}\right)}{\frac{N_{i,q}(t)\cdot\left(f_i s_i\right)\cdot r_i}{1+\left(r_i/\left\{\sum_{h=1}^{H}\left[\left(K_{ih}\cdot F_h\right)\div\left(N_{i,q}(t)f_m\right)\right]\right\}\right)}}. \quad (3.12)$$

Since $\lambda_{i,q}(t)$ is only calculated for patches occupied by species i, $N(i,q)$ is assumed to be 1. The term $N(m,q)$ is either 1 or 0, depending on the occupancy of the competitor. If the terms in the numerators are cancelled and it is assumed that $f_m = f_i \forall i$, $K_{m,h} = K_{i,h} \forall i, h$, equation (3.12) becomes

$$\lambda_{i,q}(t) = 1 - \left[1 + r_i / \sum_{h=1}^{H} F_h\right] / \left\{1 + r_i / \left[\sum_{h=1}^{H} F_h \div \sum_{m=1}^{M} C_{mih} N_{m,q}(t)\right]\right\}, \forall H \text{s.t. } c_{ih} > 0 \quad (3.13)$$

where the parameter r, the probability of successful infestation, is defined as

$$r_i = \sum_{h=1}^{H} (F_h \cdot c_{ih}), \quad (3.14)$$

and C_{mih}, the competitive effect of species m on species i for host h, is defined as

$$C_{mih} = c_{mh} / c_{ih}. \quad (3.15)$$

The range of the λ parameter is (0,1); if species i experiences no competition on patch x, $\lambda_{m,x}(t) = 0$.

Long-distance dispersal

Under the assumption of long-distance dispersal associated with metapopulation dynamics, the probability of gaining a species becomes

$$g_{m,x}(t) = 1 - \prod_{q=1}^{X} [1 - d_{m,q,x}(t)], \quad (3.16)$$

where $d_{m,q,x}(t)$ is the probability of dispersal of species m from patch q to patch x, and X is the total number of patches in the system. That is, all occupied patches potentially contribute propagules to a target patch. Similarly, the probability of losing a species (l) becomes

$$l_{m,x}(t) = \varepsilon_m\left(\prod_{q=1}^{X}[1-d_{m,q,x}(t)]\right), \forall q \neq x. \tag{3.17}$$

Under the assumption of metapopulation dynamics, the probability of dispersal of species m from a patch q to a target patch x at time t, $d_{m,q,x}(t)$, is given by

$$d_{m,q,x}(t) = N_{m,q}(t)\,\rho_m D_q \tag{3.18}$$

where $N_{m,q}(t)$ is a 1 or zero, representing the presence or absence, respectively, of species m on patch q; ρ_m is the probability that a population of species m successfully produces offspring during a time step (given in equation (3.4)); and the term D_q is $D_q = \Delta, \forall q$.

When competition is introduced to a system of long-distance dispersal, the probability of gaining a species becomes

$$g_{m,x}(t) = \left(1-\left\{\prod_{q=1}^{X}[1-d_{m,q,x}(t)]\right\}\right)\cdot[1-\lambda_{m,x}(t)] \tag{3.19}$$

and the probability of losing a species becomes

$$l_{m,x}(t) = \left(\left\{\prod_{q=1}^{X}[1-d_{m,q,x}(t)]\right\}\cdot\varepsilon_m^{[1-\lambda_{m,x}(t)]}\right), \forall q \neq x. \tag{3.20}$$

Competition decreases the probability of a species successfully producing propagules:

$$d_{m,q,x}(t) = N_{m,q}(t)\,\{\rho_m[1-\lambda_{m,q}(t)]\}D_q. \tag{3.21}$$

The equation for the competition parameter (λ) is given in equation (3.13).

Four scenarios were considered: neither competition nor long-distance dispersal, competition, long-distance dispersal, and both processes occurring (Table 3.2).

Table 3.2. Summary of equations used for four model scenarios.

Scenario	Gaining a species (g)	Losing a species (l)	Dispersal probability(d)
Neither process (local dispersal)	Equation 3.1	Equation 3.2	Equation 3.3
Competition	Equation 3.6	Equation 3.7	Equation 3.8
Long-distance dispersal	Equation 3.16	Equation 3.17	Equation 3.18
Competition and long-distance dispersal	Equation 3.19	Equation 3.20	Equation 3.21

Analytic solution

An approximate analytic solution for the average number of species per patch at equilibrium is developed for the two scenarios without competition, for the purpose of comparing to simulation results. To develop a solution, it is necessary to first derive an equation for the probability of occupancy for a single species. This probability can be derived by simplifying the state transition matrix given in Table 3.1 to describe a two-state system, where states 1 and 2 correspond to patches being empty and occupied, respectively. The probability for a particular patch of being in each of these states at a given time t is $n_1(t)$ and $n_2(t)$, respectively, where $n_2(t) = 1 - n_1(t)$. The probability of a patch being occupied at a particular time t+1 is given by

$$n_2(t) = g_x(t)\, n_1(t-1) + [1 - l_x(t)]\, n_2(t-1) \qquad (3.22)$$

The equation for n_2 at equilibrium can be derived by substituting for $n_1(t)$ in equation (3.22), setting $n_2(t+1) = n_2(t)$, and rearranging:

$$n_2 = g_x / (g_x + l_x)\,. \qquad (3.23)$$

Equation (3.23) is solved by substitution of equations from Table 3.2.

For the scenario of local dispersal, equations (3.1) and (3.2) can be approximated as

$$g_x = 1 - (1 - \rho_m D_q)^{n_2(\kappa_x - 1)} \text{ and } l_x = \varepsilon_m \cdot (1 - \rho_m D_q)^{n_2(\kappa_x - 1)}, \tag{3.24}$$

respectively, where κ_x represents the equilibrium number of contributing patches to a given patch x. For a particular patch i, κ_i is given by

$$\kappa_i = \sum_{q=-Q}^{Q} \left[e^{(-|q|+2)}\right], \ \forall [q \neq 0, \ (q+i) \leq X, \ (q+i) > 0] \ . \tag{3.25}$$

For a given system of X patches, $\kappa_x = \left(\sum_{i=1}^{X} \kappa_i \right) / X$. If the term $(\rho_m D_q)$ is sufficiently small, the term $(1 - \rho_m D_q)^{n_2(\kappa_x - 1)}$ can be approximated as $1 - [n_2(\kappa_x - 1) \cdot \rho_m D_q]$. When this approximation is substituted in the equations in (3.24), and these equations in turn are substituted in equation (3.23), the resulting approximation for n_2 at equilibrium is

$$n_2 \approx \frac{1}{(1 - \varepsilon_m)} - \frac{\varepsilon_m}{(1 - \varepsilon_m) \cdot \rho_m D_q \cdot (\kappa_X - 1)} . \tag{3.26}$$

For the long-distance dispersal scenario, equations (3.16) and (3.17) are approximated as

$$g_x = 1 - (1 - \rho_m D_q)^{n_2(x-1)} \text{ and } l_x = \varepsilon_m \cdot (1 - \rho_m D_q)^{n_2(x-1)}, \tag{3.27}$$

respectively. Using an approximation for the equations in (3.27) similar to that discussed above and the substitution that $\kappa_x = X$, the resulting approximation for n_2 at equilibrium is

$$n_2 \approx \frac{1}{(1 - \varepsilon_m)} - \frac{\varepsilon_m}{(1 - \varepsilon_m) \cdot \rho_m D_q \cdot (X - 1)} . \tag{3.28}$$

Equations (3.26) and (3.28) describe equilibrium occupancy for a single species under local and long-distance dispersal scenarios, respectively. Differences among species in the simulation model occur only in the parameters that specify their use of hosts, which are assigned randomly according to the same rules for each species. As such, the single species' expression for equilibrium occupancy probability can be multiplied by the number of species in the system to get expected average number of species per patch. Probabilities from equations (3.26) and (3.28) are multiplied by 7 to compare to model results.

Simulations

The model was parameterized for 7 mussel species on a series of 20 patches. These numbers are designed to mimic three real systems described below. All seven species are assumed to be present in the model, that is, the immigration probability into patch 1 is 100% for all species. Because this model envisions the series of patches as a headwater stream, the upstream boundary of the system is assumed to contribute no propagules. For the initial condition, species occurred on the first five patches, and all other patches were empty. each simulation used a set value of dispersal ability ($\Delta = 0.05$) and a different randomly generated input matrix. For scenarios including local dispersal, simulations were performed at six approximately evenly spaced intervals within the range 0.005 - 0.125 for the extinction parameter. For simulations including metapopulation dynamics, simulations were performed at six approximately evenly spaced intervals within the range 0.05 - 0.55 for the extinction parameter. Simulation runs were iterated for 1000 time steps, and the average number of species per patch was calculated for the last time step.

An index of nestedness, a measure of whether each patch of successively lower species richness is a subset of the previous one, was also calculated for species x sites matrix at the last time step of each simulation (Patterson and Atmar 1986) (e.g., equation 3.29).

$$Nested = \begin{bmatrix} 1 & 1 & 1 \\ 1 & 1 & 0 \\ 1 & 0 & 0 \end{bmatrix}, \quad Non\text{-}nested = \begin{bmatrix} 1 & 1 & 0 \\ 0 & 1 & 0 \\ 1 & 0 & 1 \end{bmatrix} \tag{3.29}$$

Nestedness was examined by first ordering rows of the mussel distribution matrix from most common to least common species, and ordering columns from most diverse to least diverse patch. The formulation of Atmar and Patterson (1993) was applied to determine a matrix "temperature" on a scale of 0 - 100, 100 being maximally disordered (non-nested). Atmar and Patterson (1993) define "local unexpectedness" as $\tau_{ij} = v_{ij}/V_{ij}^{2}$, where V_{ij} is the length of the full diagonal line running through the jth species in the ith island, and v_{ij} is the species length along the line. Total unexpectedness is $\Phi = [1/(MX)] \sum_i \sum_j \tau_{ij}$, where M is the number of species and X is the number of patches. Matrix "temperature" is $[(100 \cdot \Phi)/\Phi_{max}]$ where $\Phi_{max} \approx 0.04145$, a value derived by Atmar and Patterson (1993) to normalize the metric. High nestedness is indicated by a low "temperature", and low nestedness related to alternative states is indicated by a high "temperature."

MODEL RESULTS

For the scenario with neither process operating, the average number of species per patch ranged from 1.4 - 6.9, and the nestedness index ranged from 0 - 39.1 (Figure 3.1).

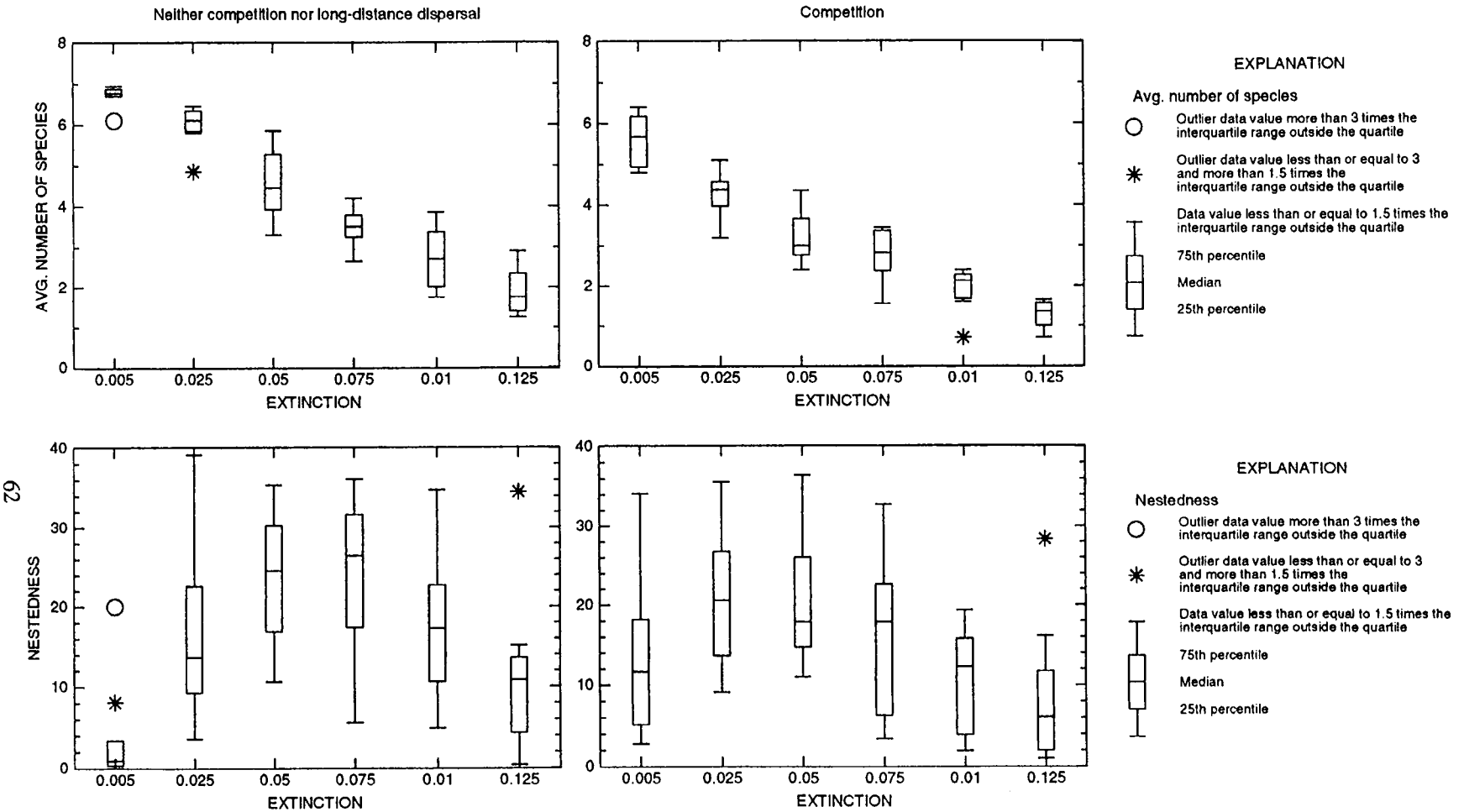


Figure 3.1. Average number of species per patch (top) and index of nestedness (bottom) for 10 simulations for of each of two scenarios: neither long-distance dispersal consistent with metapopulation dynamics nor competition operating (left) and competition (right). Conditions are $\Delta = 0.05$, $T = 1000$.

The median of the average number of species per patch for ten simulations decreased sharply and approximately linearly with increasing extinction. The median values are similar to the values resulting from the analytic solution (Figure 3.2). The median values of the index of nestedness for 10 simulations exhibited a unimodal pattern with extinction (Figure 3.3). The two lowest median values of the index of nestedness resulting from these simulations, 0.9 and 11.0, occurred at the high and low endpoints of the range of extinction parameter examined (at extinction levels of 0.005 and 0.125, respectively). These values also correspond with the highest (6.8) and lowest (1.75) median values, respectively, of the average number of species per patch resulting from these simulations. The highest median index of nestedness for this scenario was 26.5, which corresponded to a median average number of species per patch for 10 runs of 3.5.

For the scenario with competition operating, the average number of species per patch ranged from 0.7 - 6.4, and the index of nestedness ranged from 2.8 to 36.4 (Figure 3.1). The median values of the average number of species per patch showed a decline with increasing extinction (Figure 3.2). The competition scenario gave consistently lower values for the median of average number of species per patch than the scenario of local dispersal without competition. The difference between these two scenarios was more pronounced at lower levels of extinction. For example, the introduction of competition caused a 34.8% decline in median average number of species per patch for 10 simulations at $\varepsilon_m = 0.05$, and a 22.2% decline at $\varepsilon_m = 0.1$. The median values of the index of nestedness for 10 simulations exhibited a unimodal pattern with extinction (Figure 3.2). The two lowest median values of index of nestedness resulting from these simulations, 13.2

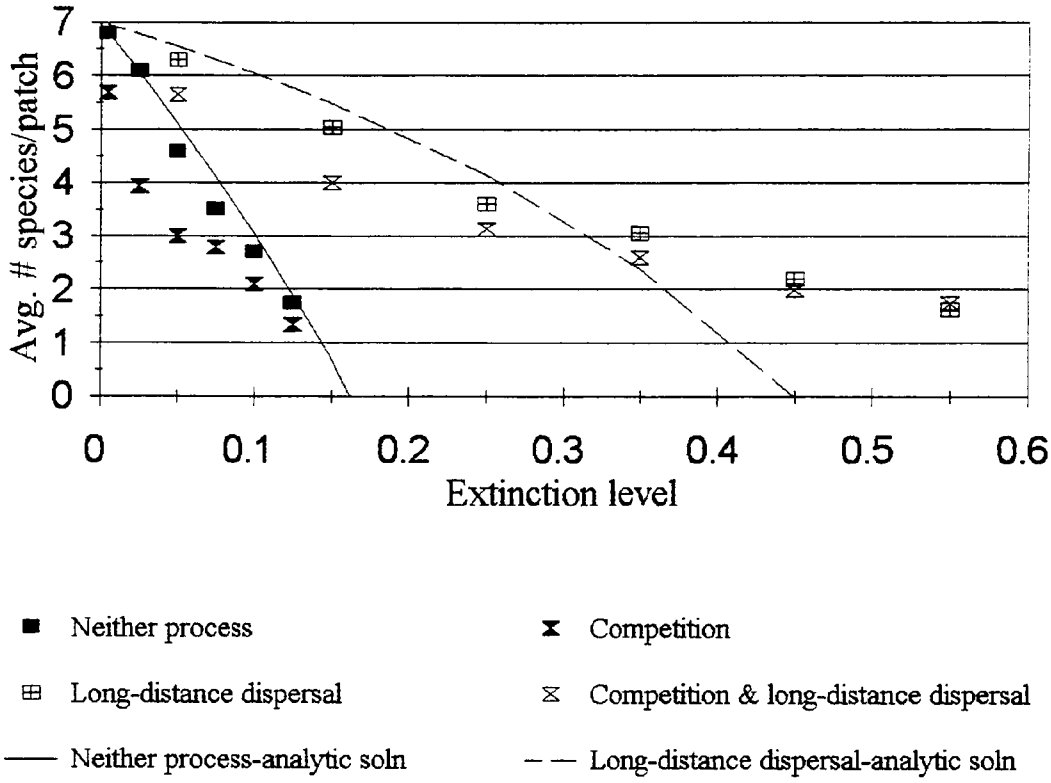


Figure 3.2. Median values of average number of species per patch from Figures 3.1 and 3.4 plotted on equally scaled extinction axis. Approximate analytic solutions for scenarios of neither process operating and long-distance dispersal associated with metapopulation dynamics, derived from equations (3.26) and (3.28), are also included for comparison.

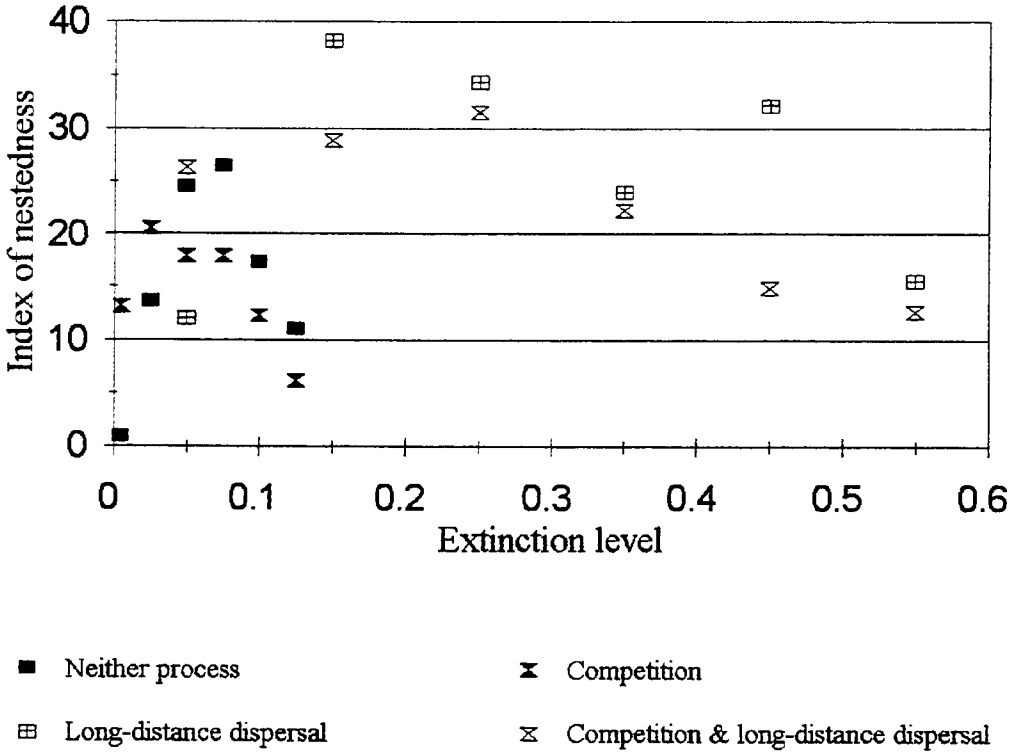


Figure 3.3. Median values of index of nestedness from Figures 3.1 and 3.4 plotted on equally scaled extinction axis. This figure allows comparison of local and long-distance dispersal scenarios.

and 6.1, occurred at the high and low endpoints of the range of extinction parameter examined (at extinction levels of 0.005 and 0.125, respectively). These values also correspond with the highest (5.7) and lowest (1.35) median values, respectively, of the average number of species per patch resulting from these simulations. The highest median index of nestedness was 20.6 (the lowest of the four scenarios), which corresponded to a median average number of species per patch for 10 runs of 3.95.

Under the scenario of long-distance dispersal consistent with metapopulation dynamics, the average number of species per patch ranged from 1.1 - 6.6 and the index of nestedness ranged from 1.8 to 53.6 (Figure 3.4). The median value of average number of species per patch for ten simulations decreased approximately linearly with increasing extinction (Figure 3.2). The simulations matched the analytic solution for low to moderate values of ε_m, but at high values of ε_m, the simulations gave higher median values than predicted (Figure 3.2). The median average number of species per patch was consistently higher for the scenario of long-distance, as opposed to local dispersal (e.g., the long-distance dispersal scenario had a value 37% higher than the local dispersal scenario at $\varepsilon_m = 0.05$). Median values of the index of nestedness for 10 simulations under the scenario of long-distance dispersal appeared bimodal along the extinction gradient. Medians at $\varepsilon_m = 0.25$ and $\varepsilon_m = 0.45$ were higher than the median of the index at $\varepsilon_m = 0.35$. The two lowest median values of index of nestedness resulting from these simulations, 12.0 and 15.6, occurred at the high and low endpoints of the range of extinction parameter examined (at extinction levels of 0.05 and 0.55, respectively) (Figure 3.3). These values

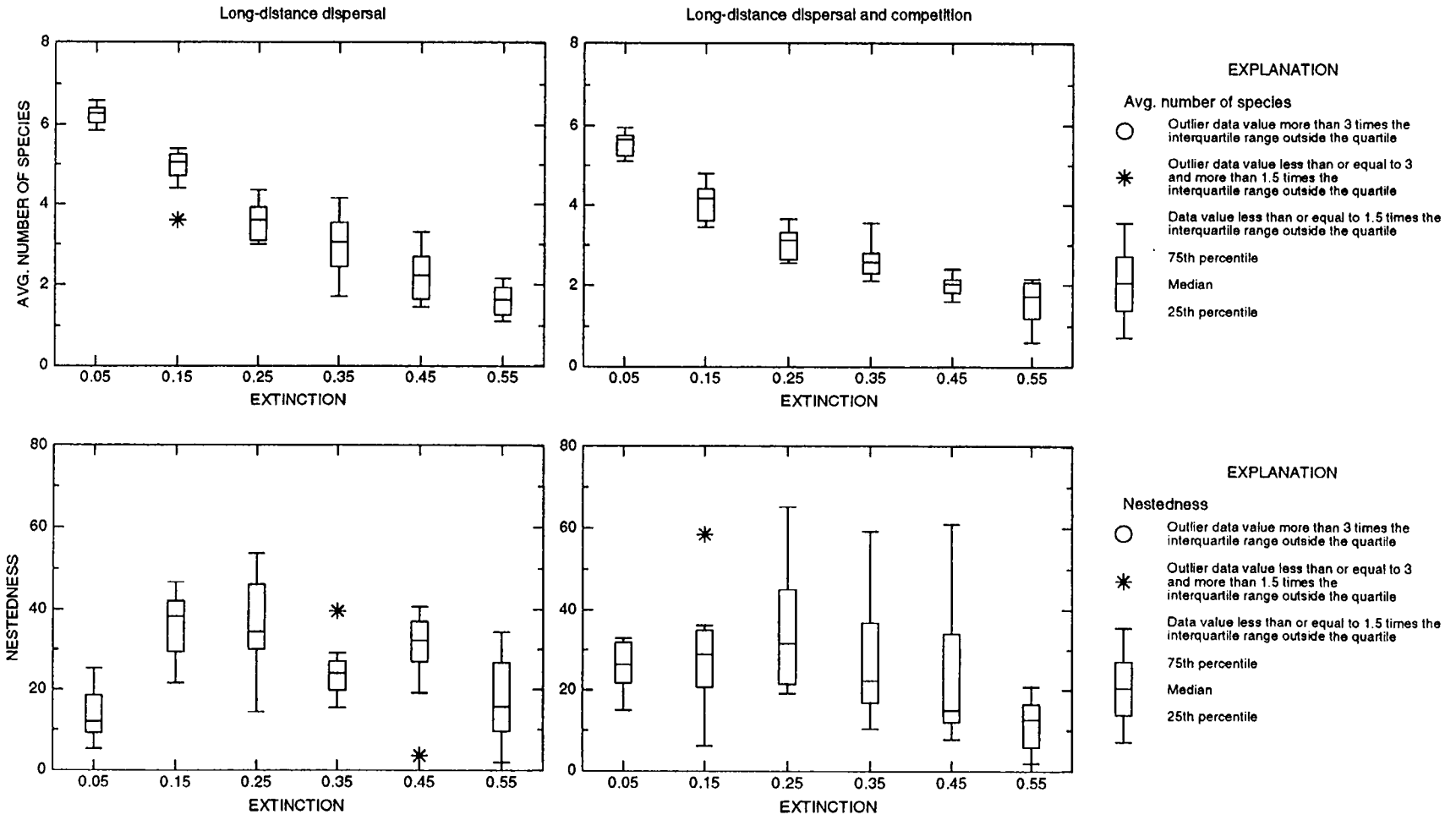


Figure 3.4. Average number of species per patch and index of nestedness for 10 simulations for of each of two scenarios: long-distance dispersal consistent with metapopulation dynamics (left) and both long-distance dispersal consistent with metapopulation dynamics and competition (right). Conditions are $\Delta = 0.05$, $T = 1000$.

also correspond with the highest (6.3) and lowest (1.6) median values of the average number of species per patch from these simulations. The highest median index of nestedness was 34.4 (highest among the four scenarios), which occurred at $\varepsilon_m = 0.25$ and corresponded to a median average number of species per patch for 10 runs of 3.6 (Figure 3.4).

Under the scenario of long-distance dispersal combined with competition, the average number of species per patch ranged from 0.6 - 6.0 and the index of nestedness ranged from 1.8 to 65.1 (Figure 3.4). Median values of the average number of species per patch formed a slightly hollow curve, where median values were lower than in the scenario of long-distance dispersal alone, particularly at levels of extinction that were intermediate in the range examined. For example, competition caused a 10.5%, 26.2%, and 8.4% decline at $\varepsilon_m = 0.05$, $\varepsilon_m = 0.15$, and $\varepsilon_m = 0.45$, respectively. However, the average number of species per patch in this scenario was consistently higher than values found with neither process operating. That is, the negative influence of competition on number of species was weaker than the positive influence of long-distance dispersal associated with metapopulation dynamics. The median values of the index of nestedness for 10 simulations exhibited a unimodal pattern with extinction (Figure 3.3). The highest median index of nestedness for this scenario was 31.6, which corresponded to a median average number of species per patch for 10 runs of 3.2. The finding that the highest median value of the nestedness index occurred at an intermediate value of average number of species per patch is consistent with all other scenarios.

COMPARISON OF MODEL RESULTS TO FIELD DATA

Results of the model were compared to the data from mussel collections in 3 streams of the upper Tennessee River basin: Nolichucky River, North Fork Holston River, and Copper Creek (Figure 3.5). Nolichucky River drains 1,756 square miles and empties into French Broad River mile 69.1. North Fork Holston drains 729 square miles and joins with the South Fork Holston to form the Holston River. Copper Creek drains 133 square miles and empties into Clinch River mile 211.6. Nolichucky River, North Fork Holston River, and Copper Creek are moderately shallow with alternating riffle and pool areas. The riffle areas support mussel beds, which correspond to the patches in this model.

Mussel spatial distribution data were collected at sites on each of the three rivers (Appendix B). The lower *Nolichucky River* was sampled in a 34-mile stretch below Nolichucky Dam (river mile 46.0) by Ahlstedt (1991) at 41 sites in 1980: he found 887 specimens comprising 21 species (two of these sites were located below Enka Dam, and were omitted from this analysis). The *North Fork Holston River* was surveyed by the U.S. Geological Survey at 18 sites in a 113 mile reach in 1995 (Figure 3.6). Sites were selected based on quality of riffle habitat and were surveyed with approximately equal level of effort. All mussels encountered were identified and counted. A total of 15 species and 2023 specimens were found (Appendix C). *Copper Creek* was surveyed at 36 sites in a 53 mile stretch in 1984 by Ahlstedt (1991); he found 1639 specimens comprising 19 species. The subset of the species found in these streams in the Ambleminae/Lampsilini taxa (Davis and Fuller 1981), numbering 10, 9, and 10, for the Nolichucky River, North Fork Holston, and Copper Creek, respectively, were used for this analysis (Table 3.3).

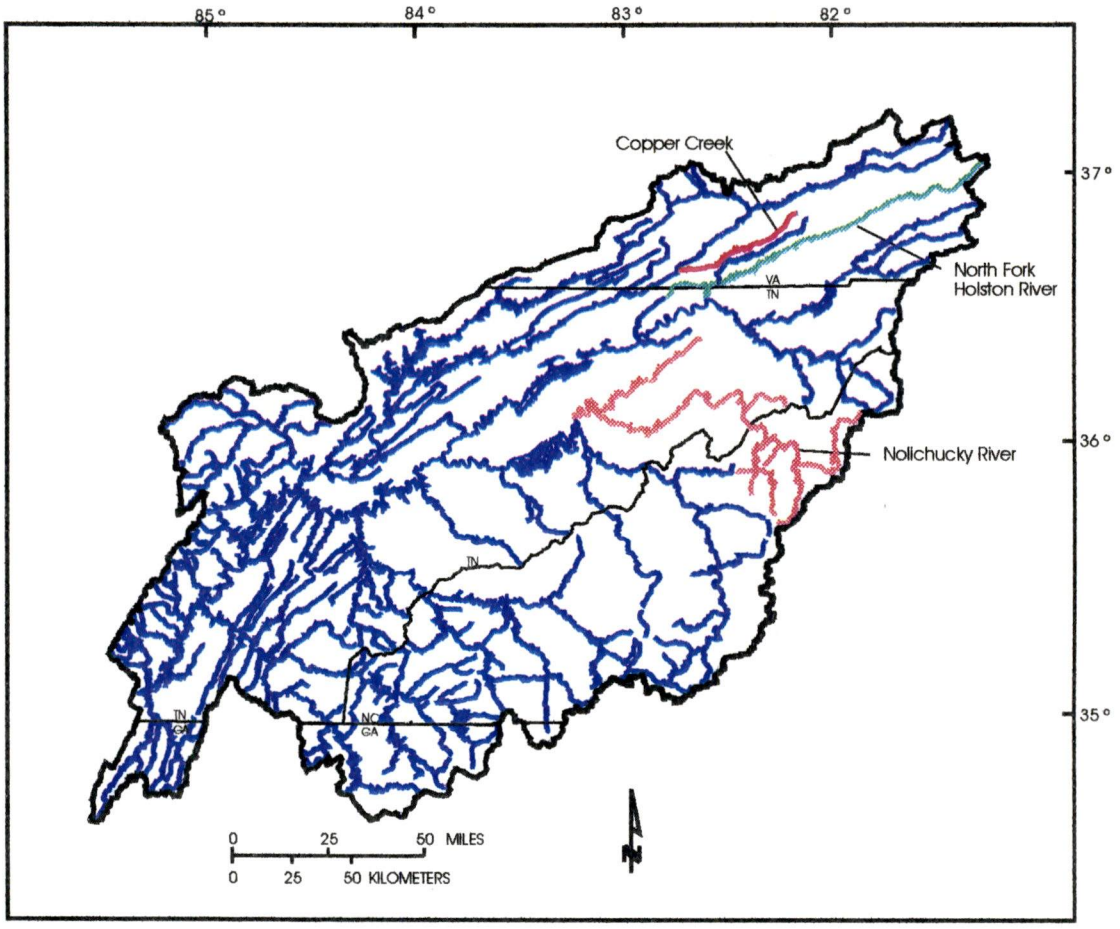


Figure 3.5. Location of the three mesoscale study areas chosen for analysis.

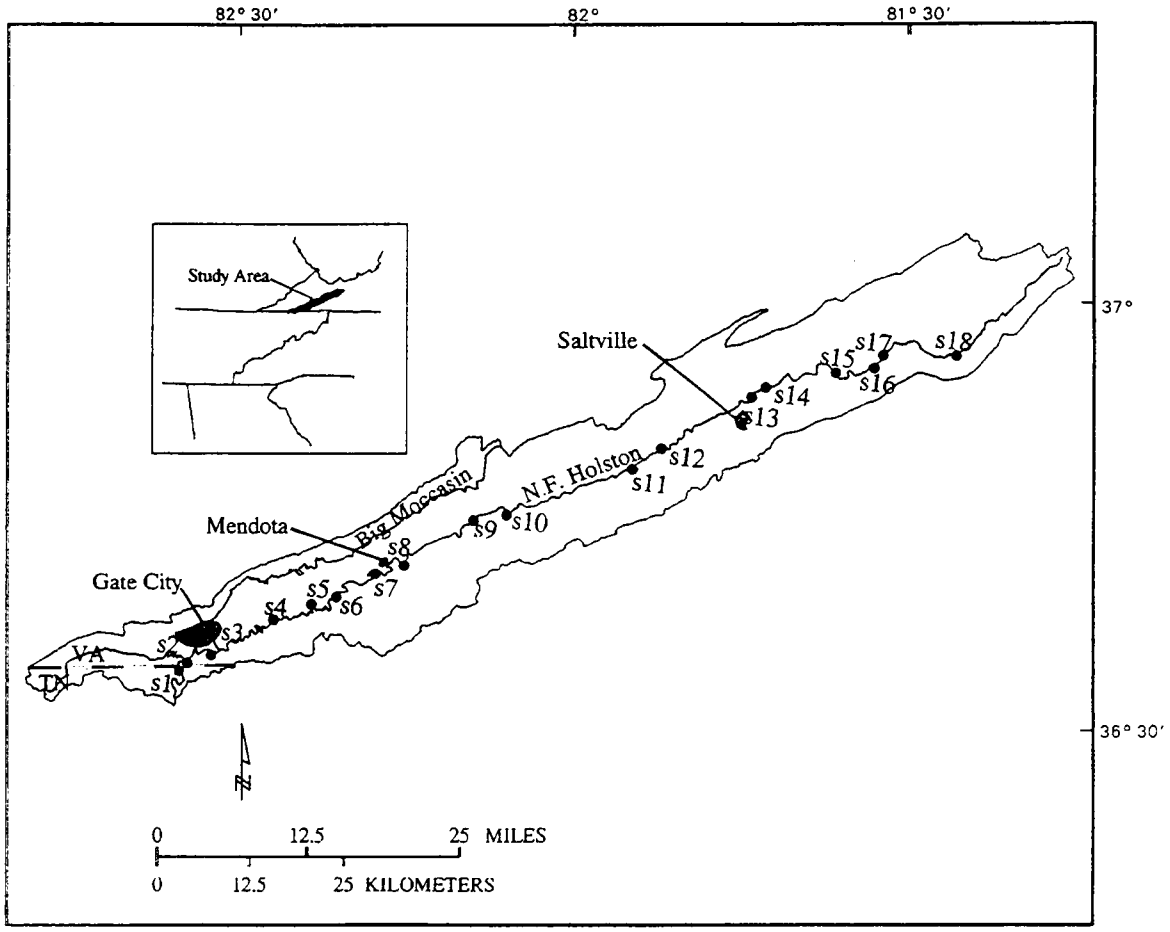


Figure 3.6. North Fork Holston sampling sites. Information corresponding to site numbers is given in Appendix B.

Table 3.3. Occurrence of lampsiline species found in each stream. Data are reported as number of sites occupied divided by total number of sites sampled.

Species	Abbreviation	Nolichucky R.	N. F. Holston	Copper Creek
Actinonaias ligamentina	Al	0.08	0.06	--
Actinonaias pectorosa	Ap	--	0.17	0.11
Epioblasma capsaeformis	Ec	0.03	--	0.11
Epioblasma triquetra	Et	0.03	--	--
Lampsilis fasciola	Lf	0.56	0.83	0.51
Lampsilis ovata	Lo	0.77	0.33	0.06
Ligumia recta	Lr	0.05	--	--
Medionidus conradicus	Mc	--	0.33	0.83
Potamilus alatus	Pa	0.21	--	--
Ptychobranchus fasciolaris	Pf	0.36	0.17	0.11
Ptychobranchus subtentum	Ps	--	0.17	0.20
Truncilla truncata	Tt	0.03	--	--
Villosa iris	Vi	--	0.89	0.91
Villosa perpurpurea	Vp	--	--	0.34
Villosa vanuxemensis	Vv	0.03	0.50	0.09
Total number of species in system		10	9	10
Total number of patches		39	18	32
Average number of species per patch[1]		2.10	3.42	3.20
Ratio of average number of species per patch/total number of species		0.21	0.38	0.32
Equivalent number of species (for comparing to model)[2]		1.47	2.66	2.24
Nestedness index of matrix		10.8	8.3	15.0

1. Calculated in Appendix B.
2. Calculated as the ratio of the average number of species per patch multiplied by 7. Although actual number of species was in the range 9-10, the model used only 7 because the number of community states increased exponentially with the number of species.

Table 3.4. Host-use matrix for lampsiline mussels known from three streams. Stream abbreviations are Nolichucky River (NO), North Fork Holston (NF), and Copper Creek (CC). An "X" in the streams column indicates that the fish species has been identified from that stream. Mussel species name abbreviations are given in Table 3.3. An "X" in the mussel species column indicates that the fish species has been identified as a host for the mussel species. Hosts are unknown for *Actinonaias pectorosa* (Ap) and *Ptychobranchus fasciolaris* (Pf), so these mussel species are omitted from table.

Fish species[2]	Streams			Mussel species[1]												
	NO	NF	CC	Al	Ec	Et	Lf	Lo	Lr	Mc	Ps	Pa	Tt	Vi	Vp	Vv
Ambloplites rupestris	X	X	X	X										X		
Aplodinotus grunniens	X		X									X	X			
Cottus baileyi		X														X
Cottus bairdi	X	X													X	X
Cottus carolinae	X	X	X		X	X					X				X	X
Etheostoma blennioides	X	X	X												X	
Etheostoma flabellare	X	X	X							X	X				X	
Etheostoma rufilineatum	X	X	X		X					X	X					
Etheostoma vulneratum	X	X	X		X											
Lepomis macrochirus	X	X	X	X				X	X							
Lepomis cyanellus	X	X	X	X												
Micropterus dolomieu	X	X	X	X			X	X						X		
Micropterus punctulatus	X	X	X											X		
Micropterus salmoides	X	X	X	X				X	X					X		
Percina caprodes	X	X	X			X										
Percina sciera	X	X	X		X											
Pomoxis annularis	X	X		X				X	X							
Pomoxis nigromaculatus	X	X		X												

1. Host use data taken from Luo 1993, Watters 1994b, and references therein, Hove 1995, Hove et al. 1995, Layzer and Madison 1995, and Watson and Neves 1996.
2. Common names are given in Appendix E. Fish species occurrences taken from Ahlstedt and Rashleigh (in review).

A host-use matrix for the lampsiline species of each stream was constructed from host fish information (Table 3.4). From each of the host-use matrices, a ratio of number of hosts used to the number of mussel species was calculated. The host:mussel ratio was 1.44, 2.14, and 1.38, for Nolichucky River, North Fork Holston, and Copper Creek, respectively. A ratio of 1.75, intermediate among these values, was used in the model. That is, for the 7 mussel species included in the model, 12 host fish were included. The sum of the number of hosts used by each species divided by the product of the number of hosts and the number of mussel species was also calculated: values were 0.20, 0.22, and 0.24, for Nolichucky River, North Fork Holston, and Copper Creek, respectively. A value of 0.25 was used in the model, that is, each species had a 25% chance of using each host.

The ratio of the average number of species per patch to the total number of species in the system and nestedness index were calculated for mussel data from each of the three streams, in order to compare field data to model results (Table 3.4). This ratio for each stream was multiplied by 7, the number of mussel species included in the model, in order to derive the value of average number of species per patch for real data that would be comparable to model results. The equivalent average number of species per patch and the nestedness indices of real communities were then compared to model output. The extinction level for which the average number of species per patch was closest to the median was identified. The actual nestedness index was compared to model results at this extinction value and rated as either consistent with model results (C) (i.e., within the interquartile range), within the range of the model results (R), or outside the range of model results (O) (Table 3.5).

Table 3.5. Comparison of model results to field data. For each scenario, table lists the extinction level (Ext.) for which the average species number per patch from field data on three streams was closest to the median of ten simulations; and indicates whether nestedness index (Nest.) from field data was consistent with (C) (within interquartile range), within (R), or outside (O) the range of the model results at that extinction level.

Model scenario	Nolichucky		N. Fork Holston		Copper Creek	
	Ext.	Nest.	Ext.	Nest.	Ext.	Nest.
Neither process	0.125	C	0.10	R	0.10	C
Competition	0.125	C	0.075	C	0.10	C
Long-distance dispersal	0.55	C	0.35	O	0.45	O
Competition and long-distance dispersal	0.55	C	0.35	O	0.45	C

Because extinction levels were adjusted so that number of species matched the simulations, only the nestedness index can be used to discriminate among scenarios. Real data were most consistent with the model scenario where competition occurred, and secondly with the scenario where neither process occurred.

This model can be used, for example, to examine impacts such as the alteration or elimination of some patches in the system, which would decrease the number of patches (X) and the dispersal probability Δ. The competition model scenario can be parameterized with $\varepsilon_m = 0.10$, an intermediate extinction value taken from Table 3.5. If both the number of patches and the dispersal probability decreased by 25%, the median of average number of species per patch would decline by 19.1% and the index of nestedness would decline by 10.5% (mean values for 10 simulations). Species' occupancy on patches is affected by the configuration and number of patches. Parameterization and validation with field data from specific sites would allow the model to be used for predictive purposes.

DISCUSSION

The opposite effects of competition and long-distance dispersal consistent with metapopulation dynamics on the average number of species per patch were not unexpected: other models have demonstrated that including competition reduces the number of species that coexist locally in models with metapopulation dynamics (Hanksi 1983) and without metapopulation dynamics (Lotka 1925), and conversely, that metapopulation dynamics increases the number of locally coexisting species for scenarios with competition (Slatkin 1974) and without competition (Hanksi 1982). The weakness of competition in affecting species number, relative to metapopulation dynamics, could be related to the low species overlap specified in the input host-use matrices. It is possible that freshwater mussel communities have been influenced by competition in the past, and poorer competitors are already extinct (Connell 1980). The relatively weak competitive interactions in the input matrix could also explain the relatively high nestedness in model results including competition, which contradicts other findings about the role of competition in metacommunities (Case 1991, Wilson 1992).

Competition may have increased nestedness by emphasizing differences in immigration and/or extinction rates. Rates for immigration and extinction among species in this model were assigned to be similar, and this assumption may not be realistic. Gotelli and Kelley (1993) concluded that the assumption that species are similar in probabilities of immigration and extinction was not appropriate for modelling mangrove insects. Wright and Reeves (1992) have noted that factors leading to consistent differences in species' immigration and extinction rates generate strong nestedness. Patterson and Brown (1991)

have determined that hierarchical organization of niche relationships is a necessary condition for nested subsets. The lack of nested subsets when neither process was operating may be due to the model assumption that species were similar.

The decrease in nestedness with the inclusion of long-distance dispersal associated with metapopulation dynamics is unexpected, since Wright and Reeves (1992) note that the "rescue effect" of long-distance dynamics leads to negative correlations between species' immigration and extinction rates, which would increase nestedness. The decrease in nestedness observed here may be due to either the off-setting influence of increased overall species dispersal--Hecnar and McCloskey (1997) found that for amphibians, species grouped as good dispersers were less nested than species grouped as poor dispersers--or possibly the influence of the assumption that the downstream patch received input from all species, and the "rescue effect" magnified this influence under long-distance dispersal scenarios (particularly at high extinction levels).

The generally unimodal pattern of nestedness is to be expected. Communities with relatively high occupancy are expected to be nested because most sites are occupied. Ryti and Gilpin (1987) found that matrices with a higher proportions of occurrences are more ordered. Similarly, sites with relatively low occupancy are expected to be nested because most sites contain only one or a few species. None of the scenarios appeared particularly nested at intermediate numbers of species. This may be due to the fact that nestedness has been attributed to certain environmental characteristics, such as differences in patch size or isolation (MacArthur and Wilson 1967, Patterson and Atmar 1986), and the patches in this model were assumed to be equal in size and spacing.

Mussel communities in the three streams examined here exhibited a relatively low average number of species per patch and high nestedness. This type of distribution pattern, where a few species are common and most are rare, is prevalent in ecological communities (Preston 1948). High nestedness is also commonly found in ecological communities: nestedness has been demonstrated for such diverse taxa as insects (Patterson 1990), fish in springs (Kodric-Brown and Brown 1993), and plants (Wright and Reeves 1992). Layzer and Madison (1995) found that the numbers of freshwater mussel species in communities of the Cumberland River system (Tennessee/Kentucky) were positively correlated with each other. Positive, rather than negative, associations have also been identified in communities of fish (Jackson et al. 1992) and desert plants (Silvertown and Wilson 1994).

Patterns of species number and composition in the three freshwater mussel communities examined here were most consistent with the model scenarios involving local, rather than long-distance dispersal. The characterization of mussels as having local dispersal agrees with the observation that they are the quickest element of the fauna to decline and the slowest to rebound (Cairns et al. 1971). Because dispersal is local, locally impacted sites within a mesoscale site network may need restoration, and preserves should maintain sufficient patch proximity in order to insure success. Patterns in the three mussel communities were most consistent with structuring by competition, however, at the low species number per patch exhibited in real communities, differences between scenarios with and without competition were relatively minor. The low influence of competition may be due to the low host overlap, the result of past competition: artificially restored or constructed mesoscale communities should include species with these characteristics.

SUMMARY AND CONCLUSIONS

Upper Tennessee River basin lampsiline freshwater mussel communities that occupy patches connected by dispersal differ in species number and composition, despite similarities in habitat. A model was developed to examine the role of competition and long-distance dispersal associated with metapopulation dynamics in generating the patterns. The model specified transition probabilities between community states for each patch as a function of species dispersal and extinction, and considered the average number of species per patch and index of nestedness under a range of parameters for extinction. Results of the model were then compared to mussel data from three streams in the upper Tennessee River basin.

Competition decreased the average number of species per patch, and metapopulation dynamics increased this parameter when compared to the scenario where neither process was operating, as expected. Long-distance dispersal dominated the effects of competition, possibly because matrices were assigned based on real data, which did not contain strong interactions. The index of nestedness appears unimodal for almost all scenarios. The scenario with neither process operating was not strongly nested, due to the random assignment of species abilities that was an assumption of the model. Competition was not strong enough to generate alternative states, and instead increased nestedness by emphasizing species' differences. The positive feedback associated with long-distance dispersal led to low nestedness. Real communities exhibit fairly low average number of species per patch, and are strongly nested, which is most consistent with the scenario where competition, or neither process, generated structure.

CHAPTER IV. REGIONAL SPECIES RICHNESS, VARIABILITY, AND SPECIALIZATION IN A UNIONID TAXON

INTRODUCTION

One of the highest diversities of freshwater mussel species of the family Unionidae in the world is found in the region of the upper Tennessee River basin, a 21,400 square mile drainage in Tennessee/Virginia/North Carolina/Georgia. Ahlstedt and Rashleigh (in review) report 93 species from this basin. Several of these species are endemic to the Tennessee River drainage (van der Schalie and van der Schalie 1950), and many are at risk of extinction. Over half of the mussel species known from this basin are federally protected, and seven are presumed extinct (Williams et al. 1992). Conservation efforts for these species recognize the need to manage fauna at large scales (Williams and Neves 1992). However, there is little understanding of how patterns of mussel species richness at the regional scale develop, and what conditions are likely to characterize highly diverse communities. Two hypotheses, based on the processes of competition and spatio-temporal heterogeneity, respectively, can be considered as possible explanations.

Classical competition theory considers species richness patterns across a region as predictably structured by local competition for limiting resources (Schluter and Ricklefs 1993). Competition between species has negative effects on the growth, reproduction, and/or survival of both species, which at competitive equilibrium lead to the exclusion of the poorer competitor (Lotka 1925, Volterra 1926). Species that coexist are expected to differ by a limiting similarity (MacArthur and Levins 1967). Local species richness at competitive equilibrium is assumed to be invariably determined by the limiting similarity

between species and the amount of available resources (MacArthur 1965). The abiotic conditions expected to lead to highest regional richness are not known (Brown 1995).

An alternate view is that communities are predominantly structured by the spatial and temporal heterogeneity of the environment, rather than by biotic interactions. Hubbell and Foster (1986) hypothesized that the unpredictability introduced into competition by the environment may lead to generalization and similarity among species. If communities are predominantly structured by the spatial and temporal heterogeneity of the environment, history and chance may determine local species richness (Shmida and Ellner 1984, Hubbell and Foster 1986, Cornell 1993). Highest regional species richness would be expected under certain abiotic conditions, such as intermediate colonization levels (Huston 1979, Hubbell and Foster 1986, Huston 1994), that may reduce gene flow among local communities, and therefore prolong coexistence.

Freshwater mussel species richness in the upper Tennessee River basin may be influenced by either competition or environmental heterogeneity. Although it is unlikely that freshwater mussel species compete for food or space (Bronmark and Malvquist 1982, Gordon and Layzer 1993), it is possible that they experience competition for fish hosts, on which their larvae are obligate parasites for a period of weeks to months. Phenological changes in mussel species through time have occurred primarily in the reproductive tissues (Heard and Gucket 1971, Davis and Fuller 1981), so it is possible that the fish-mussel interaction has driven speciation of freshwater mussels. However, the upper Tennessee River basin experiences a wide range of environmental conditions, and richness in the basin may be influenced primarily by environmental heterogeneity.

Here, a modelling approach is developed in which fauna are allowed to repeatedly build up on a fixed background (Haydon et al. 1994). The model considers a single mussel taxon, the Lampsilini tribe, because different taxa use different groups of host fish species, and competition for hosts would only be expected to occur among species of the same taxon. The model includes competition for hosts and spatio-temporal heterogeneity in community processes of colonization, speciation, and extinction. Model output (regional species richness, variability in species richness among simulations, and measures of specialization) was compared to predictions of alternative hypotheses: communities structured by competition exhibit low variability in richness and high specialization among species, whereas communities structured by environmental heterogeneity exhibit a peak in richness with intermediate colonization rates, high variability among replicate runs, and generalization among species. Regional freshwater mussel species richness patterns in the upper Tennessee River basin were evaluated for consistency with the model, and compared to model results to infer structuring processes.

THE MODEL

Model description

A model to simulate the buildup of the lampsiline taxon in the region of the upper Tennessee River basin was developed. The model tracked the number of taxon members, or "species" in the region and their occupancy across the 19 subregions of the basin. Here, subregions corresponded to hydrologic units, divisions of the basin designated by the U.S. Department of Agriculture that represent large breaks in hydrology (Figure 4.1).

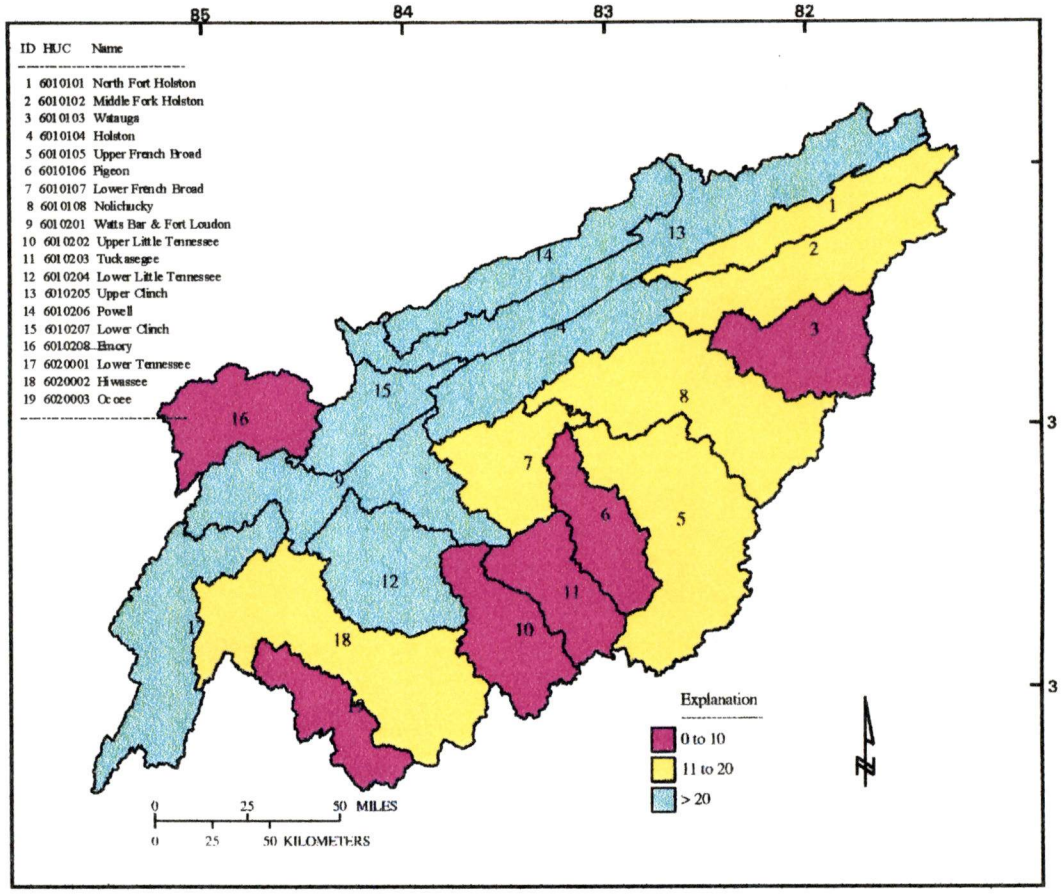


Figure 4.1. Lampsiline species richness by hydrologic unit. The upper Tennessee River basin (North Carolina/Tennessee/Virginia/Georgia) is divided into hydrologic units, which represent large breaks in hydrology. The hydrologic unit code (HUC) corresponding to the hydrologic unit number was assigned by the U.S. Department of Agriculture. This figure gives the richness of species of the Lampsilini tribe of freshwater mussels of the family Unionidae by hydrologic unit. A species list is provided in Appendix D and summarized in Table 4.3.

Connections between units were assigned to mimic the real drainage pattern for this region. All units were assumed to be equal in size, to possess identical environmental characteristics, and to differ only in the number and identity of resident fish species. Fish species number and identity were assigned based on field data (described below).

The number of mussel species present in the region was represented as $M(t)$, and the number of host fish species was given by H (definitions of all parameters are given in Appendix A). It was assumed that mussel species colonized a fixed pool of hosts (Jermy 1984), rather than evolving simultaneously with hosts (Ehrlich and Raven 1964). Mussel species were represented as binary strings ("genotypes") of length H. Each element, or locus, on the string ($G_{m,h}(t)$) corresponded to the potential of mussel species m to use a particular host resource h. This 1:1 assumption for parasites to hosts has been used to describe other host-parasite systems (e.g., Hamilton 1993). Each locus was represented with either a "1", indicating that the resource is used, or a "0", indicating that the resource is not used. The $M(t)$ x H matrix $\boldsymbol{G}(t)$ represents the set of mussel species' genotypes at a particular time t.

The model was run with a time step approximating a generation. Each generation consisted of the steps of mutation, determination of fitness, colonization, and extinction. Mutation is the change in the form of the gene at a particular locus. Fitness is the ability, relative to others species in a system, to generate offspring (Allaby 1994). Extinction is defined here as the loss of species from a hydrologic unit. Colonization is defined as the movement of species from one hydrologic unit to another in evolutionary time. The mathematical representation of these processes in the model is explained below.

Mutation

Mutation occurred at each time step for each species in each unit at each locus with the probability μ (set at 0.001). That is, with probability μ, each locus ($G_{m,h}(t)$) switched from either a "0" to a "1", or vice versa, depending on its original state. A newly mutated string, if unique, was added to the set of genotypes for the basin and recorded as occurring in the unit where it originated. The string from which the mutant was derived was either deleted, with probability 1- ς, or retained, with probability ς (set at 0.9). Retention of the old string represents sympatric speciation, the development of a new taxon from an older taxon in the same geographic range (Allaby 1994). Sympatric speciation may be common in mollusks (Davis 1982). The model also included back-mutation based on host immunity. That is, with probability A,

$$A_h(t) = \mu \cdot \sum_{m=1}^{M(t)} G_{m,h}(t), \tag{4.1}$$

$G_{m,h}(t)$ was set to "0" for all mussel species m for host species h. It was assumed that back-mutation was positively related to the number of parasites using fish species h.

Determination of relative fitness

Fitness (w) of genotype i in hydrologic unit u was given by

$$w_{i,u}(t+1) = \rho_i [1 - \lambda_{i,u}(t)], \tag{4.2}$$

where ρ_i represents the overall ability of species i in generating offspring (which in this model is equivalent to its ability in attracting hosts), and $\lambda_{i,u}$ represents competition experienced by species i in hydrologic unit u at time t. Each species was randomly

assigned an ability ρ_i in the range (0,1). The term representing competition, $\lambda_{i,u}(t)$, was taken from equation (3.13) as:

$$\lambda_{i,u}(t) = 1 - \left\{ \frac{1 + \left[r_i(t) / \sum_{h=1}^{H} F_{h,u} \right]}{1 + r_i(t) / \left\{ \sum_{h=1}^{H} \left[F_{h,u} \div \sum_{m=1}^{M(t)} C_{mih}(t) N_{m,u}(t) \right] \right\}} \right\}, \tag{4.3}$$

where the parameter $N_{m,u}(t)$, the occurrence of species m in unit u at time t, is defined as

$$N_{m,u}(t) = \begin{cases} 1, w_{m,u}(t) > 0 \\ 0, w_{m,u}(t) = 0 \end{cases}, \tag{4.4}$$

the parameter r, the probability of successful infestation, is defined as

$$r_i(t) = \sum_{h=1}^{H} [F_{h,u} \cdot c_{ih}(t)], \tag{4.5}$$

the parameter $C_{mih}(t)$, the competitive effect of species m on species i, is defined as

$$C_{mih}(t) = c_{mh}(t) / c_{ih}(t), \tag{4.6}$$

and $F_{h,u}$ is the occupancy (1,0) of fish species h in hydrologic unit u.

The reproductive ability of species i on host h at time t, $c_{ih}(t)$, is calculated as the species' overall ability to attract hosts divided by number of hosts used, to represent the trade-off between the number of hosts used and the ability to use each host:

$$c_{ih}(t) = \rho_i / \left[\sum_{h=1}^{H} G_{i,h}(t) \right]. \tag{4.7}$$

The substitution of equation for competition (4.3) in the equation for fitness (4.2) gives

$$w_{i,u}(t) = \rho_i \left(\frac{1 + \left[r_i(t) / \sum_{h=1}^{H} F_{h,u} \right]}{1 + r_i(t) / \left\{ \sum_{h=1}^{H} \left[F_{h,u} \div \sum_{m=1}^{M(t)} C_{mih}(t) N_{m,u}(t) \right] \right\}} \right) \quad (4.8)$$

which reduces to

$$w_{i,u}(t) = \rho_i \left(\left\{ \sum_{h=1}^{H} \left[F_{h,u} \div \sum_{m=1}^{M(t)} C_{mih}(t) N_{m,u}(t) \right] \right\} / \left(\sum_{h=1}^{H} F_{h,u} \right) \right). \quad (4.9)$$

If species *i* experiences no competition in hydrologic unit *u*, equation 4.9 reduces to $w_{i,u}(t) = \rho_i$, that is, its fitness is equal to its overall ability in attracting hosts. It was assumed that if a species evolved to use ten or more hosts, its fitness was set to zero.

Colonization and extinction

In this model, a species' colonization ability was assumed to be a function of a species' fitness and occupancy among hydrologic units. For a time step *t*, each hydrologic unit *u* was categorized as either "1" or "0" for each species *i*, based on whether or not the fitness of species *i* in unit *u*, $w_{i,u}(t)$, was above or below a critical value, respectively. The critical fitness value, $\omega_c(u,t)$, was derived from the introduction of Gaussian noise with small standard deviation (sd=0.1) to a constant critical fitness value for colonization ω_c. Noise was added to simulate natural variability in the system. The occupancy state of a hydrologic unit at time t+1 depends its state and the state of its upstream and downstream neighbors at time *t*. It is assumed that the most downstream unit has a downstream state of "0". A unit's "neighborhood" can be characterized as a three-bit string representing upstream, target, and downstream units (Table 4.1).

Table 4.1. Transition rules for a target hydrologic unit. Neighborhood sequence represents upstream hydrologic unit--target hydrologic unit--downstream hydrologic unit.

	Neighborhood sequence at time t							
	111	110	101	100	011	010	001	000
State of target hydrologic unit at time t+1	1	1	1	1	1	1	1	0

Table 4.1 specifies which of the eight possible neighborhood sequences will lead to an empty hydrologic unit, represented by a "0", and which will lead to a colonized unit, represented by "1". A target unit will be occupied by a species at time t+1 unless neither it nor its neighbors contain the species at or above the critical fitness value $\omega_c(u,t)$.

Extinction of a species was assumed to be a function of its fitness: species within a hydrologic unit u at time step t with fitness less than a critical value became extinct in that unit. The critical fitness value, $\omega_e(u,t)$, was derived from the introduction of Gaussian noise with small standard deviation (sd=0.1) to a constant critical fitness value for extinction ω_e. If the critical fitness value was high enough to remove all species from the system, the model specified that the species with the highest mean fitness remained, in order to maintain the system.

Simulations

The initial condition of the model was 5 randomly generated genotypes present in each of the first 2 downstream hydrologic units (u = 9 and u = 17, see Figure 4.1). The five initial genotypes were generated such that each species had a 10% chance of using each

host fish species. Ten model runs of T=500 generations were conducted at each of 25 different combinations of critical fitness values for colonization and extinction: five values for colonization (0.5, 0.6, 0.7, 0.8, 0.9) and five for extinction (0.1, 0.2, 0.3, 0.4, 0.5). Means of output parameters were reported for the last 50 time steps. Regional species richness means over 10 simulation runs were graphed as functions of critical fitness values for colonization and extinction. Coefficients of variation (CV) across sets of simulations, calculated as standard deviations divided by means, multiplied by 100, were plotted against regional richness. Means over 10 simulation runs for host overlap and average number of hosts per mussel species were calculated and regressed with regional richness to detect specialization. An overlap, or link, occurs between two mussel species in the region when they have at least one host in common. Host overlap for the system (χ) is calculated as the fraction of actual links (L) over all possible links, $M(M-1)$. Ten additional simulations were run at intermediate critical fitness values for colonization and extinction (0.8 and 0.2, respectively), when the mutation rate and speciation rate were each decreased by 50%, to determine the model's sensitivity to these parameters.

MODEL RESULTS

According to the model for the region of the upper Tennessee River basin, species richness increased with decreasing critical fitness values for colonization and extinction (Figure 4.2). Regional richness reached its highest value within the parameter space considered, a mean value of 66.7 for 10 simulations, at critical fitness values of 0.5 and 0.1 for colonization and extinction, respectively. Regional richness reached its lowest

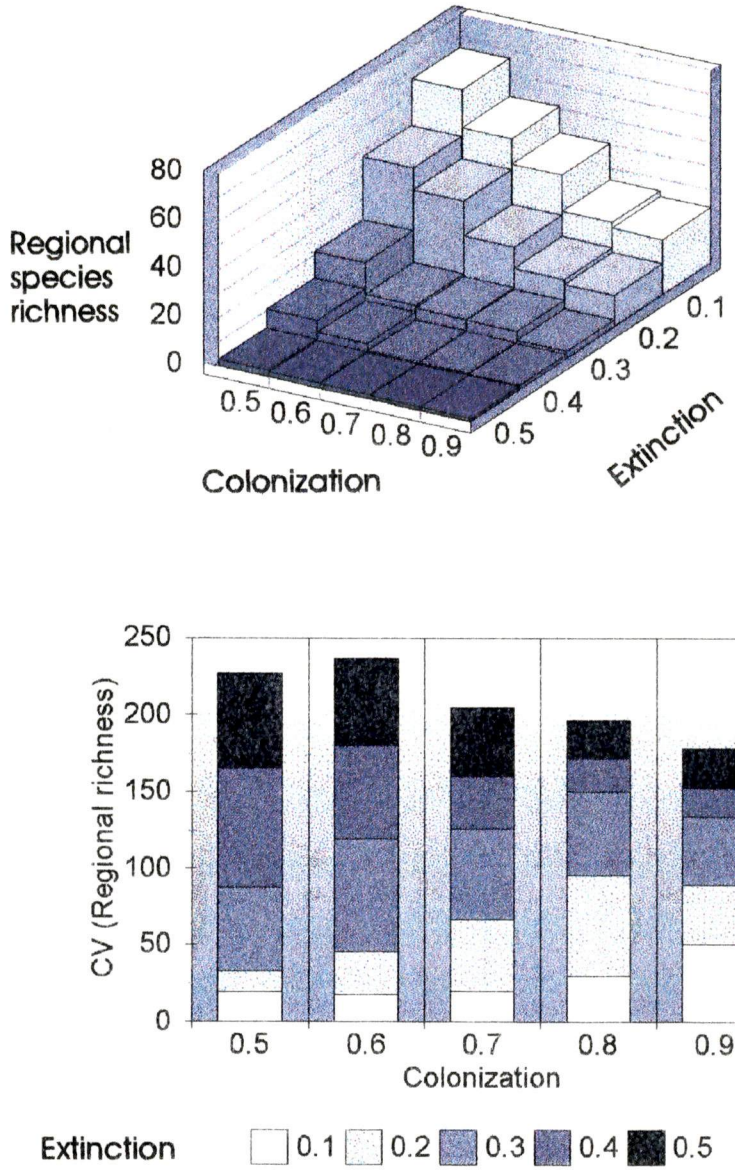


Figure 4.2. Regional species richness and environmental conditions. Figure shows mean values (top) and coefficient of variation (CV) (bottom) for 10 simulations as a function of the critical fitness values for colonization and extinction.

value, a mean of 1.3 for ten simulations, at critical fitness values of 0.9 and 0.5 for colonization and extinction, respectively. The value of the coefficient of variation (CV) among each set of ten simulations for regional species richness was not constant with species richness (Figure 4.3). Over the range of regional richness of approximately 1 to 10, the CV increased with richness. The highest value of the CV, 77.7, occurred at a regional species richness of 10.4. Over the range of richness of approximately 10-30, CV declined. The CV remained approximately constant and consistently low (equal or less than 20) for the range of regional richness values from 30 to 66.7, the highest value that occurred in the model. The minimum value for the CV, 13.8, occurred at a regional richness value of 47.4. Sensitivity of regional richness and the CV to changes in the mutation and speciation parameters is given in Table 4.2.

Table 4.2. Results of sensitivity analysis. Sensitivity is change in the mean over 10 model runs compared to results for $\omega_c = 0.8$, $\omega_e = 0.2$. Default values are $\mu = 0.001$ and $\varsigma = 0.9$.

Parameter value (% change)	Regional richness	CV (Regional richness)	Host overlap	Avg. number of hosts
Mutation rate (μ) 0.0005 (-50%)	5.6 (-50.9%)	36.4 (-47.4%)	0.42 (+10.5%)	3.1 (+24%)
Speciation (ς) 0.45 (-50%)	5.9 (-48.2)	61.4 (-11.3%)	0.39 (+2.6%)	3.0 (+20%)

A 50% decrease in either the mutation rate or speciation parameter caused approximately a 50% decrease in the mean value of regional richness for 10 simulations. Both parameter changes decreased the CV, which is expected with the decrease in richness predicted by the model.

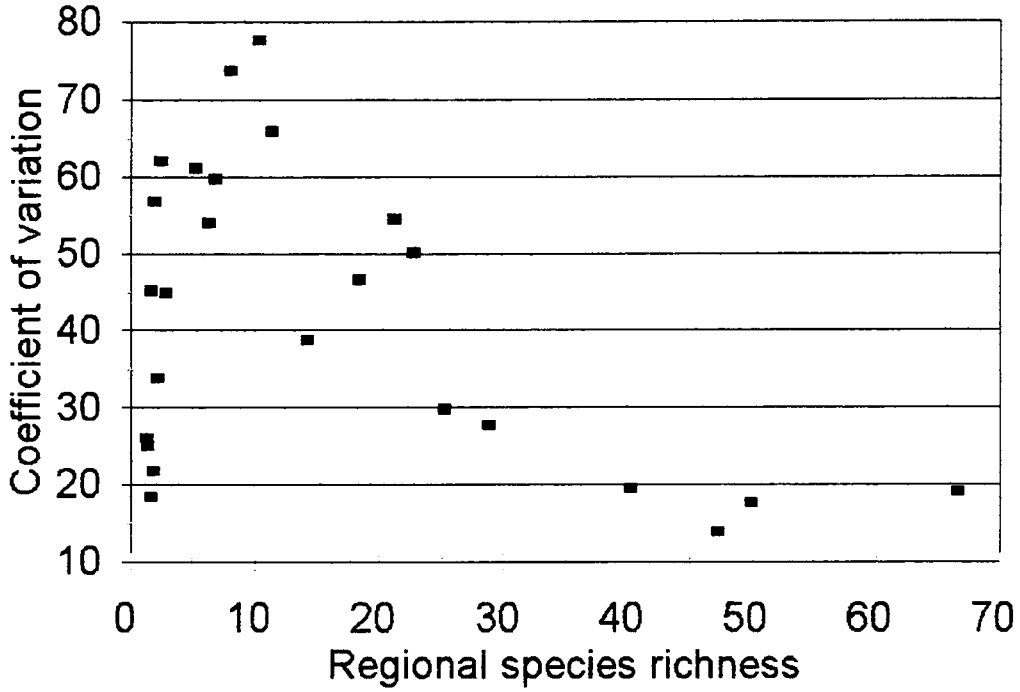


Figure 4.3. Coefficient of variation as a function of regional species richness. Each value for regional species richness represents the mean of 10 model runs. The coefficient of variation for each value of regional species richness is calculated as [(Std/Mean)*100], where Std = the standard deviation from the 10 model runs, and Mean = the mean regional species richness over the 10 model runs.

Host overlap and average number of hosts per species were negatively related to regional richness (Figure 4.4). Although both parameters exhibited a recognizable decline at relatively low levels of mussel species richness, these parameters appear nearly constant above a regional richness level of approximately 30. These characteristics were correlated with each other (r=0.7442, P=0.0001). Decreases in both the mutation rate and the probability of sympatric speciation slightly increased host overlap and average number of hosts use per mussel species (Table 4.2). These changes are most likely related to the decrease in regional species richness that occurred with a decrease in mutation and speciation parameters.

COMPARISON WITH LAMPSILINE DATA

The model results were compared to data for lampsiline freshwater mussel species richness in the upper Tennessee River basin (UTEN). Lists of the lampsiline species in the basin and hosts used by these mussel species were compiled (Appendix D and E, respectively). The occurrence of fish species by hydrologic unit (Appendix F, Table 4.3) was used as input for the model. Richness of the subset of lampsiline mussels for which hosts were known (indicated as bold in Appendix D) is given in Table 4.3, 4.4.

Table 4.4. Actual mussel data for the upper Tennessee River basin.

Regional richness (Appendix D)	Mean hydrologic unit richness (Table 4.3)	Number of host fish (Appendix E)	Host overlap	Average # of hosts
29	13.2	30	0.21	2.8

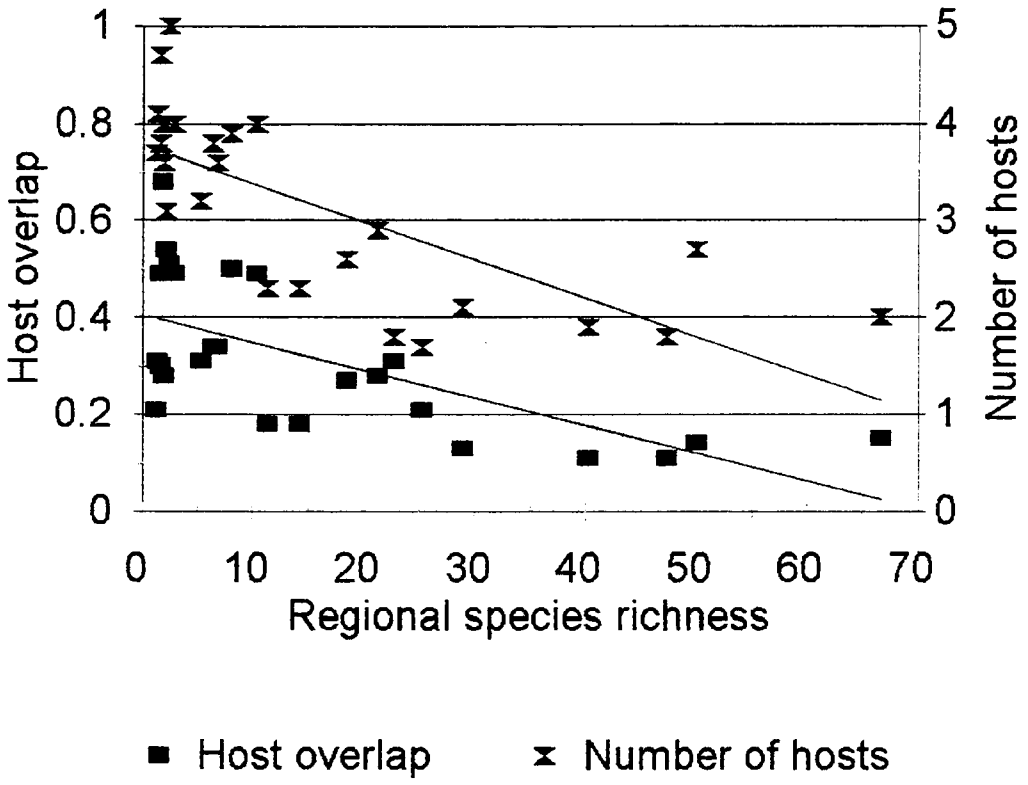


Figure 4.4. Host overlap and average number of hosts per mussel species as a function of regional species richness. Data points represent the means of ten simulations. The linear regression of host overlap with richness is given by y = 0.406 - 0.0006x (F=17.763, Pr>F 0.0003), and the linear regression of average number of hosts per species with richness is given by y = 3.778 - 0.0394x (F=26.423, Pr>F 0.0001).

Table 4.3. Lampsiline mussel species and host species richness by hydrologic unit.

Major drainage	Hydrologic unit (Abbreviation)	Hydrologic unit number (u)	Lampsiline species richness	Number of hosts
Holston River	North Fork Holston River (Nf)	1	16	22
	South Fork Holston River (Sf)	2	12	25
	Watauga River (Wa)	3	4	23
	Holston River (Ho)	4	22	28
French Broad River	Upper French Broad River (Uf)	5	9	24
	Pigeon River (Pi)	6	1	23
	Lower French Broad River (Lf)	7	20	27
	Nolichucky River (No)	8	16	21
Watts Bar - Little Tennessee River	Watts Bar-Fort Loudon (Wb)	9	22	29
	Upper Little Tennessee River (Ul)	10	2	20
	Tuckaseegee River (Tu)	11	0	15
	Lower Little Tennessee River (Ll)	12	24	24
Clinch-Powell Rivers	Upper Clinch River (Uc)	13	23	28
	Powell River (Po)	14	20	26
	Lower Clinch River (Lc)	15	24	25
	Emory River (Em)	16	7	19
Lower Tennessee-Hiwassee Rivers	Lower Tennessee River (Tn)	17	17	24
	Hiwassee River (Hi)	18	11	26
	Ocoee River (Oc)	19	0	17
	Mean values (Standard deviation)		13.2 (8.4)	23.5 (3.8)

Host overlap and average number of hosts per mussel species were calculated from these data (Table 4.4). Regional and mean hydrologic unit richness for model and actual data were plotted, and the euclidean distance between actual data and the nearest point in the plot was calculated. Host overlap and average number of hosts for actual data were compared to real data at this point.

UTEN richness values are within the range of the model results (Figure 4.5).

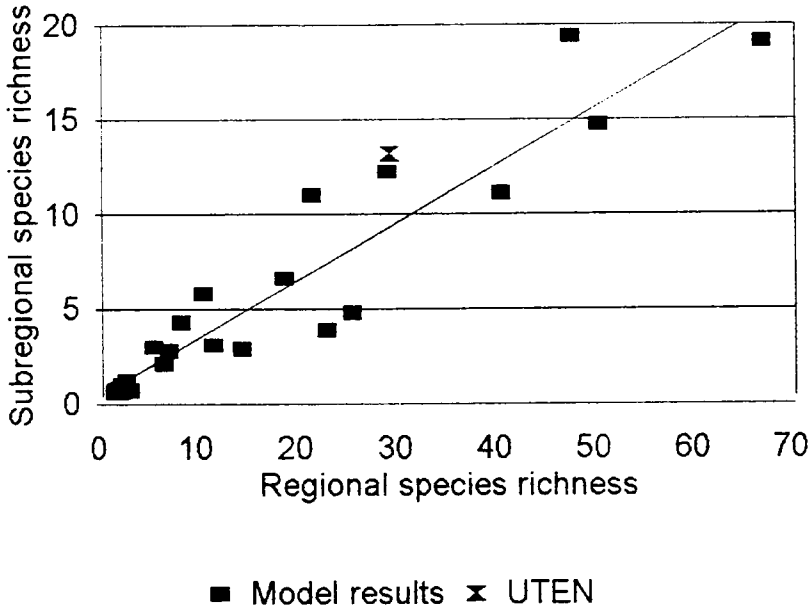


Figure 4.5. Comparison of model results to actual UTEN data for regional vs. subregional richness. Model results are means of ten simulations. The best-fit regression line is $y = 0.31 + 2.94x$ ($F=188$, $Pr>F$ 0.0001).

Field data from the UTEN are most similar to a model regional richness of 28.9, where critical fitness values for colonization and extinction are 0.6 and 0.2, respectively (Euclidean distance 1.0). At this richness value, model results showed a relatively low CV of regional richness of 27.6 (Figure 4.3). However, actual data showed a 62% higher overlap (0.13 vs. 0.21) and 33% higher average number of hosts (2.1 vs. 2.8) than model results (Figure 4.4). In other words, model species were more specialized that actual species.

DISCUSSION

Over the range of parameter space examined, the model did not exhibit a peak in regional richness with intermediate colonization rate, as expected if spatio-temporal heterogeneity generated structure. Instead, regional richness increased with decreasing critical value of fitness for colonization. That is, richness increased as the barriers to colonization decreased. However, a decrease in the barriers to colonization did not actually increase colonization rate in this model, as evidenced by the linear relation between regional and subregional richness. A low critical fitness value for colonization promoted richness, but in this model, increased richness decreased fitness, due to increased competition. Because colonization is dependent on fitness, the decrease in fitness reduced actual colonization. This is similar to the positive feedback mechanisms described by Hurtt and Pacala (1995) for the local scale, where increasing species richness causes species to become more recruitment limited, further promoting richness.

The relatively low, constant values of variability in species richness among simulations, host overlap, and average number of hosts per species at high regional richness were suggestive of the effects of competition. The finding of high variability at low richness is similar to that of Haydon et al. (1993), who also found that chance had the greatest effect for low species richness scenarios in an evolutionary model. The result of low overlap at high richness is similar to that of Ginzburg et al. (1988), who developed a theoretical model where new species were derived from existing species, and found that competitive interactions between model species evolved to be weak. Maxwell and Constanza (1993) simulated evolutionary dynamics using competition coupled with mutation, and found that

most simulations converged to the same configuration of discrete species in niche space. Kauffman (1993) and Kauffman and Johnsen (1991) have also demonstrated that species in evolutionary models may adjust to a constant overlap.

Mussel species richness patterns in the upper Tennessee River basin were most consistent with competition as structuring the communities. As such, communities under similar conditions are expected to exhibit similar levels of richness. This is a reasonable prediction: neighbors of the upper Tennessee River basin unconnected by waterways (i.e., Coosa River, Cumberland River) do support similar levels of richness (Hurd 1974, Gordon and Layzer 1989). This model characterizes communities with high richness as having relatively low fitness, which is consistent with the susceptibility of highly diverse mussel communities to extinction, and the ease of invasibility of mussel communities by species from the outside with high fitness. The model predicts a decrease in regional richness with increasing critical values of fitness for colonization and extinction. Barriers to colonization in nature have recently increased due to impoundments, while extinction has increased, due to reduction in suitable habitat, environmental stress, and pollution. Changes in these characteristics are associated with mussel decline.

Model results showed species to be more specialized than in actuality. The model assumed each mussel species used each of its host species equally well. This assumption simplifies the modelling, but is not realistic: experimental work has shown that different species of fish do not serve equally well as hosts for a given mussel species (Hill 1986). A relaxation of the assumption that a mussel species used all of its hosts with equal ability would allow for resource partitioning, which would permit more overlap. Also, this evolu-

tionary model for mussel species in the upper Tennessee River basin did not include variability in fish host densities or occurrences. Maxwell and Constanza (1995) found in an evolutionary model that variation in resources can reduce the number of species that are specialists. These assumptions about mussels' ability and variability in host densities could account for the differences in specialization between the model and actual data.

Two additional assumptions about the system are relevant: that the model does not allow input from outside the system, and that no geological/climatological changes can occur during the simulation. It is reasonable to expect that a portion of lampsiline mussels evolved in the basin - lampsilines originated in North America and diversified in the Southeast (Banarescu 1971, Watters 1994a). However, species have undoubtedly entered the system from downstream, and also from stream capture in the headwaters, and the inclusion of these processes in the model would make the model more realistic. This analysis does not include processes in geological time and at the continental spatial scale, such as changing environmental means or past climatic and geological events. Several studies have shown that these large-scale conditions and events influence ecological communities (Holling 1992, Cornell 1993). Clench and Turner (1956) have noted that the southern Appalachians have been relatively undisturbed by glaciers or changing sea level, so it is possible that large-scale influences are less important in this region than in other regions. Despite these cautions, this model is an early attempt to understand these communities at this scale, and can serve as a tool on which to build the predictive capability necessary for success of a long-term recovery plan for the freshwater mussels in this basin.

SUMMARY AND CONCLUSIONS

Regional freshwater mussel species richness may be determined by either competition or environmental heterogeneity. Communities structured by competition are expected to exhibit low variability among replicate runs and specialization among species, whereas communities structured by environmental heterogeneity should exhibit a peak in richness with intermediate colonization rates, high variability among replicate runs, and generalization among species. A simulation model that incorporated mutation, determination of fitness, and fitness-based colonization and extinction was used to generate regional patterns of species richness under different critical fitness values for colonization and extinction, in order to evaluate possible structuring mechanisms.

Highest regional richness was found at lowest critical fitness values for colonization and extinction, not at intermediate colonization levels as would be expected if spatio-temporal heterogeneity generated pattern. High species richness reduced average individual species' fitness, which inhibited colonization and further promoted richness through speciation. High-richness communities exhibited low variability among replicate scenarios and high resource specialization among species, consistent with classical competition theory.

Model results were compared to lampsiline freshwater mussel data from the upper Tennessee River basin. Regional scale patterns were consistent with model results that indicated structuring by competition, where variability was low and regularities in terms of host use were exhibited. Although this model contains many simplifying assumptions, it can lead to the development of the predictive capability necessary for conservation.

CHAPTER V. SYNTHESIS ACROSS SCALES

A multi-scale modelling approach was used to understand freshwater mussel community structure in the upper Tennessee River basin. Patterns were considered at local, meso, and regional spatial scales, which correspond to ecological, historical, and evolutionary time scales, respectively. The local scale included a detailed description of population dynamics and species interactions that could be solved analytically. The mesoscale model used elements of metapopulation and Markov chain models to describe species dynamics across a set of habitat patches. The regional scale was represented by a combination of a genetic algorithm and a cellular automaton to simulate evolution of species. A multi-scale approach was used in this dissertation because communities may appear to be structured by different processes at different scales (Rahel et al. 1984, Levin 1992, Holling 1992, Ricklefs and Schluter 1993).

These models were used to explore the patterns generated in communities when either biotic or abiotic processes were specified. At each scale, the biotic process of species competition for fish hosts was considered. Classical competition theory predicts resource partitioning at the local scale, alternative states at the mesoscale, and regularities at the regional scale, such as determinism among replicate runs and host specialization under high richness. Alternatively, the hypothesis that abiotic processes, such as temporal variability at the local scale, spatial processes at the mesoscale, and spatio-temporal heterogeneity at the regional scale, prevent the outcome of competition. At each scale, the structuring process for freshwater mussel communities in the upper

Tennessee River basin was inferred by comparing patterns generated by model processes to field data representing nested spatial scales.

The processes consistent with the pattern in freshwater mussel communities at each scale varied with scale. At the local scale, there was no evidence that either resource partitioning or temporal variability in hydrology determined patterns of local coexistence, as would be expected if biotic and abiotic processes, respectively, structured local communities. Local occurrence may be due to mortality unrelated to competition, or to the effects of processes operating at different scales. At the mesoscale, real communities exhibit fairly low average number of species per patch, and are strongly nested, which is most consistent with the scenario where competition generated structure. However, at the low average number of species per patch demonstrated in actual communities, the influence of competition is very low, compared to the scenario without competition. Regional scale patterns were consistent with model results that indicated structuring by competition, where variability was low and regularities in terms of host use and host overlap were exhibited.

Freshwater mussel communities appear more structured by biotic processes with increasing scale. This trend is a common feature of hierarchical ecological systems (Wu and Loucks 1995). Similarly, Poulin (1997) noted that processes determining species richness of parasite assemblages become less detectable as focus shifts from larger to smaller scales. DeAngelis and Waterhouse (1987) hypothesized that stochastic dynamics are more important at small scales, and that equilibrium competition models cannot be extrapolated to these small scales. Smaller-scale patterns may reflect disturbance and

environmental fluctuation, as has been hypothesized for other freshwater systems (Townsend 1989, Reice 1994). Abiotic conditions did not appear to control structure by preventing exclusion, rather, they influenced pattern for specific times and locations.

Results appeared to be consistent across scales. The inability to predict local coexistence can be explained by the stochastic influence of local dispersal and extinction at the mesoscale. The relatively weak competitive interactions at the mesoscale can be explained by regional evolutionary effects of competition, through which mesoscale community members are selected from the regional species pool. Ginzburg et al. (1988) note that while competition is strong during evolution, the final community will typically contain a majority of weakly interacting species. Regional scale patterns are the result of local species competition for host fish. Simple rules of local competitive interaction appeared to constrain larger scales, which in turn feed back and control local levels (Collins and Glenn 1990, Kawata and Toquenaga 1994, Bascompte and Sole 1995).

Results of this work are applicable to mussel conservation. These models can be used to develop predictive tools for mussel communities in the upper Tennessee River basin. They can be used, for example, to examine effects of different management scenarios, and to predict the effect of restoration activities. Results can also be used to interpret patterns of decline: the recognition of patterns of decline can be combined with the knowledge of the processes that structure communities, to infer the mechanisms by which these systems are affected by activities such as human-induced change. Conservation efforts, based on an understanding of the mussel ecology, will be crucial to the protection of this fauna.

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APPENDICES

APPENDICES

Appendix A. Definition of terms used in models.

Parameter	Definition
$A_h(t)$	Probability of a change in the immune system in host species h at time t in response to infection pressure.
α_{mi}	Competitive effect of adults of mussel species m on adults of mussel species i.
$B(t)$	State of all patches at a particular time t; matrix has dimensions YxX.
C_{mih}	Competitive effect of species m on species i for host h.
c_{mh}	Probabilities of species m obtaining resource h (range 0-1).
χ	Host overlap.
D	Proportion of propagules successfully dispersing from a patch.
$d_{m,q,x}$	Dispersal of mussel species m from patch q to patch x.
ε_m	Background extinction probability of mussel species m.
F_h	Density of resource h in system.
f_m	Species-specific fecundities per individual of species m.
$g_{m,x}$	Probability of gaining species m to patch x.
γ_{mi}	Competitive effect of adults of species m on larvae of species i.
H	Number of resources (h=1 to H). The matrix $\boldsymbol{H}$ is used in Chapter 4 to represent host occurrence by hydrologic unit (HxU).
i,j	Arbitrary mussel species.
K_{mh}	Carrying capacity of mussel species m on fish host species h.
κ_x	The number of contributing patches to a given patch.
L	Number of links (used for calculating host overlap).
$l_{m,x}$	Probability of losing species m from patch x.
$\lambda_{m,x}(t)$	Effect of competition experienced by species m on patch x.
M	Number of species in species pool (m=1 to M).

Appendix A. Definition of terms used in models.

Parameter	Definition
μ	Mutation probability.
$N_m(t)$	Number densities of species m at time t (Chapter 2); species' occurrences in a particular patch (Chapter 3); occupancy of subbasin (Chapter 4).
$P(y,y')_x(t)$	Transition probability from state y to state y' for patch x at time t. The matrix $\boldsymbol{P}$ is the transition probabilities among all states.
Q	Number of adjacent patches in one direction contributing dispersers under stepping-stone dispersal assumption.
q	Index for patches.
r_m	Probabilities of successful infestation of larvae of species m on a host.
ρ_m	Probability of reproducing.
S_m	Survival probability for adults of species m.
s_m	Survival probability for larvae of species m.
ς	Probability of sympatric speciation (deletion of old string).
T	Number of iterations (t=1 to T).
Φ	Total unexpectedness (used for calculating matrix "temperature").
τ	Unexpectedness (used for calculating matrix "temperature").
U	Number of hydrologic units in system (u=1 to U).
V, v	Parameters for calculating nestedness.
$w_{m,u}$	Fitness of genotype m on patch u.
ω_c, ω_e	Critical fitness values for colonization and extinction, respectively.
X	Number of patches in mesoscale system (x=1 to X).
Y	Number of possible community states (y=1 to Y).
$\boldsymbol{Z}$	Array of possible states for the community; matrix dimensions MxY.

Appendix B. Site characteristics for three streams used in mesoscale analysis (Chapter 3). Timed qualitative surveys were conducted at these sites. Number of lampsiline species collected is given.

Site #[1]	Site name	County (State)	River mile	# species
Nolichucky River (Ahlstedt 1991)				
3	*Thomas Island*	*Cocke/Hamblen (TN)*	8.5	4
4	*Above Thomas Island*	*Cocke/Hamblen (TN)*	9.5	5
5	*Island at Beech Bottoms*	*Cocke/Hamblen (TN)*	11.4	4
6	*Beech Bottoms*	*Cocke/Hamblen (TN)*	11.8	3
7	*Below Johnson Island*	*Cocke/Hamblen (TN)*	12.4	1
8	*Johnson Island*	*Cocke/Hamblen (TN)*	13.0	1
9	*Below Susong Bridge*	*Cocke/Hamblen (TN)*	13.5	1
10	*Below Bent Creek*	*Cocke/Hamblen (TN)*	14.8	2
11	*Below Cooper Branch*	*Cocke/Green (TN)*	15.2	0
12	*Island at Lick Creek*	*Cocke/Green (TN)*	16.0	5
13	*Above Lick Creek*	*Cocke/Green (TN)*	16.6	3
14	*Soloman Island*	*Cocke/Green (TN)*	17.7	2
15	*Above Soloman Island*	*Cocke/Green (TN)*	18.5	2
16	*Below Steele Island*	*Cocke/Green (TN)*	19.2	2
17	*Below Steele Island*	*Cocke/Green (TN)*	19.3	0
18	*Steele Island*	*Cocke/Green (TN)*	19.6	3
19	*Above Steele Island*	*Cocke/Green (TN)*	21.0	1
20	*Above Little Chucky Creek*	*Cocke/Green (TN)*	24.0	2
21	*Above Stillhouse Branch*	*Cocke/Green (TN)*	25.0	2
22	*Island above Needmore Branch*	*Cocke/Green (TN)*	25.5	3
23	*Below Bewley Island*	*Cocke/Green (TN)*	27.0	2
24	*Bewley Island*	*Green (TN)*	27.9	2
25	*Island below Pate Hill*	*Green (TN)*	28.5	2
26	*Island above Pate Hill*	*Green (TN)*	29.1	0
27	*Island above Pate Hill*	*Green (TN)*	29.4	3
28	*Evans Island near Arch Cave*	*Green (TN)*	31.0	2
29	*Island above Evans Island*	*Green (TN)*	31.3	2
30	*Below Easterly Bridge*	*Green (TN)*	31.9	3
31	*Evans Island above Cochran Bend*	*Green (TN)*	33.8	0
32	*Island in Linebaugh Bend*	*Green (TN)*	35.4	5
33	*Island in Linebaugh Bend*	*Green (TN)*	35.7	2
34	*Island above Love Bridge*	*Green (TN)*	36.8	3

Appendix B. Site characteristics for three streams used in mesoscale analysis (Chapter 3). Timed qualitative surveys were conducted at these sites. Number of lampsiline species collected is given.

Site #[1]	Site name	County (State)	River mile	# species
35	*Island above Gregg Creek*	*Green (TN)*	38.0	1
36	*Jones Island*	*Green (TN)*	39.0	1
37	*Island above Jones Island*	*Green (TN)*	39.5	2
38	*Grays Island*	*Green (TN)*	40.3	1
39	*Russell Island*	*Green (TN)*	40.8	1
40	*Below Johnson Island*	*Green (TN)*	41.7	2
41	*Johnson Island*	*Green (TN)*	42.0	3
Mean (Standard deviation)			--	2.37 (1.17)
North Fork Holston (USGS - Appendix C)				
1	*Cloud Ford*	*VA/TN*	4.6	3
2	*Click Island*	*Scott (VA)*	6.1	7
3	--	*Scott (VA)*	9.3	2
4	*Hilton Bridge*	*Scott (VA)*	21.8	3
5	--	*Scott (VA)*	27.3	3
6	*Jett Ford*	*Scott (VA)*	31.5	2
7	*Barker Mill Dam*	*Washington (VA)*	38.4	2
8	*Fleenor Mill Ford*	*Washington (VA)*	44.5	3
9	*North Fork Church*	*Washington (VA)*	53.0	3
10	*Hines Island*	*Washington (VA)*	56.5	3
11	*Hwy 80 bridge crossing*	*Washington (VA)*	70.1	0
12	--	*Smyth (VA)*	78.0	0
13	*Broadford gage*	*Smyth (VA)*	85.0	5
14	*North Holston Ford*	*Smyth (VA)*	86.9	5
15	*Hwy 630 bridge*	*Smyth (VA)*	97.8	5
16	*Upper NF Bridge to Ridgedale*	*Smyth (VA)*	105.1	4
17	*Olinger Cemetary*	*Smyth (VA)*	107.0	4
18	*Nebo Bridge*	*Smyth (VA)*	117.5	2
Mean (Standard deviation)			--	3.50 (1.41)
Copper Creek (Ahlstedt 1991)				
1	*Mouth of Copper Creek*	*Scott (VA)*	0.2	3
2	*Below Swinging Bridge*	*Scott (VA)*	0.9	3
3	*Below road bridge*	*Scott (VA)*	1.4	5
4	*Above road bridge*	*Scott (VA)*	1.8	7
5	*At small tributary*	*Scott (VA)*	2.1	5
6	*Below Jennings Ford*	*Scott (VA)*	2.3	4

Appendix B. Site characteristics for three streams used in mesoscale analysis (Chapter 3). Timed qualitative surveys were conducted at these sites. Number of lampsiline species collected is given.

Site #[1]	Site name	County (State)	River mile	# species
7	*Jennings Ford*	*Scott (VA)*	2.7	2
8	*Below Spivey Ford*	*Scott (VA)*	3.5	5
9	--	*Scott (VA)*	4.5	3
10	--	*Scott (VA)*	4.8	4
11	*Unnamed ford below Bellamy*	*Scott (VA)*	5.9	3
12	*Unnamed ford below Bellamy*	*Scott (VA)*	6.3	1
13	*Swinging bridge*	*Scott (VA)*	7.0	1
14	*Above swinging bridge*	*Scott (VA)*	7.3	1
15	*Below Spivey Mill Dam*	*Scott (VA)*	7.7	2
16	*At Blackoak Branch*	*Scott (VA)*	8.5	3
17	*Below Powerline*	*Scott (VA)*	11.0	5
18	*Above Carter cemetary*	*Scott (VA)*	11.5	5
19	*Below Plank Camp Creek*	*Scott (VA)*	12.0	3
20	*Above Plank Camp Creek*	*Scott (VA)*	13.0	4
21	*Swinging bridge*	*Scott (VA)*	13.8	4
22	--	*Scott (VA)*	20.6	1
23	*Below unnamed bridge*	*Scott (VA)*	20.8	1
24	*Below unnamed bridge*	*Scott (VA)*	23.8	4
25	*Below unnamed bridge*	*Scott (VA)*	29.0	3
26	*Unnamed ford*	*Scott (VA)*	30.3	3
27	*Below unnamed bridge*	*Scott (VA)*	32.7	1
28	*Dorton Fort*	*Scott (VA)*	34.7	3
29	*Below unnamed bridge*	*Scott (VA)*	40.1	2
30	--	*Scott (VA)*	41.2	3
31	--	*Scott (VA)*	42.0	2
32	*Above Tracy Hollow*	*Scott (VA)*	44.0	2
33	*Below Jessee Cemetary*	*Russell (VA)*	48.2	2
34	*Bridge below Dorton Cemetary*	*Russell (VA)*	49.7	2
35	*Unnamed bridge*	*Russell (VA)*	51.1	3
36	--	*Russell (VA)*	53.0	2
Mean (Standard deviation)			--	2.97 (1.44)

1. Numbers correspond to original authors.

Appendix C. Number of individuals found in U.S. Geological Survey 1995 freshwater unionid mussel timed qualitative survey of equally sized reaches on the North Fork Holston River, Tennessee/Virginia.

Site 1. Cloud Ford. RM. 4.6 7/31/95

Amblema plicata - 1

Fusconaia barnesiana - 1

Fusconaia cuneolus - 1

Lampsilis fasciola - 2

Lampsilis ovata - 3

Villosa iris - 274

Site 2. Click Island. RM. 6.1 8/1/95

Actinonaias ligamentina - 17

Actinonaias pectorosa - 82

Amblema plicata - 2

Fusconaia barnesiana - 2

Fusconaia cuneolus - 2

Lampsilis fasciola - 19

Lampsilis ovata - 12

Lasmigona costata - 1

Lexingtonia dollabelloides - 1

Medionidus conradicus - 2

Ptychobranchus fasciolaris - 1

Ptychobranchus subtentum - 3

Villosa iris - 25

Villosa vanuxemensis - 10

Site 3. North Fork Holston RM. 9.3

Lampsilis fasciola - 2

Villosa iris - 11

Site 4. Hilton Bridge, RM. 21.8

Lampsilis fasciola - 4

Lampsilis ovata - 2

Villosa iris - 88

Site 5. North Fork Holston RM. 27.3

Lampsilis fasciola - 5

Villosa iris - 86

Site 6. Jett Ford, RM. 31.5

Lampsilis fasciola - 8

Lampsilis ovata - 2

Villosa iris - 28

Site 7. Barker Mill Dam, RM. 38.4

Lampsilis fasciola - 2

Villosa iris - 16

Site 8. Fleenor Mill Ford, RM. 44.5

Lampsilis fasciola - 1

Villosa iris - 12

Site 9. North Fork Church, RM. 53.0

Lampsilis fasciola - 7

Lampsilis ovata - 1

Villosa iris - 10

Villosa vanuxemensis - 2

Appendix C. Number of individuals found in U.S. Geological Survey 1995 freshwater unionid mussel timed qualitative survey of equally sized reaches on the North Fork Holston River, Tennessee/Virginia.

Site 10. Hines Island, RM. 56.5

Lampsilis fasciola - 9

Villosa iris - 15

Site 11. Hwy 80 Bridge Crossing, RM. 70.1

No mussels

Site 12. RM 78.0

No mussels.

Site 13. Broadford gage, RM. 85.0

Actinonaias pectorosa - 3

Fusconaia barnesiana - 13

Fusconaia cor - 7

Lampsilis fasciola - 10

Lexingtonia dollabelloides - 17

Medionidus conradicus - 8

Ptychobranchus fasciolaris - 2

Ptychobranchus subtentum - 4

Villosa iris - 16

Villosa vanuxemensis - 4

Site 14. North Holston Ford, RM. 86.9

Actinonaias pectorosa - 4

Fusconaia barnesiana - 4

Fusconaia cor - 3

Lampsilis fasciola - 4

Lampsilis ovata - 2

Lexingtonia dollabelloides - 5

Medionidus conradicus - 4

Ptychobranchus fasciolaris - 3

Villosa iris - 23

Villosa vanuxemensis - 2

Site 15. Hwy 630 bridge at Riverside, RM. 97.8

Fusconaia barnesiana - 4

Lampsilis fasciola - 8

Medionidus conradicus - 6

Ptychobranchus subtentum -6

Villosa iris - 41

Villosa vanuxemensis - 26

Site 16. Upper NF Bridge to Ridgedale, RM. 105.1

Fusconaia barnesiana - 47

Lampsilis fasciola - 17

Medionidus conradicus - 3

Villosa iris - 367

Villosa vanuxemensis - 151

Site 17. Bridge at Olinger Cemetary, RM. 107.0

Fusconaia barnesiana - 81

Lampsilis fasciola - 27

Medionidus conradicus - 5

Villosa iris - 116

Villosa vanuxemensis - 104

Site 18. Nebo Bridge, RM. 117.5

Fusconaia barnesiana - 25

Villosa iris - 40

Villosa vanuxemensis - 35

Appendix D. Lampsiline mussel species of the upper Tennessee River basin.[1] Species' distributions among major drainages are given (see Table 4.3, Figure 4.1 for drainages).

Species name (Turgeon et al. 1988)	Common name	Holston	French Broad	Watts Bar	Clinch Powell	Lower Tenn.
Actinonaias ligamentina[2]	mucket	X	X	X	X	X
A. pectorosa	pheasantshell	X	X	X	X	0
Cyprogenia stegaria	fanshell	X	X	X	X	X
Dromus dromas	dromedary pearlymussel	X	X	X	X	X
Ellipsaria lineolata	butterfly	0	X	X	X	X
Epioblasma arcaeformis	sugarspoon	X	X	X	X	X
E. biemarginata	angled riffleshell	X	0	0	X	0
E. brevidens	Cumberlandian combshell	X	X	X	X	X
E. capsaeformis	oyster mussel	X	X	X	X	X
E. flexuosa	leafshell	0	0	0	0	X
E. florentina florentina	yellow blossom	0	X	X	X	X
E. florentina walkeri	tan riffleshell	X	0	0	X	X
E. haysiana	acornshell	X	X	X	X	X
E. lenoir	narrow catspaw	X	0	X	X	0
E. lewisi	forkshell	X	0	X	X	0
E. obliquata	catspaw	0	0	0	X	X
E. propinqua	Tennessee riffleshell	X	0	X	X	X
E. stewardsoni	Cumberland leafshell	X	X	X	X	X
E. tortulosa torulosa	tuberculed blossom	X	X	X	X	X
E. tortulosa gubernaculum	green blossom	X	X	X	X	0
E. triquetra	snuffbox	X	X	X	X	X
E. turgidula	turgid blossom	X	0	X	X	X
Lampsilis abrupta	pink mucket	X	X	X	X	X
L. cardium	plain pocketbook	0	0	X	0	0
L. fasciola	wavy-rayed lampmussel	X	X	X	X	X
L. ovata	pocketbook	X	X	X	X	X
L. virescens	Alabama lampmussel	0	0	0	X	0

Appendix D. Lampsiline mussel species of the upper Tennessee River basin.[1] Species' distributions among major drainages are given (see Table 4.3, Figure 4.1 for drainages).

Species name (Turgeon et al. 1988)	Common name	Holston	French Broad	Watts Bar	Clinch Powell	Lower Tenn.
Lemiox rimosus	birdwing pearlymussel	X	X	X	X	X
Leptodea fragilis	fragile papershell	X	X	X	X	X
L. leptodon	scaleshell	X	0	X	X	0
Ligumia recta	black sandshell	X	X	X	X	X
Medionidus conradicus	Cumberland moccasinshell	X	X	X	X	X
Obliquaria reflexa	threehorn wartyback	0	0	X	X	X
Obovaria olivaria	hickorynut	0	0	0	0	X
O. retusa	ring pink	X	0	X	X	X
O. subrotunda	round hickorynut	X	X	X	X	X
Potamilus alatus	pink heelsplitter	X	X	X	X	X
P. ohiensis	pink papershell	0	0	X	0	0
Ptychobranchus fasciolaris	kidneyshell	X	X	X	X	X
P. subtentum	fluted kidneyshell	X	X	X	X	X
Toxolasma lividus	purple lilliput	X	X	X	X	0
T. parvus	lilliput	0	0	X	0	0
Truncilla donaciformis	fawnsfoot	0	0	X	X	0
T. truncata	deertoe	X	X	X	X	0
Villosa fabalis	rayed bean	X	X	X	X	0
V. iris[3]	rainbow	X	X	X	X	X
V. perpurpurea	purple bean	X	0	X	X	0
V. taeniata	painted creekshell	0	0	0	X	0
V. trabalis	Cumberland bean	0	X	X	X	X
V. vanuxemensis vanuxemensis	mountain creekshell	X	X	X	X	X
TOTAL: 50		37	31	43	45	34

1. Taken from Ahlstedt and Rashleigh (in review), which compiled records from: Ortmann (1918), Cahn (1936), Hickman (1937), Neves et al. (1980), Parmalee et al. (1982), Bogan and Parmalee (1983), Parmalee and Bogan (1986), Parmalee (1988), Starnes and Bogan (1988), Parmalee and Hughes (1994). Taxonomy according to Davis and Fuller (1980).
2. Species for which hosts are known are given in bold.
3. Records of both *Villosa iris* and *Villosa nebulosa* from the basin are referred to collectively as *V. iris*.

Appendix E. Known fish host species for lampsiline mussel species considered in regional scale analysis.[1]

Species	Common name	Abbreviation
Ambloplites rupestris	rock bass	*Ar*
Aplodinotus grunniens	freshwater drum	*Ag*
Carassius auratus	goldfish	*Ca*
Cottus baileyi	black sculpin	*Cb*
Cottus bairdi	mottled sculpin	*Cbr*
Cottus carolinae	banded sculpin	*Cc*
Etheostoma blennioides	greenside darter	*Eb*
Etheostoma caeruleum	rainbow darter	*Ec*
Etheostoma camurum	bluebreast darter	*Ecm*
Etheostoma flabellare	fantail darter	*Ef*
Etheostoma rufilineatum	redline darter	*Er*
Etheostoma simoterum	snubnose darter	*Es*
Etheostoma vulneratum	wounded darter	*Ev*
Etheostoma zonale	banded darter	*Ez*
Lepomis cyanellus	green sunfish	*Lc*
Lepomis gulosus	warmouth	*Lg*
Lepomis macrochirus	bluegill	*Lm*
Lepomis megalotis	longear sunfish	*Lmg*
Micropterus dolomieu	smallmouth bass	*Md*
Micropterus punctulatus	spotted bass	*Mp*
Micropterus salmoides	largemouth bass	*Ms*
Morone chrysops	white bass	*Mc*
Perca flavescens	yellow perch	*Pf*
Percina caprodes	logperch	*Pc*
Percina sciera	dusky darter	*Ps*
Pomoxis annularis	white crappie	*Pa*
Pomoxis nigromaculatus	black crappie	*Pn*
Scaphirhynchus platorynchus	shovelnose sturgeon	*Sp*
Stizostedion canadense	sauger	*Sc*
Stizostedion vitreum	walleye	*Sv*

1. Sources: Luo (1993), Watters (1994, and references therein), Hove (1995), Hove et al. (1995), Layzer and Madison (1995), Watson and Neves (1996), and Watters (1996). Taxonomy of Robins et al. (1991).

Appendix F. Host fish occurrence by river basin used for model input (Ahlstedt and Rashleigh, in review).

	River basins (abbreviations given in Table 4.3)																		
Sp[1]	Nf	Sf	Wa	Ho	Uf	Pi	Lf	No	Wb	Ul	Tu	Ll	Uc	Po	Lc	Em	Tn	Hi	Oc
Ar	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ag	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Ca	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	0
Cb	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cbr	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1
Cc	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Eb	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ec	1	1	1	1	1	0	1	1	1	1	0	0	1	1	0	1	0	1	0
Ecm	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	0
Ef	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	0	0
Er	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Es	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Ev	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0	1	0	0	0
Ez	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1
Lc	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lg	0	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0
Lma	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lmg	1	1	0	1	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1
Md	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Mp	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Ms	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Mc	0	1	1	1	1	1	1	0	1	1	0	1	1	1	1	0	1	1	1
Pf	0	0	0	0	0	1	1	0	1	1	0	1	0	0	1	1	1	1	1
Pc	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Ps	1	0	0	1	1	1	1	0	1	0	0	1	1	1	1	1	0	1	0
Pa	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	0
Pn	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	0
Sp	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Sc	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	0	1	1	0
Sv	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	0

1. Species names corresponding to abbreviations are given in Appendix E.

VITA

Brenda Rashleigh was born in Burlington, Vermont. She graduated from Colchester High School in Colchester, Vermont in 1984, and from the University of Vermont in Burlington, Vermont in 1988. She began graduate school at Indiana University in Bloomington, Indiana in 1990 and graduated in 1992 with a Masters of Science in Environmental Science. After graduation, Brenda worked at the Environmental Sciences Division of Oak Ridge National Laboratory in Oak Ridge, Tennessee. She enrolled in the Ph.D. program at the University of Tennessee in 1994. She began work for the U.S. Geological Survey National Water Quality Assessment Program in Knoxville, Tennessee in 1995 and continues to work there. She will receive her doctorate in Ecology and Evolutionary Biology from the University of Tennessee in August 1998.