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Integrating Fluvial Geomorphology and Stream Ecology: Processes Shaping the Distribution of Freshwater Mussels in Connecticut

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**Project title: Integrating Fluvial Geomorphology and Stream Ecology:
Processes Shaping the Distribution of Freshwater Mussels in
Connecticut**



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EXECUTIVE SUMMARY

Purposes of the Project

- Freshwater mussels are a group of benthic, burrowing, filter-feeding bivalves. Most are in the family Unionidae that includes species living in North and Central America, and throughout the Palearctic region.
- Unionids are among the most imperiled groups of animals worldwide. Of the 297 species in North America, approximately 72 percent are considered endangered, threatened, or of special concern. Sixty-nine species are listed by the U.S. Fish and Wildlife as endangered or threatened, and 21 are endangered and presumed extinct. In Connecticut, six of the twelve native freshwater mussel species are listed as special concern, threatened, or endangered. In samples of lotic waters of the Willimantic River watershed, we have found 2 of the species (*Elliptio complanata* and *Pyganodon cataracta*) known to occur in Connecticut. These species are not listed species, but it is expected that analysis of the factors affecting the distribution of these species will be helpful in identifying likely areas of occurrence for other species, including those that are species of concern.
- A better understanding of habitat use will assist in conservation and management of mussel populations. Freshwater mussels are patchily distributed at multiple spatial scales. At the microhabitat scale, variables such as flow velocity and substratum are not strongly predictive of mussel presence. On a broader spatial scale, several hydraulic variables appear to successfully predict the distribution of unionids. In particular, factors that reduce the shear forces acting on river bottoms could be important in creating flow refuges. The availability of flow refuges or sediment stability is affected by structural features at the stream reach and watershed level, suggesting that a multiple-scale analysis incorporating geomorphology may yield good predictions of mussel presence.

Objectives

- The primary goal of this study was to examine the factors affecting the distribution of freshwater mussel at multiple spatial scales. We addressed two specific objectives: 1. Determine the distribution, abundance, size, and species composition of adult unionid communities in four sub-watersheds; 2. Delineate the location of mussel beds with respect to sediment stability, substrate characteristics and channel hydraulics.

Methods

- This project took place in northeastern Connecticut within four subwatersheds of the Willimantic River watershed: Edson Brook, Hop River, Middle River, and Roaring Brook. Data used for this study were collected in the field during Summer 2008.
- We conducted sampling in multiple phases: identification of potential study reaches (Phase 1), timed search assessment of mussel abundance (Phase 2), surveying selected reaches (Phase 3), and quadrat sampling of selected reaches (Phase 4).
- Phase 1 was performed in May and early June. Maps were analyzed for accessibility of watercourses, with respect to roadway proximity. These sites were

visited and potential study reaches, defined as segments of streams up to 50 m long, were further evaluated based on three criteria: access, wadeability, and the likelihood that there would be a complete line of sight for surveying equipment down the length of the reach.

- In phase 2, timed searches were conducted in stream sections that were selected in phase 1. We searched 45 reaches, approximately 10 reaches from each subwatershed. In the timed search, each reach was waded in an upstream direction for a predetermined period of 30 minutes. Mussels encountered during the search were counted without disturbing the animals. Based on the results of the timed search, we selected from each subwatershed three reaches that had no mussels, three that had a low abundance of mussels and three that had a high abundance of mussels, for a total of twelve reaches.
- In phase 3, surveying of selected reaches was conducted. A Totalstation was employed to survey study reaches and obtain point elevations of the stream bottom. Survey data was pre-processed and ArcGIS 9.3 was primarily used to develop maps and derive digital elevation models (DEM) of study reaches.
- In phase 4, quadrat sampling of selected reaches was conducted using a systematic sampling method. A detailed sampling map was developed for each reach depicting locations of all possible quadrat sites along with their horizontal coordinates in order to perform field sampling. The quadrats to be sampled within the set of possible quadrats were determined by a method called systematic sampling with multiple random starts. Biotic sampling entailed counting, identifying and measuring all mussels within a quadrat. Mussels were replaced into the substrate after handling. Abiotic variables were also determined at each quadrat at the same time using established methods. Coverage of each of three broad sediment types (fine, medium and coarse) was estimated. Substratum stability was assessed as embeddedness, the degree to which larger particles (boulder, cobble and gravel) were surrounded or covered by fine sediment. In-situ morphologic features, such as run/riffle/pool distribution, sand bars, debris pile-up were identified and mapped. Flow velocity was measured in the center and lateral margins of the quadrat with an electromagnetic current meter. We obtained dissolved Oxygen (DO) and water temperature at every quadrat by using a YSI 556 MPS.
- Reach-scale variables were also characterized. Channel depth, width, length, elevation, gradient and shear stress were ascertained from elevation maps. Water temperature was measured with HOBO® Water Temp pro temperature loggers.
- We utilized an information-theoretic approach to develop resource selection functions (RSF) that evaluate the predictors of mussel abundance. An array of microhabitat-scale and reach-scale habitat parameters hypothesized to affect occurrence of freshwater mussels was identified based on available literature. We then developed all possible models incorporating the identified habitat parameters and fitted each with logistic regression. At the microhabitat (quadrat) scale, all unique combinations of 5 parameters and 4 interactions were combined to develop 2102 logistic regression models. At the reach scale, analyses were conducted using data on both detailed-sampling reaches (i.e. the twelve sampled reaches in which we conducted quadrat analysis) and timed-search reaches (i.e.

the 45 reaches that were subjected to timed searches for mussels in Phase 2 of the sampling design). The variables used in these two reach-scale analyses differed. We used eleven variables in the detailed-sampling reach analyses. All combinations of these eleven parameters were combined to develop 83 logistic regression models. We did not have information on all of these variables for all 45 of the timed-search reaches and used only 4 reach-scale variables, yielding 15 logistic regression models. In each set of analyses, candidate models were ranked using Akaike's information criterion (corrected for small sample bias in the reach-scale analyses). Diagnostics such as AIC weights and evidence ratios were also used to assess the weight of evidence favoring highly-ranked models. In order to address model selection uncertainty among competing models, we used multimodel averaging and calculated model-averaged estimates of the coefficients for the RSF equations.

Key Findings

- At the quadrat scale of analysis, four main effects (medium sediment, depth, embeddedness, and embeddedness²) and two interactions (geomorphic unit*medium sediment and geomorphic unit*depth) were equally the most important microhabitat features. Mussels select medium sediment over fine and coarse sediments, runs over pools and riffles, and microhabitat with greater embeddedness. Interactions among these main effects indicate that the effect of fine substrate, medium substrate, depth and embeddedness on mussel presence vary with geomorphic unit.
- At the reach scale, analysis of data from sites at which quadrat sampling was conducted indicated that mussels selected medium substrate over fine and coarse substrate types, and habitats with lower shear stress. The probability of mussel occurrence in a reach increased with increasing embeddedness. Analysis of data from all 45 reaches subjected to timed searches for mussels indicated that the probability of mussel occurrence in a reach increased with decreasing gradient, sinuosity, and distance to a dam.
- Water temperature was not found to affect habitat selection at microhabitat and reach-scales.
- Mussels ranged in age from 1 to 19 years with a mean age of five years. The age-frequency distribution indicated a similar age variation for Eastern Elliptio and Eastern Floater. There is no apparent density-dependent suppression of growth rate.
- Data on the fish assemblages in subwatersheds of the Willimantic River watershed were obtained from the Connecticut Department of Environmental Protection to identify mussel host fish species in our study reaches. We identified five host fish species of which three were known to be host fish for Eastern Elliptio and two were known to be host for Eastern Floater.

Conclusions

- Selection of mussels for habitats with medium-size substrate, high embeddedness, and reaches of low gradient suggests the importance of substrate stability and flow refuge. The effect of some habitat variables, such as depth, varies among geomorphic unit (pool, riffle or run).

- The information-theoretic approach enabled us to identify and rank habitat features predicting mussel occurrence from an array of features hypothesized to predict occurrence.
- RSFs are a powerful way of assessing resource selection when combined with GIS because (1) RSFs offer a quantitative characterization of resource use; (2) RSFs can accommodate virtually any type of resource being selected, including both categorical and scalar variables; and (3) RSF models easily accommodate spatial structure and can be interfaced with GIS to facilitate rapid analysis and use of remote sensing and other types of spatial data.
- The associations between mussels and physical habitat parameters should be measured across multiple spatial scales.

Recommendations

- Eastern Elliptio, the most common mussel species, coexists with many state and federally listed species, including Dwarf Wedgemussel and Brook Floater and Tide Watermucket. Therefore, the analysis of the factors affecting the distribution of common species will be helpful in identifying likely areas of occurrence for other species, including those that are species of concern. The RSF model that developed based on rapid-assessment data can be used as a robust tool to identify likely areas for mussel occurrence before employing expensive and detailed sampling methods.
- Our microhabitat-scale and reach-scale RSF models can assist in relocation programs. Freshwater mussels are typically relocated from sites that will be impacted by restoration efforts such as dam removals. In such circumstances, the habitat suitability of selected relocation sites can be evaluated with our multiple-scale RSF models.

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INTRODUCTION

Freshwater mussel biology

Freshwater mussels are a group of benthic, burrowing, filter-feeding bivalves (Vaughn et al. 2004). They are large (up to 150 mm in length) bivalved organisms enclosed by two shells connected by a ligament (Morales et al. 2006). The shells are formed largely out of calcium carbonate that has been extracted from the waters where mussels live (Nedeau 2008). Freshwater mussels come under 3 different subclasses, separated into 5 separate orders and divided among 19 families within the Class Bivalvia (Borgan 2008). Of these families, the family Unionidae is the largest family that includes species living in North and Central America, and throughout the Palearctic region. The family Unionidae is characterized by the possession of gill septa in the demibranchs (v-shaped structure of gills that is common to Bivalvia) and a complex diaphragm (Douglas 1995).

Freshwater mussels are endobenthic and use their muscular foot and shell to burrow in the sediment (Allen and Vaughn 2009). Studies conducted by Amyot and Downing (1998) and Watters et al. (2001) documented the burrowing behavior of individual mussel species can vary with season and reproductive cycle, flow regime, substrate type and disturbance and parasite abundance, but also varies greatly among species.

Recent studies reveal that mussels can access benthic, as well as planktonic, food supplies (Nichols et al. 2005). Mussels filter food from both the water column and sediment with ciliated gills located on the inner surface of the mantle, demibranchs, and visceral mass (Vaughn et al. 2008). The synchronous movement of the cilia generates water currents inside and outside the shell. The currents bring a continuous supply of fresh water with oxygen and food inside the shell and remove the waste products (Vaughn et al. 2008)

Freshwater mussels have a complex life history in which the larvae are obligate parasites on the gills or fins of fish (Vaughn 1997). Reproduction is initiated when an upstream male releases sperm into the water column and a downstream female collects it via the incurrent aperture (Smith 2001). Fertilization occurs internally, with embryo

development ensuing within the marsupia (gill pouches). The resulting larva, termed glochidium, parasitizes the gills of freshwater fishes, including darters, minnows and bass (Layzer 2003). The larvae use the host fish for dispersal and cause them little to no harm. Several of the mussels attract host fish by mimicking lures, minnows, worms, leeches or aquatic insects (Watters 1998; Layzer 2003). Juvenile and adult mussels live either partially or completely buried in the substrate, filtering algae, detritus and microorganisms from the water column (Zimmerman, 2003). Most species prefer clean, silt-free, shoals of cobble and gravel interspersed with sand (Williams et al. 1992).

Unionids are among the most imperiled groups of animals worldwide (Masters 1990). The maximum diversity and abundance of mussels are found in North America where 297 species have been documented (Turgeon et al. 1998 and Graf et al. 2007). Of these species, approximately 72 percent are considered endangered, threatened, or of special concern (Williams et al, 1992). Sixty-nine species are listed by the U.S. Fish and Wildlife as endangered or threatened, and 21 are endangered and presumed extinct (Zimmerman 2003). The combined effects of anthropogenic activities over-harvesting, habitat alteration, and invasive species have placed freshwater mussels among the most endangered faunal groups (Strayer et al. 2004). Habitat modifications through man-made structures like dams and channel alterations have destroyed free-flowing water habitats. Mussels reach their greatest diversity in running waters and damming of rivers has caused precipitous declines in freshwater mussels both upstream and downstream of dams. Many species are unable to tolerate impounded environments (Neddeau et al, 2000). In addition to habitat modifications, mussel populations are exposed to point and non-point source pollution (toxic runoff containing fertilizers, herbicides and pesticides from land use practices). The combined stresses restrict many mussels from dispersing which results in small, isolated populations. A better understanding of mussel habitat requirements will assist in developing recovery plans.

Freshwater mussels play a number of important roles in aquatic ecosystems. They provide critical ecosystem functions such as particle processing, nutrient release, and sediment mixing (Morales et al. 2006). As filter-feeders, mussels are capable of removing large amounts of particles such as sediment, organic matter, bacteria, and phytoplankton from the water column and transfer these resources to the river bottom as biodeposits

(Howard and Cuffey 2006). The cycling of fine particulate matter is critical for the sustenance of stream ecosystems, providing nutrients and energy to both suspension feeders and deposit feeders (Zweig and Rabeni, 2001). The biomass of healthy unionid assemblages can exceed the biomass of all other benthic organisms by an order of magnitude, and production by mussels (range from 1 to 20 g dry mass m⁻²y⁻¹) can equal that by all other macrobenthos in many streams (Layzer et al. 1993; Strayer et al. 1993; and Vaughn et al. 2004). Mussels also interact with stream sediments. The burrowing behavior of unionids mixes sediment pore water, releasing nutrients and oxygenating substrates (Vaughn and Hakenkamp 2001). Particularly dense assemblages of mussels may influence substrate stability and provide nutrients and microrefugia for benthic life (Vaughn and Hakenkamp 2001; Zimmerman and de Szalay 2007). They serve as good indicators of ecosystem health because they remain essentially in one place for a long time and require good water and sediment quality and physical habitat. For example, freshwater mussels have been used to establish base level nitrogen isotope ratio values ($\delta^{15}\text{N}$) used in trophic position and food web studies in freshwater ecosystems (McKinney et al, 1999). Freshwater mussels also provide food for a number of terrestrial and aquatic species. The spent valves of freshwater mussels play a role in aquatic ecosystems as well. Shells provide habitat for a variety of life, including fish, periphyton, crustaceans, molluscs, and macroinvertebrates (Vaughn et al. 2008)

Freshwater mussel populations have patchy distributions at multiple spatial scales (Strayer 2004; Newton et al 2008). These multispecies assemblages are known as mussel beds (Strayer et al. 1994; Vaughn et al. 2008). Zoogeographic factors strongly influence the broad-scale distribution of freshwater mussels (Mcrae et al 2004; Strayer 1993). The effect of other ecological factors on the distribution of unionids is poorly understood (Mcrae et al. 2004). Mussel beds may be the product of differential mortality, so that juveniles settle evenly on the river bottom but are destroyed in unsuitable habitats (Morales et al 2006; Strayer 1999). Another suggestion is that areas without juveniles could mean that juveniles have not yet arrived there (Morales et al. 2006). Early workers documented a strong association between some taxa and specific microhabitats (cited in Gangloff et al. 2007). However, recent empirical studies (Strayer and Rally 1993; Strayer

1993; and Vaughn 1997) have noted few linkages between local habitat variables such as flow velocity and substratum, and mussel abundance (Gangloff et al. 2007).

Some authors (Tevesz & McCall, 1979; Strayer 1981; Holland-Bartels, 1990; Layzer & Madison, 1995) have documented the incompetence of microhabitat scale variables in predicting mussel occurrence in lotic systems (Mcrae et al. 2004). Strayer (1983, 1993) noted the importance of macrohabitat variables (e.g. stream size) as opposed to microhabitat descriptors, in predicting broad-scale mussel distribution (Mcrae et al. 2004). Therefore, it could be more valuable to examine habitat variables determining mussel distribution across broad spatial scales compare to a single-scale microhabitat approach (Strayer and Ralley, 1993, Mcrae et al. 2004).

Several hydraulic variables appear to successfully predict the distribution of unionids (Morales et al. 2006). Recent workers (Howard and Cuffey 2003; Layzer and Madison 1995; Hardison and Layzer 2001) have noted the factors that reduce the shear forces acting on river bottoms could be important in creating flow refuges (Morales et al. 2006). These flow refuges enable mussels to persist in during floods. Flow refuges can be broadly defined as areas in or near a stream where currents or shear stresses remain moderate during floods, and thus where stream organisms can survive or even accumulate (Strayer et al. 1999). The flow refuge concept could provide considerable explanation for unionid patchiness. Strayer et al. (1999) demonstrated that all beds occupied flow refuges, but that not all flow refuges were occupied by beds. Mussel absence in certain flow refuges may be due to lack of favorable habitat conditions such as interstitial dissolved oxygen, sediment grain size, frequency of desiccation (Strayer et al 1999). Conversely unoccupied patches could represent refuges that are too new or ephemeral for unionids to colonize (Strayer et al 1999).

In contrast to microhabitat-scale habitat descriptors, recent studies have been attempted to test combinations of reach and catchment-scale habitat variables to explain mussel distribution. For example, Macrae et al. (2004) identified flow stability, substratum composition, and overall reach habitat quality as the most effective reach-scale variables, and measures of surficial geology as catchment-scale variables. Gangloff et al. (2007) suggest that mussel abundance and assemblage structure may be sensitive to any changes in channel geomorphology and hydraulic condition that result from land use

in the catchment. Brainwood et al. (2008) investigated the role of geomorphically derived microhabitat factors in determining the distribution of mussel species. Their findings reveal that the structure of the substratum patches was strongly influenced by geomorphic reach type, especially roughness elements such as boulders and cobbles that create a flow refuge.

Freshwater Mussels in Connecticut

In Connecticut, six of the twelve native freshwater mussel species are listed as special concern, threatened, or endangered (Nedea and Victoria 2003). In samples of lotic waters of the Willimantic River watershed, we have found 2 of the species (*Elliptio complanata* and *Pyganodon cataracta*) known to occur in Connecticut. These species are not listed species, but it is expected that analysis of the factors affecting the distribution of these species will be helpful in identifying likely areas of occurrence for other species, including those that are species of concern.

The Eastern Elliptio (*Elliptio complanata*) is the most abundant and widespread freshwater mussel in northeastern North America (Nedea and Victoria 2003). Eastern Elliptio is a medium sized mussel, less than 127mm in length. The shape is highly variable but most often elliptical or trapezoidal (Nedea and Victoria 2003). Shells are laterally compressed and strong. Beaks are not prominent and not raised above the hinge line. Pseudocardinal teeth are well developed, the left valve has two and the right valve has one. Lateral teeth are also well developed – the left valve has two and right valve has one. The periostracum is usually tan or brownish in younger individuals to dark brown or black in adults, and there are usually rays on the periostracum. The nacre is purplish, rose-colored, or white in fresh specimens (Nedea 2008). The Eastern Elliptio is able to parasitize a variety of different host fish (Kneeland and Rhymer 2008), inhabit both flowing and standing water, and withstand many forms of habitat disturbances and environmental stresses (Nedea and Victoria 2003). Host fish include banded killifish, green sunfish, pumpkinseed, orange-spotted sunfish, largemouth bass, yellow perch, and white crappie (Watters et al., 2005)

The Eastern Floater (*Pyganodon cataracta*) is widespread and abundant in Connecticut (Nedea and Victoria 2003). The Eastern Floater is a medium sized to large mussel that may exceed 150mm in length. Shells are ovate or elliptical and they are

laterally inflated and extremely thin and fragile (Nedea 2008 ; Nedea and Victoria 2003) . Beaks are prominent and raised above the hinge line. The hinge is either straight or has a slight upward curve. Hinge teeth are entirely absent. Shells are smooth with prominent growth annuli and may have faint rays. The periostracum is yellowish , greenish or brownish-black. The nacre is usually silvery white or metallic blue, sometimes with a yellowish tinge (Nedea 2008). The Eastern Floater is found in a wide variety of habitats and substrate type (Nedea and Victoria 2003). It has the ability to thrive in silt and mud- substrates. In addition to its tolerance for muddy substrates, it is tolerant of other parameters that are typically undesirable for mussels, such as warm water temperature, low dissolved oxygen, and eutrophic condition (Nedea 2008). The Eastern Floater has a variety of hosts, most prominent of which include the common carp, bluegill, pumpkinseed, yellow perch, white sucker, rock bass, and the threespine stickleback (Nedea 2000).

Objectives

The primary goal of this study was to examine the factors affecting the distribution of freshwater mussel at multiple spatial scales. The associations between mussels and physical habitat parameters measured across multiple spatial scales might be more useful than a single-scale microhabitat approach. Recent studies found that multiple-spatial scale approaches can provide a more spatially relevant estimate of the importance of local habitat models.

We addressed two specific objectives;

1. Determine the distribution, abundance, size, and species composition of adult unionid communities in four sub-watersheds.
2. Delineate the location of mussel beds with respect to sediment stability, substrate characteristics and channel hydraulics.

METHODOLOGY

Study Area

This project took place in northeastern Connecticut within four subwatersheds of the Willimantic River watershed. The four subwatersheds that we sampled were Edson Brook, Hop River, Middle River, and Roaring Brook. The Willimantic River watershed

is a sub-basin of Thames River basin, which drains an area of approximately 225 square miles in southern Massachusetts and northeastern Connecticut (Figure 1). The headwaters of the Willimantic watershed begin in the towns of Monson and Wales, Massachusetts. The watershed includes the Connecticut towns of Stafford, Union, Ellington, Tolland, Willington, Ashford, Vernon, Bolton, Coventry, Mansfield, Andover, Columbia, Windham, Hebron, and Lebanon. A total of 11 subregional drainage basins (subwatersheds) are contained within the Willimantic Watershed. The Willimantic River originates at the confluence of Middle River and Furnace Brook in Stafford, Connecticut and then flows for approximately 25 miles before it joins the Natchaug River to form the Shetucket River. Natural stream flow in the Willimantic River is regulated by Staffordville Reservoir, located in the upper Furnace Brook Basin (Stahl and Smith 2001). The Connecticut Department of Environment Protection (CT-DEP) identified the Willimantic River as one of the diverse and most utilized fishery resources in eastern Connecticut. The Willimantic River has approximately 18 species of freshwater fish and is designated as a Wild Trout Management Area (WTMA: CT-DEP 2001). The Willimantic River is designated as Class B surface water with a water quality goal of Class A in Connecticut's Water Quality Standards. A Class B surface water designation indicates suitability for recreational use, swimming, fish and wildlife habitat, agricultural and industrial supply, and other legitimate uses including navigation. Discharges from public or private drinking water treatment systems, industrial and municipal wastewater treatment facilities are restricted to class B surface water bodies (CT-DEP 2009).

The surficial geology of the Willimantic river watershed is composed of schists, gneisses and phyllites of the Ornage-Milford belt and Connecticut Valley Synclinorium. The upper basin has small hills and valleys draped with glacial deposits. The lower basin is moderately undulating, consisting of moraines and till. Present land cover of the basin is dominated by deciduous and conifer forests. In the upper catchment, wetlands and small lakes are abundant, and impervious cover is limited. The lower region of the basin has more agricultural lands and impervious cover than the upper catchment (Figure 2).

Field Sampling

Selecting the appropriate sampling design entails several important aspects such as: clear definition of the survey goals, identification of the target population, evaluation

of the resources available for sampling, and prior knowledge about site characteristics and the mussel population in the watershed (Villella et al. 2005, Strayer and Smith 2003). As mentioned in the previous chapter freshwater mussel populations have patchy distributions at multiple spatial scales. When sampling this kind of population quantitatively, more sampling effort and resources should be allocated in locations where the organism occurs than it does not occur (Villella et al. 2005). Consequently, optimal allocation of sampling effort and resources is difficult without *a priori* knowledge on mussel distribution in a river (Villella et al. 2005). A multiple phase sampling design can resolve the sampling-effort and resource allocation problems effectively because *a priori* information on mussel population distribution acquired during early phases can be used to allocate sampling effort effectively in later stages (Villella et al. 2005). Further, a multiple phase sampling design is capable of controlling sampling costs because a large initial set of sites could be sampled using a quick and inexpensive method, and some fraction of the initial sites could further be resampled in detail by employing a more costly method to gather precise information (Villella et al. 2005).

We therefore conducted sampling in multiple phases: identification of potential study reaches (phase 1), timed search assessment of mussel abundance (phase 2), surveying selected reaches (phase 3), and quadrat sampling of selected reaches (phase 4). Data used for this study were collected in the field during Summer 2008.

Phase 1, identification of potential study reaches, was performed in May and early June. Maps were analyzed for accessibility of watercourses, with respect to roadway proximity (Figure 3). These sites were visited and potential study reaches, defined as segments of streams up to 50 m long, were further evaluated based on three criteria: access, wadeability, and the likelihood that there would be a complete line of sight for surveying equipment down the length of the reach. Some judgment had to be exercised with respect to the last criterion because lines of site changed over the season with the completion of leaf-out. Reaches that satisfied all criteria were marked on site and obtained GPS coordinates for future reference.

In phase 2, timed searches were conducted in stream sections that were selected in phase 1. We searched 45 reaches, approximately 10 reaches from each subwatershed. In the timed search, each reach was waded in an upstream direction for a predetermined

period of 30 minutes. Mussels encountered during the search were counted without disturbing the animals. Based on mussel count, reaches were categorized into three classes: no mussels, low mussel abundance (1 – 10 mussels), and high mussel abundance (> 10 mussels). We randomly selected reaches within strata so that each abundance stratum was represented by one reach in each subwatershed. These randomly selected reaches numbered 3 in each subwatershed and 12 in all four subwatersheds. We selected a 100 m stream segment at each site and GIS analysis was performed to obtain reach scale variables: sinuosity, gradient and, distance to nearest dam. The hydrography GIS layers available online at Connecticut Department of Environmental Protection (www.ct.gov/dep) in conjunction with statewide mosaic of 2004 digital orthophotos (25 cm spatial resolution) at UCONN CLEAR (www.clear.uconn.edu) were used to determine sinuosity and distance to dam. Sinuosity (S) was measured as the ratio of channel distance to valley distance (Gordon et al. 1992).

$$S = \frac{\text{Channel (thalweg) distance}}{\text{Downvalley distance}}.$$

Elevations at study sites were acquired by using the statewide LiDAR (Light Detection And Ranging) derived DEM (Digital Elevation Model) dataset (3m spatial resolution) available online at UCONN CLEAR (www.clear.uconn.edu). Subsequently, gradient (G) was computed with the equation:

$$G = \frac{(E_u - E_d)}{L_r} * 1000,$$

where E_u and E_d are elevations (m) at upstream and downstream boundaries, respectively and L_r is the length of the reach (Arend 1999). StreamStats, a web-based GIS tool developed by USGS, was utilized to obtain peak flows at each reach.

In phase 3, surveying of selected reaches was conducted. A Totalstation (Model 202 TOPCON, Livermore, California) was employed to survey study reaches and obtain point elevations of the stream bottom. Survey control points were established on river banks and local coordinate systems were defined for each reach. The trigonometric heighting method was used to ascertain point elevations of the stream bottom. Point

heights were obtained with an approximate spacing of 3 feet because a dense point cloud captures morphological variation of the river bottom more accurately than a sparse point cloud. Survey data was pre-processed and ArcGIS 9.3 was primarily used to develop maps and derive digital elevation models (DEM) of study reaches.

In phase 4, quadrat sampling of selected reaches was conducted using a systematic sampling method. The systematic sampling method is easy to implement under field conditions (Strayer and Smith 2003). This is an efficient method of sampling rare, clustered, and auto-correlated populations (Smith et al. 2005; Strayer and Smith 2003). Systematic sampling is efficient when systematic sample means are similar but units within systematic samples vary widely (Strayer and Smith 2003). These conditions tends to be met for spatially patchy populations: some quadrats within the systematic sample will place on top mussel beds and others will not, but these highs and lows average out so that the multiple systematic samples are similar, thus sampling variance is reduced (Smith et al. 2005; Strayer and Smith 2003). Interpolation methods such as kriging can be applied for the data acquired from systematic sampling method because this method satisfies the uniformity condition needed (Smith et al. 2005). Finally, systematic sampling can incorporate a random component that allows valid statistical inference (Smith et al. 2005).

A detailed sampling map was developed for each reach depicting locations of quadrats along with their horizontal coordinates in order to perform field sampling. A grid of 1m x 1m was digitally overlaid on each reach map. This grid represented the possible quadrats that could be sampled. Each cell was given a number for reference. The quadrats to be sampled within the set of possible quadrats were determined by a method called systematic sampling with multiple random starts (Strayer and Smith 2003). Setting up the sampling design at each reach involved decisions about the rough number of quadrats to be sampled and the number of random starts. We set the desired number of quadrats at 50 and the number of random starts at 3 (Strayer and Smith 2003). These decisions, along with the size of the reach, determined the interval or distance between quadrats (d) within a single systematic sample. That was done according to the following equation:

$$d = \sqrt{\frac{L.W}{n/k}},$$

where L is the length of the study reach, W is the width of the study reach, n is the total number of quadrats, and k is the number of random starts (Strayer and Smith 2003). All the random starts were placed downstream of the reach. A random location was set for each random start and a quadrat was placed at each of random starts. Once the quadrat was placed at a random start, it was then propagated over the reach with a separation distance of (d). Then the procedure was iterated for the other random starts as well. An example is illustrated in Figure 4.

After the location of quadrats to be sampled was determined, quadrat sampling of mussels was conducted. A weighted PVC quadrat (1x1m) was placed at each selected sampling locations. Biotic sampling entailed counting, identifying and measuring all mussels within a quadrat. Mussels were replaced into the substrate after handling. *In-situ* identification was done by using a current field guide to unionid mussels in Connecticut (Nedeau and Victoria 2003).

Abiotic variables were also determined at each quadrat at the same time using established methods. We subdivided the quadrat into 25 squares (20cm x 20cm). The dominant sediment type (clay, silt, sand, gravel, mix of sand and cobbles, cobbles, or boulders) were encoded for each of the nine diagonal squares. The quadrat's dominant sediment type was estimated as the sediment particle mean of these nine values (Strayer 1999). Substratum stability was assessed as embeddedness, the degree to which larger particles (boulder, cobble and gravel) were surrounded or covered by fine sediment. We employed a visual assessment of embeddedness developed by Platts et al. (1983). In each quadrat, embeddedness was rated according to values listed in Table 1. In-situ morphologic features, such as run/riffle/pool distribution, sand bars, debris pile-up were identified and mapped. Flow velocity was measured in the center and lateral margins of the quadrat with an electromagnetic current meter. We obtained dissolved Oxygen (DO) and water temperature at every quadrat by using a YSI 556 MPS.

Reach-scale variables were also characterized. Channel depth, width, length, elevation, gradient and shear stress were ascertained from elevation maps. Water temperature was measured with HOBO® Water Temp pro temperature loggers

manufactured by Onset Computer Corp. (Pocasset, Massachusetts). Temperature loggers were placed at each reach and the temperatures were recorded from late summer 2008 through the end of spring 2009. In the middle of each reach we anchored a logger to the stream bottom to prevent dislodging and floating. The loggers were placed in a transition zone of a riffle and pool because we wanted to be consistent with anchoring point throughout the study reaches.

Data Analysis

We utilized an information-theoretic approach to develop resource selection functions (RSF) that evaluate the predictors of mussel abundance. An RSF is defined as any function that is proportional to the probability of use by an organism (Boyce et al. 2002). Information-theoretic methods are relatively simple to understand and practical to employ across a large class of empirical situations and scientific disciplines (Anderson et al. 2000). Amadio et al. (2005) noted that the information-theoretic approach employs strength of evidence context to assess a set of a priori alternative hypotheses rather than statistical tests of null hypotheses with decision based on P-values. This approach develops several types of evidence for alternative hypotheses: the rank of each hypothesis, expressed as a model; an estimate of the formal likelihood of each model, given the data; a measure of precision incorporating model selection uncertainty; and approaches to allow the use of alternative models in making formal inference (Amadio et al. 2005 and Anderson et al. 2000).

We practiced an exploratory approach to understand the habitat use of freshwater mussels. An array of microhabitat-scale and reach-scale habitat parameters hypothesized to affect occurrence of freshwater mussels was identified based on available literature. We then developed all possible models incorporating the identified habitat parameters and fitted each with logistic regression. We considered 7 parameters as main effects in the quadrat-scale analysis (Table 2): (1) geomorphic unit (2) proportion of fine sediment (3) proportion of medium sediment (4) depth, (5) depth², (6) embeddedness, and embeddedness². We also considered 3 interactions of geomorphic unit with sediment type, embeddedness, and depth. Habitat variables were not strongly intercorrelated ($|r| < 0.50$). All unique combinations of 5 parameters and 4 interactions were combined to develop 2102 logistic regression models.

Logistic regression analysis was performed by using the PROC LOGISTIC method in SAS (SAS Institute, 2003). We initially decided to implement ordinal polytomous logistic regression to predict the probability of mussel occurrence based on a dataset categorized into three ordinal responses representing the number of mussels sampled within a reach (none, low, and high). We then implemented model diagnostics which included the Score Test for Proportional Odds Assumption, to determine the validity of choosing ordinal over nominal polytomous logistic regression. Model diagnostics indicated that we violated the Proportional Odds Assumption. Therefore dichotomous (presence/absence) logistic regression was used for model development.

We developed a RSF at the microhabitat (quadrat) scale based on presence/absence data sets. Regression models of all possible combinations of these predictors were assessed with Akaike's information criterion (AIC; Burnham and Anderson 2002). The value of AIC is given by:

$$AIC = -2\log_e L(\hat{\theta} | data) + 2K, \text{ where:}$$

$\log_e(L)$ is the log-likelihood, $\log L(\hat{\theta} | data)$ is the value of the maximized log-likelihood over the unknown parameters (θ), K is the number of model parameters, and n represents the sample size. The AIC weights (w_i) were used to rank models:

$$w_i = \frac{e^{(-0.5*\Delta_i)}}{\sum e^{(-0.5*\Delta_i)}},$$

Where Δ_i is equal to $AIC_i - AIC_{\text{minimum}}$, and AIC_{minimum} is the lowest AIC value among the set of competing models. The model with the largest w_i is considered to best fit the data (Anderson et al. 2000). Models with w_i values that are 10% or more of the maximum w_i are identified as competing models (Amadio et al. 2005). Evidence ratios can be used to assess the strength of competing models with respect to the best fit model (Burnham and Anderson 2002). Such ratios present the evidence about fitted models as to which is better in a K-L information sense (Burnham and Anderson 2002). The evidence ratio (E_r) for a given competing model is given by:

$$E_r = \frac{w_1}{w_j},$$

where w_i is the estimated best model and w_j is a competing model in the set. In order to address model selection uncertainty among competing models, we used multimodel averaging and calculated model-averaged estimates of the coefficients and their standard errors (Burnham and Anderson 2002).

Reach-scale habitat feature selection and model development followed similar procedures to those used at the microhabitat scale. RSFs were created for habitat variables in both detailed-sampling reaches (i.e. the twelve sampled reaches in which we conducted quadrat analysis) and timed-search reaches (i.e. the 45 reaches that were subjected to timed searches for mussels in Phase 2 of the sampling design). The variables used in these two reach-scale analyses differed. We used eleven variables in the detailed-sampling reaches (Table 3). All combinations of these eleven parameters were combined to develop 83 logistic regression models. We did not have information on all of these variables for all 45 of the timed-search reaches and used only the last 4 of the variables listed in Table 3, yielding 15 logistic regression models.

Reach-scale candidate models were ranked using Akaike's information criterion which was corrected for small sample bias (AIC_c ; Burnham and Anderson 2002). The value of AIC_c is given by:

$$AIC_c = \frac{-2\log_e(L) + 2(K) + [2K(K+1)]}{(n-K-1)},$$

where $\log_e(L)$ is the log-likelihood, $\log L(\hat{\theta} | data)$ is the value of the maximized log-likelihood over the unknown parameters (θ), K is the number of model parameters, and n represents the sample size. The model with highest w_i values was considered to best fit the data and competing models were identified as models with $w_i \geq 10\%$ of the highest ranking model (Burnham and Anderson 2002).

RESULTS

Quadrat scale sampling data from 12 (50m long) study reaches were used for habitat analysis. Of the developed models, we identified 7 competing models that had a w_i value within 10% of the best fit model (Table 4). The top ranked model contained six of the main effects and two of the four interaction terms. The calculated evidence ratio for best fit model models versus model 2 is only 1.20. An RSF was developed by averaging the best fit model and seven competing models. Table 5 shows the results of the multimodel average of the eight competing models. The summed w_i values indicated four main effects (medium sediment, depth, embeddedness, and embeddedness²) and two interactions (geomorph unit*medium sediment and geomorph unit*depth) were equally the most important microhabitat features. These four main effects and two interactions are appeared in the top eight models. The model variable 'proportion of fine sediment type' indicated a summed w_i value of 0.62 and occurred in six top ranked models (Table 4). Proportion of geomorphic unit (pool, run, and riffle) had the lowest summed w_i (0.03) value, the least influential variable among the main effects, and appeared only in the sixth ranked model. However, the interaction of geomorphic unit with the proportion of medium sediment and depth indicated a higher summed w_i value of (0.70). Model-averaged coefficients were used to create a mussel RSF (Table 6). In summary, the values of averaged coefficients and summed w_i values (Table 5) of the competing models suggest that mussels select medium sediment over fine and coarse sediments, runs over pools and riffles, and microhabitat with greater embeddedness (which, because of the scale used for this variable, has a lower score; Table 1). However, the habitat preference of mussels changes when the main effects interact with each other. The positive slope for the pool*fine sediment interaction indicates that fine substrate has a stronger effect on mussel occurrence in pools than outside pools; in combination with a positive slope for the run*fine sediment interaction, this means that mussels are less likely to occur in riffles with fine substrate. The other interactions indicate that the effects of medium substrate, depth and embeddedness vary with geomorphic unit.

An RSF was created for detailed-sampling reaches (i.e. those in which we conducted quadrat analysis). The top-ranked model and 11 models that had a w_i value

within 10% of top model were identified as competing models (Table 7). These 12 models were averaged to create a RSF. We further calculated evidence ratios for best fit model versus other competing models. The summed w_i values for the competing models indicated the proportion of medium substrate that appeared in three competing models, was the most important habitat variable within reaches. Shear stress had a summed w_i of 0.22 (Table 8) and appeared in five competing models. Mean embeddedness occurred in three models and had a summed w_i of 0.17, indicating that it was ranked third in relative importance among the habitat variables included in the averaged model. Geomorphic unit and peak flow had the lowest w_i (0.02) value relative to other variables, indicating that they had the minimum influence compared to other habitat features. Model-average coefficients were used to develop a RSF for predicting occurrence of freshwater mussels within a reach (Table 9). The direction of effect indicated that mussels selected medium substrate over fine and coarse substrate types, and habitats with lower shear stress. The probability of mussel occurrence in a reach increased with increasing embeddedness.

An RSF was also created for the reach scale using all 45 reaches that had been subjected to timed search. The best fit model and seven competing models were identified based on AIC and AIC weights (Table 10). All competing models were averaged to create a RSF (Tables 11 and 12). The summed w_i values for each habitat variable showed that gradient was the most important reach scale habitat feature determining mussel occurrence and appeared in the top six models. Distance to dam (summed $w_i = 0.34$) was the second most influential reach scale habitat variable. The probability of mussel occurrence in a reach decreased with increasing gradient, sinuosity, and distance to dam.

Size and age data were obtained for all mussels encountered. These data were not used for model development, however, preliminary interpretations were carried out to understand the relationship among age, growth rate, and mussel abundance. The constructed plots are depicted in Figures 5 and 6. Mussels ranged in age from 1 to 19 years with a mean age of five years. The age-frequency distribution indicated a similar age variation for Eastern Elliptio and Eastern Floater. The maximum mean mussel abundance was observed at age 4, recording 339 and 58 mussels from Eastern Elliptio and Eastern Floater respectively. The scatter plot of mean growth rate vs mean mussel

abundance suggested that there is no density-dependent suppression of growth rate (Figure 6).

Mean temperatures were calculated from temperature loggers averaged over the summer sampling period. Water temperature was not found to affect habitat selection at microhabitat and reach-scale, therefore, it was not incorporated into model development. The mean summer temperature data at reach scale are depicted in Table 13.

Data on the fish assemblages in subwatersheds of the Willimantic River watershed were obtained from the Connecticut Department of Environmental Protection to identify mussel host fish species in our study reaches. We identified five host fish species of which three were known to be host fish for Eastern Elliptio and two were known to be host for Eastern Floater (Table 14).

DISCUSSION

Resource Selection Function (RSF) models

We identified five main habitat parameters that affect the probability of mussel presence at the microhabitat-scale, with the most important being proportion of medium substrate, depth, and embeddedness. Even though the parameter geomorphic unit (pool, run) was not found as a main effect, it appeared as an influential factor in interactions with three of the five main parameters (i.e. sediment type, embeddedness and depth). Mussel occurrence was typically dominated by medium substrate (gravels and pebbles) with high levels of embeddedness.

The dominance of medium substrate could suggest the importance of flow refuges over the occurrence of mussels. This inference is consistent with Strayer's (1999) suggestion that mussel beds will generally be found in flow refuges where shear stresses during floods are too low to displace them or the sediments in which they are anchored in. In a medium substrate, roughness elements are relatively close in size (e.g. gravel and pebble) and therefore flow tend to glide over the substratum resulting in much slower flows and stable eddies in spaces between the bed elements (Holomuzki and Biggs 1999). This feature could mitigate the hydraulic stress on mussels and thereby reduce the dislodgement rates.

We know of no other published studies that have attempted to incorporate substrate embeddedness in RSF models for predicting mussel occurrence at microhabitat scale or reach scale. In this study, we introduced the substrate embeddedness as a microhabitat scale parameter (also as a reach scale parameter), because it describes the character of stream substrate in which mussel are bedded. As we expected, our results revealed a promising relationship between substrate embeddedness and mussel presence. When stream substrates become more embedded, the interstitial space between particles is reduced. As a result, streambed roughness could substantially reduce and therefore alter channel bedform, and hydraulics (Wilcock 1998). Streambed and substrate mobility can be considerably affected by the quantity and characteristics of the fine material because the critical flow initiating grain motion decreases rapidly with increasing amount of fine material in the matrix (Wilcock 1998). Similarly, several studies have also shown that particle embeddedness negatively affects bed movement at the critical flow (Matthaei et al 1999 and Buffington et al 1992). These findings further reveal the effect of substrate embeddedness on flood refuges. Highly embedded substrate types are less vulnerable to severe disturbances at peak flows because coarser particles such as cobbles could act as shields sheltering smaller roughness elements (e.g. gravel and pebble) against lift forces. These environments could provide favorable substratum condition for mussels because mussels are able to be anchored in the substratum as long as the substratum itself is stable (Strayer 1999).

Depth also contributed to the competing models and in the multimodel averages. Even though depth marked a significant AIC weight, it has relatively small averaged coefficient in the RSF in comparison with medium substrate and embeddedness. The large AIC value indicates that the depth is a critical habitat feature for predicting mussel occurrence. However, the small averaged coefficient suggests that increasing depth is less likely to considerably increase the probability of finding mussels. In the studies conducted by Valovirta (1995), the preferred depth was found to be between 1m and 3m, while depths less than 0.3m were described as unsuitable habitat because shallower water freezes in winter. In contrast, Gittings et al. (1998) noted the highest mussel densities at 0.2m depths in rivers of southern Ireland which do not freeze in winter. Our data also

recorded 0.2m as the most preferable depth for freshwater mussels in the Willimantic River watershed.

Apart from stand alone effects of main habitat features we also considered their interactions. By doing this we attempted to reveal the contribution of the combined effects of habitat features for predicting mussels and incorporate them as variables into our RSF. If there is an interaction between effects it means that the change in the dependent variable as a result in one of the variables depends on the value of the other variable.

The combined effects of medium substrate and depth with geomorphic unit also indicated a considerable contribution to the competing models and in the multimodel averages. This suggests that stand alone effect of geomorphic unit (pool and run) is less influential but the effect is critical when it interacts with other three main habitat parameters (medium substrate, depth, and embeddedness). The combined effect of pools and proportion of medium sediment indicated a positive correlation to the mussel presence, suggesting that mussels prefer pools subjected to the proportion of medium sediment. Similarly, the pool-depth interaction has also marked a significant AIC weight along with a negative correlation to the mussel occurrence. This suggests that the effect of depth is different in pools versus not-pools. Mussels prefer shallow pools dominated with medium substrate because, as discussed earlier, high sediment stability is associated with smaller roughness elements (medium substrate) and the stability is highest in low velocities such as that found in pools. A similar kind of pattern is observed for the interactions of runs with medium sediment and depth. Both run-depth and run-medium sediment interactions were negatively correlated to the mussel occurrence. Runs represent moderately turbulent flow condition, therefore, increasing runs create less favorable flow condition to mussels by decreasing sediment stability.

Several factors affected the probability of mussel occurrence at the reach scale, with medium substrate, bed shear stress, and mean embeddedness being the most important habitat features in 12 reaches where detailed assessment was employed. Similar to microhabitat-scale variables, medium substrate and mean embeddedness were also consistently important amongst the reach-scale variables. In reach-scale, the slope quantifying the importance of medium substrate is approximately ten times larger in the

reach-scale analysis than in the microhabitat-scale analysis. This suggests that proportion of medium sediment (gravel and pebble) has a strong predictive relationship with mussel occurrence in reach-scale. Our observation agrees with available literature because substrate type has been a good predictor of mussel occurrence in other studies. Early researchers such as, Gorman and Karr (1978); Salmon and Green (1983); and Lewis and Riebel (1984) have made indirect reference to substratum type influencing the abundance and local distribution of many mussel species but they were unable to find a considerable relationship between substratum and mussels. However, recent studies noted a significant relationship between substratum and mussel occurrence. Macrae et al (2004) noted substratum as one of the most influential reach-scale variable for mussel distribution. Brainwood et al (2008) found that mussel distribution has frequently correlated with the substratum character of a reach.

Reach-averaged shear stress was identified as the second most important habitat variable. The negative correlation of shear stress indicates increasing shear stress degrades the mussel habitat suitability. Our finding is analogous to the other studies conducted on habitat preference of freshwater mussels at reach-scales. Several studies predicted the distribution of mussels in small to medium sized rivers using various derivatives of shear stress (Layzer and Madison 1995, Hardison and Layzer 2001, Howard and Cuffy 2003). Morales et al 2006 simulated the spatial distribution of developing mussel beds at reach-scale based on substrate and hydrodynamic condition and found promising effect of shear stress over mussel prediction. Gangloff and Feminella 2007 also reported that mussel abundance was highly variable at sites subject to low-shear stress during spates, whereas abundance always was low at sites subject to high-shear stress. It should be noted that we have calculated the reach-averaged shear stress based on wetted channel dimensions. However, our calculations could have been further improved if the shear stress were calculated under bankfull condition. In both cases shear stress is calculated using channel depth. This condition is only valid for wide-shallow streams. For narrow deep channels, the hydraulic radius should be used for calculating shear stress instead of channel depth. Therefore, our reach scale RSF is valid only for wide-shallow streams.


In comparison to detailed assessment, gradient was accounted as the most important reach-scale predictor variable based on the data from 45 reaches where rapid-assessment was employed. Gradient marked a high negative correlation to the mussel occurrence. Gangloff and Feminella 2007 also noted channel gradient as one of the best predictor of mussel abundance. Dixon and Vokoun 2008 and Amadio et al 2005 reported that some reach scale-variables can be correlated with others. For example, gradient can be correlated with other reach-scale habitat features such as substrate type, geomorphic unit, embeddedness, shear stress, and sinuosity. In observational studies such as this one there is a high probability that some of predictor variables will be mutually dependent (Burnham and Anderson 2002). Increasing gradient directly influence flow dynamics and hydrogeomorphic variables. For example, in high gradient reaches cascades, rapids and chutes are dominant while riffles and pools are common in medium to low gradient reaches (Halwas and Church 2005). We can therefore argue that gradient may be a surrogate for several other reach-scale features affecting mussel occurrence. Although all four model parameters (gradient, sinuosity, distance to dam, and peak flow) in the rapid assessment were derived from available GIS and remote sensing data without any field efforts, we obtained a promising relationship between gradient and mussel occurrence. This finding is important because the proposed RSF model is capable of making a rapid prediction of mussel occurrence in a given area, and therefore can potentially be used in future studies to optimize sampling effort and resource allocation. However, the predictability may be limited by the resolution and scale of GIS data, especially the dependence of channel gradient estimates on the vertical resolution of DEM.

The RSF models could have been further enhanced if catchment-scale variables were integrated into the modeling because reach-scale variables such as channel morphology and substrate character are in turn dependent on catchment scale processes, including land use/cover, geology, and flood history. It would have been desirable to perform a quantitative model validation of the three RSFs in a new watershed. We believe that RSFs are the most promising of procedures proposed for studying resource selection when combined with GIS because (1) RSFs offer a quantitative characterization of resource use; (2) RSFs can accommodate virtually any type of resource being selected, including both categorical and scalar variables; and (3) RSF models easily accommodate

spatial structure and can be interfaced with GIS to facilitate rapid analysis and use of remote sensing and other types of spatial data (Boyce et al 1999).

Value of the information-theoretic approach

The information-theoretic approach enabled us to identify and rank habitat features predicting mussel occurrence from an array of features hypothesized to predict occurrence. The purpose of this approach is not to find the “true model” but to find a best approximating model, given the data, and then develop inferences from that model (Burnham and Anderson 2002). In contrast to information-theoretic framework, classical hypothesis tests have several inherent drawbacks in model selection. The fundamental issue is that hypothesis tests assume the existence of a true model (Weakliem 2004).

 Compared to information-theoretic approach, classical hypothesis tests do not always identify a single best model and therefore there may be several models that can not be rejected against any alternative (Weakliem 2004). The results from this method can be strongly influenced by sample size. In large samples, nearly all hypotheses can be rejected, so the use of classical hypothesis tests for model selection leads to very complex models (Weakliem 2004). Another issue is that classical hypothesis testing does not consider models symmetrically and therefore smaller model can be rejected without receiving a positive support (Weakliem 2004). Information-theoretic approaches gained an appealing status in model selection compare to classical hypothesis tests. However, information-theoretic approaches should not be used unthinkingly. It is critical to have a good set of a priori models, and this entails professional judgment and integration of the science of the issue into the model set (Burnham and Anderson 2004).

Value of the multiple spatial scale approach

Stream ecosystems can be considered as hierarchical environments (Dixon and Vokoun 2008). The level of geomorphic variability present in a scale of interest is a function of processes operating at range of scales (Bartley and Rutherford 2005, Thomson et al. 2001). At larger scale, a reach is controlled by regional geology and basin plan-form, which mainly affect the slope of a reach (Bartley and Rutherford 2005). At the next scale down, geomorphic variability is mainly controlled by basin area and hydrology, which produces variation in hydrogeomorphic features such as pool and riffles (Bartley and Rutherford 2005). Finally, the small scale variations observed within

a reach are attributed by factors such as woody debris and localized geological structures (Bartley and Rutherford 2005). Even though the variability produced at each of these scales is not independent, it produces the overall variability within a given reach. For example, channel morphology and substrate character are in turn dependent on longer-term larger-scale process, including sediment supply and flood history (Bartley and Rutherford 2005, Thomson et al. 2001).

Freshwater mussel populations have distributions in multiple spatial scales. Previous studies based on single-scale framework which focused only on microhabitat-scale habitat predictors, have been largely unsuccessful in predicting mussel occurrence. As discussed above, microhabitat variables such as hydrogeomorphic parameters are functions of large scale processes. For example, substrate character at microhabitat scale could be a function of channel gradient at reach scale and at the same time that could be a function of land cover at catchment scale. Therefore, understanding the associations between mussels and physical habitat parameters measured across multiple spatial scales might be more useful than a single-scale microhabitat approach. Further, multiple-spatial scale approaches can provide a more spatially relevant estimate of the importance of local habitat models.

Recommendations to state resource managers

The state of Connecticut has twelve native freshwater mussel species. Of these, six species are listed as special concern, threatened, or endangered. Understanding habitat requirements of these species is critical in well informed conservation practices and sustainable land use planning.

The two mussel species (Eastern Elliptio and Eastern Floater) we studied are not listed as species of concern. However, Eastern Elliptio, the most common mussel species, share the habitat with majority of state and federally listed species, including Dwarf Wedgemussel and Brook Floater and Tide Watermucket (Nedean 2008). Therefore, the analysis of the factors affecting the distribution of common species will be helpful in identifying likely areas of occurrence for other species, including those that are species of concern.

When exercising conservation practices on state or federally listed species, it is critical to locate their habitats rigorously and cost effectively. The RSF model that

developed based on rapid-assessment data can be used as a robust tool to identify likely areas for mussel occurrence before employing expensive and detailed sampling methods. The state resource managers can easily implement this RSF model using readily available GIS and remotes sensing data to delineate hot spots.

Our microhabitat-scale and reach-scale RSF models can assist in relocation programs. Freshwater mussels are typically relocated from sites that will be impacted by restoration efforts such as dam removals. Prior to implementing relocation, the resource managers need to make decisions about where to move the animals. In such circumstances, the habitat suitability of selected relocation sites can be evaluated with our multiscale RSF models.

Temperature, fish assemblages and mussel age/size data

Although water temperature was measured as a physical parameter, it was not considered for model selection both in microhabitat and reach scales. A direct effect of water temperature on mussel occurrence was poorly supported by literature. Thus, it was not hypothesized as a predictor variable. However, Spooner and Vaughn 2009 noted that the physiological performance of mussel species (i.e. respiration, filtration, excretion) varies along temperature gradients, thus temperature may be used by mussels to partition spatial and temporal resources. Although there is lack of support for temperature dependence of mussels, thermal preference of mussel host fish can significantly affect on mussel occurrence because freshwater mussels require a host fish to complete the life cycle (Newton et al 2008).

Studies conducted by Woolnough (2006) and Newton et al (2008) emphasized the importance of the host fish, in addition to channel hydraulic and hydrogeomorphic features, as a habitat variable for mussel abundance and richness. Although the movement of host fish occurs on large scales (e.g., > 100 m), both their distribution and abundance possibly contribute to the spatial pattern of mussel communities (Woolnough 2006). Despite the importance of host fish, reach-scale fish sampling was not conducted due to time constraints and budget availability. However, fish assemblages should have been incorporated into model development. From subwatershed scale fish assemblages, we identified five host fish species which are known to be common host fish for Eastern Elliptio and Eastern Floater. Collectively predictability of our RSFs would have been

enhanced if water temperature data and fish assemblages were also incorporated into model development

In order to determine a status of a population, the age structure must be established in addition to the number or density of individuals, as the absence or scarcity of juveniles indicates reproductive failure and population decline (Outerio 2008). Therefore, we obtained age and size data for each mussel encountered during quadrat sampling. The annual periodicity of the growth rings (annuli) in the valves was used for determining age. Recent studies indicate that the use of annuli could be erroneous (Anthony et al 2001). However, Outerio et al (2008) noted that this method is reliable enough for determining the age of individuals of up to 30-40 years. This observation validated our age data because the maximum longevity we observed was 20 years. In all four subwatersheds mean ages were ranged 2 -10 years indicating comparatively younger populations. Nedeau 2008 noted that freshwater mussels reach sexual maturity at ages ranging from 6 to 10 years. Our age frequency histogram exhibits a range of sizes, with evidence of reproduction and longevity. This reveals healthy populations with strong recruitment in all subwatersheds. High population density may indicate a healthy and stable population (Nedeau 2008). The growth-abundance scatter plot can be used to make preliminary inferences on mussel populations in high/low mussel reaches. Growth rate of three high mussel reaches (Hop River, Middle River, and Roaring Brook) were ranged from 0.5 to 1.0 and indicated a high mussel frequency within that range. Further, we observed high density of younger populations in high mussel reaches. Therefore, we can hypothesize that younger populations have high growth rates which may attributed by habitat condition (e.g., flow refuges, substratum) and resource availability (e.g., food and host fish). However, we have limited evidences to support this idea because we poorly addressed the dynamics in mussel population.

In summary, we identified main habitat features, including substrate type, embeddedness, and shear stress for predicting mussels at microhabitat scale and they are analogues with previous studies. However, to our knowledge this is the first study attempted to integrate embeddedness in mussel prediction at microhabitat and reach scales. Most important reach-scale predictors derived from detailed assessment were consistent with microhabitat-scale parameters. Our reach-scale predictors were also

promising and supported by recent studies. Gradient was identified as the best reach-scale predictor based on rapid-assessment data and it has strength to surrogate several other hydrogeomorphic variables. Although the mussel species we studied are not listed as species of concern, the analysis of the factors affecting the distribution of these species will be helpful in identifying likely areas of occurrence for other species, including those that are species of concern. The resource selection function models can be used as robust tools for delineating critical mussel habitats for land use planning, locating species of concern, and identifying suitable habitats for mussel relocations. These models can easily be interfaced with GIS framework, facilitating rigorous habitat assessments at multiple spatial scales. Collectively the results from this study can assist regional resource managers for developing effective habitat restoration and conservation strategies in Connecticut.

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TABLES AND FIGURES

Table 1. Embeddedness rating for gravel, rubble, and boulder particles (Platts et al. 1983).

Rating	Rating description
5	<5 % of surface covered by fine sediments
4	5-25% of surface covered by fine sediments
3	25-50% of surface covered by fine sediments
2	50-75% of surface covered by fine sediments
1	>75 % of surface covered by fine sediments

Table 2. Habitat variables employed in microhabitat-scale analysis.

Parameter	Description
Geomorphic unit	
<i>Pool</i>	Categorical variable identified as a region of deeper, slower-moving water with fine bed materials.
<i>Run</i>	Categorical variable identified as an intermediate region in which the flow is less turbulent than in riffles but moves faster than riffles.
<i>Riffle</i>	Categorical variable identified as a region with coarser bed materials and shallower, fast moving water.
Sediment type	
<i>Proportion of fine sediment</i>	Continuous variable calculated as the proportion of quadrat composed of silt and sand.
<i>Proportion of medium sediment</i>	Continuous variable calculated as the proportion of quadrat composed of gravel and pebble.
<i>Proportion of coarse sediment</i>	Continuous variable calculated as the proportion of quadrat composed cobble, boulder, and bedrock).
Depth	Continuous variable recorded as the mean depth of a quadrat.
Embeddedness	Continuous variable recorded as the degree to which larger particles are covered by fine sediments in quadrat.

Table 3. Habitat variables employed in reach-scale analysis (detailed sampling reaches).

Parameter	Description
Percentage of geomorphic unit	
<i>Pool</i>	Percentage of a reach composed of pool channel units.
<i>Run</i>	Percentage of a reach composed of run channel units
<i>Riffle</i>	Percentage of a reach composed of riffle channel units
Percentage of sediment type	
<i>Fine</i>	Percentage of a reach composed of silt and sand.
<i>Medium</i>	Percentage of a reach composed of gravel and pebble.
<i>Coarse</i>	Percentage of a reach composed of cobble, boulder, and bedrock.
Mean depth	Continuous variable calculated by averaging mean depths of all quadrats of a reach.
Mean embeddedness	Continuous variable calculated by averaging the embeddedness of all quadrats of a reach
Gradient	Continuous variable measured as the change in elevation in a reach over the length of reach.
Shear stress	Continuous variable calculated using slope, hydraulic radius and specific gravity of water.
Sinuosity	Continuous variable calculated as the reach channel pattern
Distance to dam	Distance to the nearest up stream dam measured from the upper boundary of a reach.
Peak flow	Peak flow at two year recurrence interval.

Table 4. Competing logistic regression models developed for variation in the occurrence of freshwater mussels at the microhabitat scale within the study reaches. The models included proportion of fine sediment (F_s), proportion of medium sediment (M_s), depth (D), embeddedness (E), pool (P), and run (R). Interactions of main effects are also considered. Models are ranked according to Akaike's information criterion weights (w_i) computed from Akaike's information criterion modified for small sample size, the number of estimated parameters (K), log likelihood ($\text{Log}_e L$), and the difference in AIC (Δ_i). The evidence ratio Er is also included for each model. Competing models with w_i values that were 10% or more of the maximum w_i are included in the table. Depth and embeddedness transformed with square transformation (D^2 , E^2)

Rank	Model	K	-2Log _e L	AIC	Δ_i	w_i	
1	$\beta_0 + \beta_1(F_s) + \beta_2(M_s) + \beta_3(D) + \beta_4(D^2) + \beta_5(E) + \beta_6(E^2) + \beta_7(P * M_s) + \beta_8(R * M_s) + \beta_9(P * D) + \beta_{10}(R * D)$	11	-271.91	565.83	0.00	0.26	
2	$\beta_0 + \beta_1(F_s) + \beta_2(M_s) + \beta_3(D) + \beta_4(D^2) + \beta_5(E) + \beta_6(E^2) + \beta_7(P * M_s) + \beta_8(R * M_s) + \beta_9(P * D) + \beta_{10}(R * D) + \beta_{11}(P * E) + \beta_{12}(R * E)$	13	-270.10	566.20	0.37	0.21	1.20
3	$\beta_0 + \beta_1(F_s) + \beta_2(M_s) + \beta_3(D) + \beta_4(E) + \beta_5(E^2) + \beta_6(P * M_s) + \beta_7(R * M_s) + \beta_8(P * D) + \beta_9(R * D)$	10	-274.43	568.86	3.02	0.06	4.54
4	$\beta_0 + \beta_1(M_s) + \beta_2(D) + \beta_3(D^2) + \beta_4(E) + \beta_5(E^2) + \beta_6(P * F_s) + \beta_7(R * F_s) + \beta_8(P * M_s) + \beta_9(R * M_s) + \beta_{10}(P * D) + \beta_{11}(R * D) + \beta_{12}(P * E) + \beta_{13}(R * E)$	14	-270.71	569.42	3.60	0.04	6.04
5	$\beta_0 + \beta_1(F_s) + \beta_2(M_s) + \beta_3(D) + \beta_4(E) + \beta_5(E^2) + \beta_6(P * M_s) + \beta_7(R * M_s) + \beta_8(P * D) + \beta_9(R * D) + \beta_{10}(P * E) + \beta_{11}(R * E)$	12	-272.85	569.696	3.87	0.04	6.91
6	$\beta_0 + \beta_1(F_s) + \beta_2(M_s) + \beta_3(D) + \beta_4(D^2) + \beta_5(E) + \beta_6(E^2) + \beta_7(P) + \beta_8(R) + \beta_9(P * M_s) + \beta_{10}(R * M_s) + \beta_{11}(P * D) + \beta_{12}(R * D) + \beta_{13}(P * E) + \beta_{14}(R * E)$	15	-269.93	569.87	4.04	0.03	7.52
7	$\beta_0 + \beta_1(M_s) + \beta_2(D) + \beta_3(D^2) + \beta_4(E) + \beta_5(E^2) + \beta_6(P * F_s) + \beta_7(R * F_s) + \beta_8(P * M_s) + \beta_9(R * M_s) + \beta_{10}(P * D) + \beta_{11}(R * D)$	12	-272.97	569.94	4.11	0.03	7.80
8	$\beta_0 + \beta_1(F_s) + \beta_2(M_s) + \beta_3(D) + \beta_4(D^2) + \beta_5(E) + \beta_6(E^2) + \beta_7(P * M_s) + \beta_8(R * M_s) + \beta_9(P * M_s) + \beta_{10}(R * M_s) + \beta_{11}(P * D) + \beta_{12}(R * D) + \beta_{13}(P * E) + \beta_{14}(R * E)$	15	-270.05	570.09	4.26	0.03	8.42

Table 5. Averaged model variables, estimated model coefficients, and sums of corrected Akaike information criterion (AIC_c) weights for a model averaged among eight competing models accounting for the variation in the occurrence of freshwater mussels in the study reaches. The proportion of coarse substrate is not shown here because it is dependent on the coefficients for the other two category levels (fines and medium).

Model variable	Averaged coefficients	Sum of AIC _c weights
Constant	-0.703	-
Proportion of substrate type		
<i>Fines</i>	1.108	0.624
<i>Medium</i>	2.278	0.698
Proportion of geomorphic unit		
<i>Pool</i>	0.134	0.034
<i>Run</i>	0.349	0.034
Depth		
<i>Depth</i>	0.078	0.698
<i>Depth</i> ²	-0.001	0.605
Embeddedness		
<i>Embeddedness</i>	-0.880	0.698
<i>Embeddedness</i> ²	-0.515	0.698
Interactions		
<i>Pool* Proportion of Fine sediment</i>	0.482	0.105
<i>Run* Proportion of Fine sediment</i>	0.702	0.105
<i>Pool* Proportion of Medium sediment</i>	0.189	0.698
<i>Run* Proportion of Medium sediment</i>	-1.367	0.698
<i>Pool*Depth</i>	-0.071	0.698
<i>Run*Depth</i>	-0.044	0.698
<i>Pool*Embeddedness</i>	0.619	0.355
<i>Run*Embeddedness</i>	0.256	0.355

Table 6. Relative probability of presence, $w(x)$, as a function of variables in freshwater mussel resource selection function at the quadrat scale. Abbreviations for parameters are: proportion of fine sediments (F_s), proportion of medium sediments (M_s), depth (D), pool (P), run (R), embeddedness (E), square transformation Depth and embeddedness (D^2 , E^2). Pool and run have binary effect on the equation. For example, if the geomorphic unit is pool then $P = 1$ and $R = 0$.

$$w(x) = -0.703 + 1.108 (F_s) + 2.278 (M_s) + 0.134 (P) + 0.349 (R) + 0.482(P*F_s) + 0.702 (R*F_s) + 0.189 (P*M_s)$$

$$- 1.366 (R*M_s) + 0.078 (D) + -0.001 (D^2) + -0.071 (P*D) - 0.044 (R*P) - 0.880 (E) - 0.515 (E^2) + 0.618 (P*E) + 0.256 (R*E)$$

Table 7. Competing logistic regression models developed for variation in the occurrence of freshwater mussels at reach-scale within the 12 detailed-sampling reaches. The models included percentage of fine sediment (F_s), percentage of medium sediment (M_s), depth (D), proportion of pool (P_p), proportion of run (P_R), embeddedness (E), distance to nearest dam (D_d), shear stress (S_s), sinuosity (S) and peak flow (P_k). Models are ranked according to Akaike's information criterion weights (w_i) computed from Akaike's information criterion modified for small sample size (AIC_c), the number of estimated parameters (K), log likelihood ($\text{Log}_e L$), and the difference in AIC_c (Δ_i). Competing models with w_i values that were 10% or more of the maximum w_i are included in the table.

Rank	Model	K	-2Log _e L	AIC	Δ_i	w_i	Er
1	$\beta_0 + \beta_1(M_s)$	2	-2.98	11.29	0.00	0.19	
2	$\beta_0 + \beta_1(S_s)$	2	-3.34	12.00	0.71	0.13	1.43
3	$\beta_0 + \beta_1(E)$	2	-3.69	12.71	1.42	0.09	2.03
4	$\beta_0 + \beta_1(M_s) + \beta_2(D_d)$	3	-1.89	12.79	1.49	0.09	2.11
5	$\beta_0 + \beta_1(F_s) + \beta_2(M_s)$	3	-2.00	13.00	1.71	0.08	2.35
6	$\beta_0 + \beta_1(D) + \beta_2(E)$	3	-2.66	14.32	3.03	0.04	4.54
7	$\beta_0 + \beta_1(E) + \beta_2(D_d)$	3	-2.79	14.58	3.29	0.04	5.17
8	$\beta_0 + \beta_1(F_s) + \beta_2(S_s)$	3	-3.20	15.40	4.11	0.02	7.82
9	$\beta_0 + \beta_1(P_p) + \beta_2(S_s)$	3	-3.27	15.54	4.25	0.02	8.38
10	$\beta_0 + \beta_1(P_k)$	2	-5.11	15.55	4.26	0.02	8.41
11	$\beta_0 + \beta_1(P_R) + \beta_2(S_s)$	3	-3.28	15.55	4.43	0.02	8.43
12	$\beta_0 + \beta_1(S_s) + \beta_2(D_d)$	2	-3.30	15.60	4.31	0.02	8.63

Table 8. Averaged model variables, estimated model coefficients, and sums of corrected Akaike information criterion (AIC_c) weights for a model averaged among 12 competing models accounting for the variation in the occurrence of freshwater mussels within the 12 detailed-sampling reaches.

Model variable	Averaged coefficients	Sum of AIC_c weights
Constant	-0.096	
Proportion of substrate type		
<i>Fine</i>	6.930	0.102
<i>Medium</i>	22.708	0.351
Proportion of geomorphic unit		
<i>Pool</i>	-2.573	0.022
<i>Run</i>	2.273	0.022
Mean Depth	0.234	0.041
Mean Embeddedness	-4.529	0.167
Shear Stress	-0.172	0.219
Distance to dam	0.000	0.145
Peak flow	0.021	0.022

Table 9. Relative probability of presence, $w(x)$, as a function of variables in freshwater mussel resource selection function. Abbreviations for parameters are, percentage of fine sediments (F_s), percentage of fine sediments (M_s), embeddedness (E), depth (D), sinuosity (S), distance to nearest dam(D_d), and peak flow (P_k).

$$w(x) = -0.096 + 6.930 (F_s) + 22.708 (M_s) - 2.573 (P_p) + 2.273 (P_R) + 0.234 (D) - 4.529 (E) - 0.172 (S_s) + 0.021 (P_k)$$

Table 10. Competing logistic regression models developed for variation in the occurrence of freshwater mussels at reach-scale within 45 study reaches (timed search). The models included gradient (G), distance to nearest dam (D_d), sinuosity (S), and peak flow (P_k). Models are ranked according to Akaike's information criterion weights (w_i) computed from Akaike's information criterion modified for small sample size, the number of estimated parameters (K), log likelihood ($\text{Log}_e L$), and the difference in AIC_c (Δ_i). Competing models with w_i values that were 10% or more of the maximum w_i are included in the table.

Rank	Model	K	-2Log _e L	AIC	Δ_i	w_i	Er
1	$\beta_0 + \beta_1(G)$	2	-20.19	44.66	0.00	0.33	-
2	$\beta_0 + \beta_1(G) + \beta_2(D_d)$	3	-19.62	45.82	1.16	0.19	1.79
3	$\beta_0 + \beta_1(G) + \beta_2(S)$	3	-20.12	46.83	2.17	0.11	2.97
4	$\beta_0 + \beta_1(G) + \beta_2(P_k)$	3	-20.14	46.87	2.22	0.11	3.03
5	$\beta_0 + \beta_1(G) + \beta_2(D_d) + \beta_3(P_k)$	4	-19.53	48.06	3.40	0.06	5.47
6	$\beta_0 + \beta_1(G) + \beta_2(S) + \beta_3(D_d)$	4	-19.60	48.20	3.54	0.06	5.88
7	$\beta_0 + \beta_1(D_d)$	2	-22.37	49.03	4.38	0.04	8.92
8	$\beta_0 + \beta_1(G) + \beta_2(S) + \beta_3(P_k)$	4	-20.06	49.13	4.47	0.04	9.34

Table 11. Averaged model variables, estimated model coefficients, and sums of corrected Akaike information criterion (AIC_c) weights for a model averaged among eight competing models accounting for the variation in the occurrence of freshwater mussels in the study reaches.

Model variable	Averaged coefficients	Sum of AIC_c weights
Constant	0.457	-
Gradient	-78.350	0.889
Sinuosity	-1.851	0.203
Distance to dam	-0.000	0.339
Peak flow	0.000	0.205

Table 12. Relative probability of presence, $w(x)$, as a function of variables in freshwater mussel resource selection function. Abbreviations for parameters are, gradient (G), sinuosity (S), distance to nearest dam (D_d), and peak flow (P_k).

$$W(x) = 0.457403 - 78.350442(G) + -1.850954(S) + -0.000177(D_d) + 0.000647(P_k)$$

Table 13. Mean and standard deviation of summer water temperature data in the sampled 12 reaches.

Subwatershed	Reach type	Mean temperature (°C)	SD
Edson Brook	High	23.89	1.36
	Low	20.22	1.38
	No	17.92	2.01
Hop River	High	24.11	1.41
	Low	19.56	2.06
	No	19.73	1.65
Middle River	High	21.77	1.71
	Low	20.72	1.17
	No	N/A	N/A
Roaring Brook	High	20.26	1.11
	Low	20.48	1.30
	No	19.66	1.23

Table 14. Identified host fish species in the sampled subwatersheds

Subwatershed	Host fish	
	Eastern Elliptio	Eastern Floater
Edson Brook	<i>Lepomis gibbosus</i> (Pumpkinseed)	<i>Lepomis macrochirus</i> (Bluegill sunfish), <i>Catostomus commersoni</i> (White sucker)
Hop River	<i>Micropterus salmoides</i> (Largemouth bass), <i>Perca flavescens</i> (Yellow perch)	<i>Catostomus commersoni</i> , <i>Perca flavescens</i>
Middle River	<i>Lepomis gibbosus</i>	<i>Catostomus commersoni</i>
Roaring Brook	<i>Micropterus salmoides</i> , <i>Perca flavescens</i>	<i>Catostomus commersoni</i> , <i>Perca flavescens</i> , <i>Lepomis macrochirus</i>



Willimantic River Watershed Towns



Willimantic River Watershed subregional basins

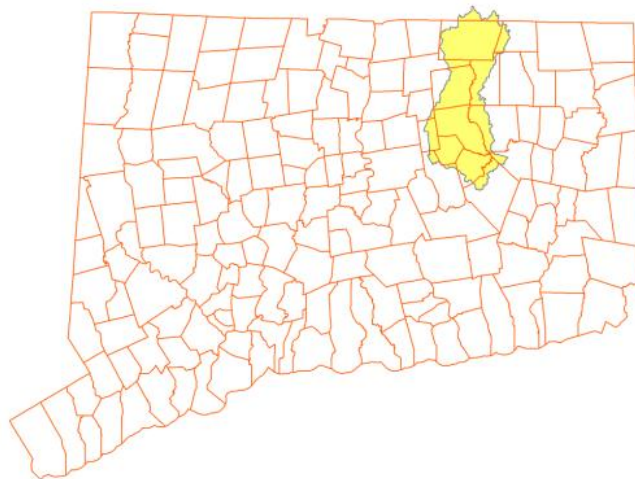
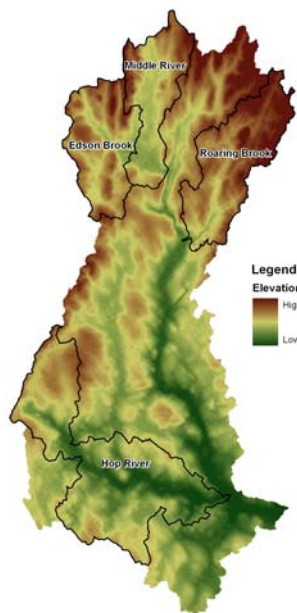
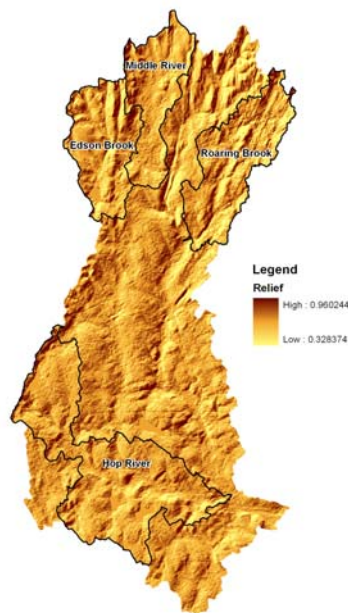


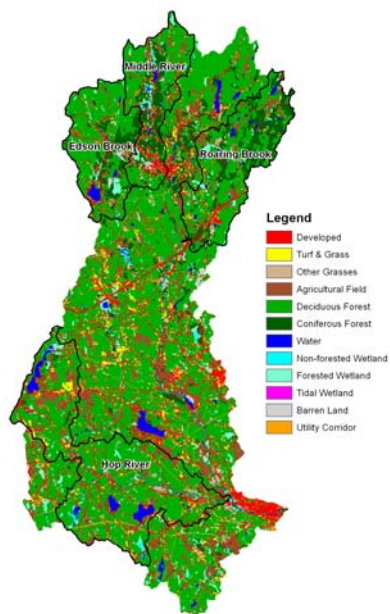
Figure 1. Willimantic River watershed, indicating political boundaries and subwatersheds.



Digital Elevation Model



Relief Map



2006 Land use/cover

Figure 2. Physiographic renderings of the Willimantic River Watershed.

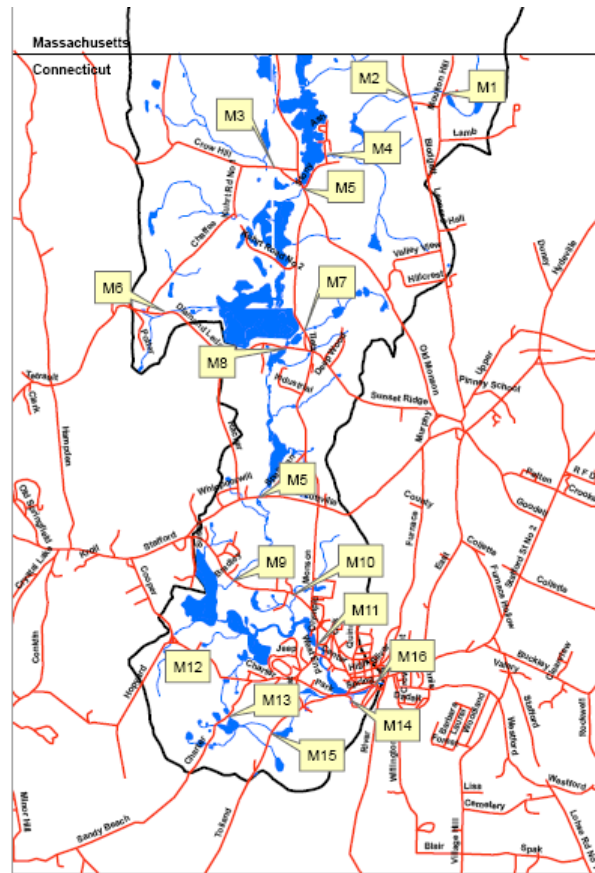


Figure 3. Middle Brook subwatershed: identification of potential reaches in phase of sampling. The letter M followed by a subscript depicts the sites we visited in phase I.

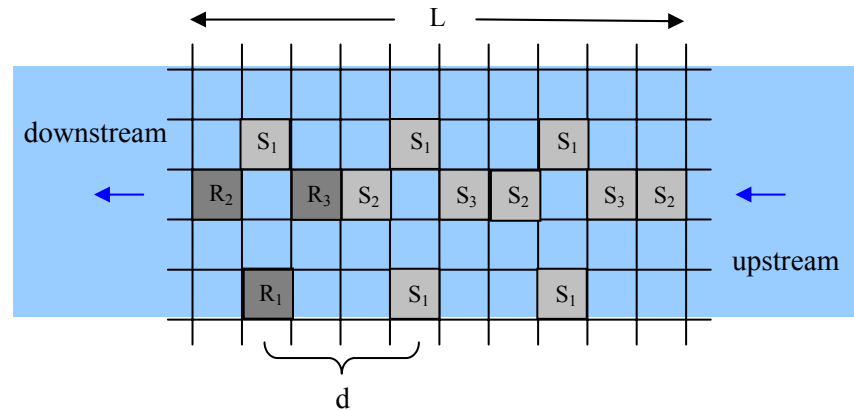


Figure 4. A systematic sampling design. In this example, a L meter long reach of stream is subdivided into 50 possible sampling units. Three random starting points are selected to serve as starting locations (dark gray cells with letter R). Additional quadrats are selected at d meter intervals. All quadrats that originate from a random starting point are part of one systematic sample. The three systematic samples are depicted as light gray squares with letter S . The subscript of the letter S corresponds to the random starting point. (Modified after Strayer and Smith 2003).

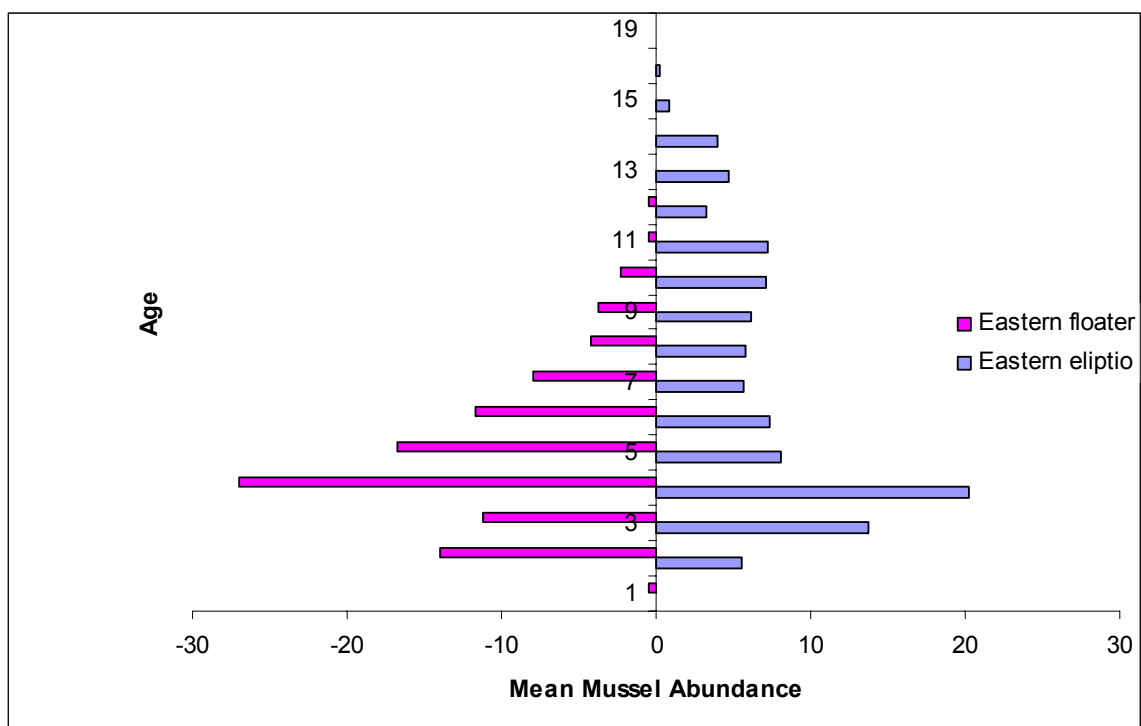


Figure 5. Age structure of mussels sampled during Summer 2008

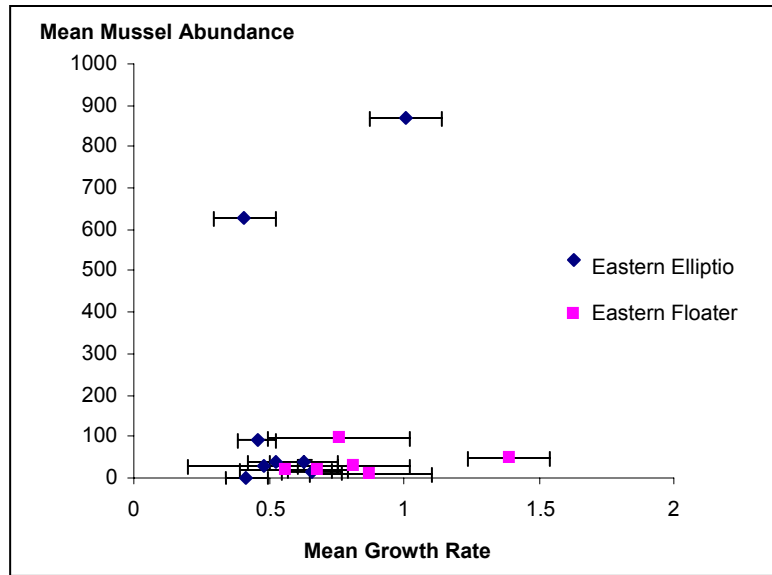


Figure 6. The relationship between growth rate and abundance of mussels sampled during Summer 2008.