THE DEVELOPMENT AND EVALUATION OF A FRESHWATER MUSSEL SAMPLING PROTOCOL FOR A LARGE LOWLAND RIVER

by

JASON RAY MEADOR

Under the direction of James T. Peterson

ABSTRACT

Freshwater mussels are among the most imperiled aquatic species within the southeastern United States. Mangers are faced with the task gathering information via monitoring, and making decisions based on available information about local mussel populations. I gathered data on mussel behavior, demography, distribution, and detection to develop a cost-effective protocol for monitoring freshwater mussel populations within the Altamaha River. Surface abundance, survival, occupancy, and detection varied spatially, temporally, and among species. I then developed sampling stratum within mesohabitats based on empirical data and evaluated the efficacy of several sampling protocols via simulation. Spatial and temporal variation among species emphasize the importance for properly estimating and evaluating habitat based on use and detection and suggest refraining from raw count indices.

INDEX WORDS: Altamaha River, Freshwater Mussels, Occupancy, Abundance, Estimation, Robust Design, Migration Patterns, Sample Design, Detection

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CHAPTER 1

INTRODUCTION

Freshwater mussels [Family *Unionidae*] are a crucial component of aquatic ecosystems. Being primary consumers, they are considered important keystone species serving as a food source for specific mammalian, avian, and fish species (Parmalee and Bogan 1998). Furthermore, mussels can be useful biotic indicators due to their sensitivity to anthropogenic degradations, such as point and non-point source pollution, and sedimentation (Neves et al. 1997). However, mussel reproduction requires species-specific host-fishes (Hoggarth 1992) that can cause them to be sensitive to factors that also affect their hosts. Consequently, anthropogenic disruptions that affect mussel hosts have caused the decline of many freshwater mussel populations within the southeastern United States (Neves et al. 1997).

Since enactment of the Endangered Species Act (ESA) in 1973, 27% of the 297 known mussels species within the United States have been listed as endangered, threatened, or extinct, with an additional 43% identified as species of special concern (i.e. low densities, restricted distribution) but not federally protected (Vaughn and Taylor 1999). The southeast United States contains the highest diversity of mussel fauna in North America, with 91% of the known species occurring in Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, and Virginia (Turgeon et al. 1988; Neves et al. 1997). Currently, 75% of those species are believed to be in decline (Neves et al. 1997). This includes over half (66%) of Georgia's approximately 122 native freshwater mussel species being either

state or federally listed or considered extirpated from the state; of these species 12 are considered globally extinct (Paul Johnson, Alabama Department of Conservation and Natural Resources, personal communication). Three of these imperiled mussels are found in the Altamaha River, a large coastal river in Georgia. The Altamaha spinymussel (*Elliptio spinosa*; Lea 1836) is listed by the state of Georgia as endangered and recognized as a candidate for federal listing under the U.S. ESA. The Savannah lilliput (*Toxolasma pullus*; Conrad 1838) is classified as a federal species of concern because of its global rarity and is considered critically imperiled in Georgia whereas the Altamaha arcmussel (*Alasmidonta arcula*; Lea 1838) is listed as state threatened (GADNR).

The conservation and restoration of mussel fauna requires the development of efficient and effective management plans. To be effective, planners need information on the current status and distribution of mussel populations combined with a means to evaluate the effectiveness of management actions. Such information is particularly difficult to collect in large rivers, such as the Altamaha River, where flow, depth, and visibility restrict the use of common and cost-effective sampling methods, such as wading and snorkeling. Currently, there is no sampling protocol for estimating the status and distribution of mussel populations in large riverine ecosystems. Therefore, the purpose of this study was to develop and evaluate different sample designs for estimating the status and distribution of mussels in large rivers.

CHAPTER 2

OBJECTIVES

The ultimate goal was to develop a cost-effective sampling protocol for monitoring the distribution and status of freshwater mussels within the Altamaha River. Therefore, I developed and evaluated various techniques for sampling mussel assemblages in the Altamaha River with the following objectives:

1) Develop sampling stratum for the Altamaha River with respect to mussel distributions based upon species-specific habitat selection.
2) Develop sampling designs for estimating the distribution and status (e.g., abundance, and density) of mussel populations.
3) Evaluate the relative effort and effectiveness of the different sampling protocols using a combination of data and model simulation.

CHAPTER 3

LITERATURE REVIEW

The development of effective and cost-efficient sampling protocols requires an understanding of the biology of freshwater mussels. For example, mussels move vertically within the river bed such that only a portion of mussel populations are near the surface and vulnerable to capture (Amyot and Downing 1997). The vertical movement can be related to factors such as reproduction, feeding, water temperature, and daylight duration (Amyot and Downing 1997; Amyot and Downing 1998; Watters et al. 2001). Thus, mussel habits (e.g., reproduction, feeding) and life history requirements should be considered when developing sampling protocols. Moreover, knowledge of mussel distribution may facilitate sampling efforts by allowing for stratification of habitat types; which ensures sampling of all habitat types while allocating weighted effort to more productive areas. Furthermore, careful planning must be considered when designing a sampling plan that maximizes statistical power/inference while minimizing cost. Sampling difficulties are further magnified as spatial coverage becomes large, such as in large rivers.

Life History

Most freshwater mussels are relatively long lived, surviving for decades or even centuries (Strayer et al. 2004; Vaughn et al. 2004), which adds difficulty when studying their life history stages. While it is believed that mussels share similar life histories, there is little species-specific

information available on specific characteristics, such as longevity, reproductive strategies, and larval host fish (Araujo et al. 2005).

The earliest life stage of a mussel begins as a larval ecto-parasite of fish, known as glochidia. Attached to the gills, fins, or skin of a host for a brief time, glochidium transform into individual juvenile mussels, detach from their host, and settle to the streambed. The clumped distribution of new recruits then is related in part to the habitat use of their respective fish hosts (Haag and Warren 1998; Vaughn and Taylor 2000). Moreover, the mobility of juvenile mussels is believed limited once they settle at a location, so that survival depends on local environmental factors, such as food availability and the presence of stable, yet permeable, substrate (Vaughn and Taylor 2000). Juvenile mussels remain completely endobenthic for a few years before becoming epibenthic where they are more likely to be detected by visual or tactile methods (Strayer et al. 2004). It is believed that juvenile mussels, while buried, acquire nutrients from the sediment with their foot, known as pedal feeding (Yeager et al. 1994).

The time required for maturation is thought to vary between mussel species. Mussel diet changes as they mature leading to filter feeding at the surface on suspended particles such as phytoplankton, protozoan, detritus, and bacteria. Therefore, mussels detected at the surface of the streambed consist of both late-stage juveniles and mature life history stages. However, it also has been suggested that juvenile and adult mussels can pedal feed during prolonged endobenthic periods (Yeager et al. 1994) making them difficult to detect. Some factors such as water temperature, suspended particle size, and bivalve size have been found to influence mussel clearance capacity suggesting unique requirements and behaviors for each species (Silverman et al. 1995; Vaughn et al. 2004). The rate at which juvenile mussels mature into reproductive

adults also is generally unknown and may range from less than 1 year to 8 years depending on the species (Haag and Staton 2003).

During spawning season, which varies by species and location, mussel eggs are contained within the marsupium of the female mussel and are fertilized by sperm filtered from the water column (Haag and Staton 2003). This type of reproductive strategy suggests that males should be located within close upstream proximity to the female for successful fertilization and that mussels form aggregated colonies to improve the chance of gamete transfer (Downing et al. 1993). Furthermore, both sexes need to be at the surface to disperse (male) and receive (female) gametes, suggesting that this period is when most mussels can be detected at the surface (Watters et al. 2001). Once fertilized, glochidia form within the gills of the female, and are brooded until mature. However, seasonal and annual spawning periodicity in unknown for many species (Strayer et al. 2004) and may not occur every year (Moles and Layzer 2008). Therefore knowledge of factors influencing spawning season and periodicity limit the ability of biologists to predict when the greatest proportion of the population will be at the surface and vulnerable to capture.

There are three known ways that females infest glochidia on host fish (Haag and Warren 2003). Mussel species that use a range of host-fish species are known as generalists and typically broadcast glochidia in a mucus web (Haag and Warren 1998). In contrast, some mussel species require specific host-fish species (specialist) and may use methods geared towards enticing specific fish to strike a glochidia sack. The first method uses a modified mantle margin as a 'lure' that resembles a fish or invertebrate. The second method requires the female to release glochidia in packages resembling food of the target fish species such as fish eggs, or larval insects or fishes (Haag and Warren 2003). Therefore, gravid females must to be at the

sediment surface to deploy either method of glochidia infestation (Watters et al. 2001). In addition to the spawning season, some studies observed that both male and female mussels remain on the surface during the period when glochidia is released, suggesting that mussel detection is greater during this period (Watters et al. 2001).

During the winter season, most mussel species undergo a 'dormant stage' where they are endobenthic. Vertical mussel migration during this period has been observed to show a direct response to decreased temperature, duration of daylight, or possibly a combination of both (Amyot and Downing 1997). However, the reason for the dormant stage is unknown.

It is easier to capture epibenthic mussels, therefore sampling during periods when most mussels are at the surface reduces bias associated with low capture probabilities. Although spawning, glochidia release, and filter feeding takes place at the substrate surface, the entire population does not surface simultaneously. The ratio of epibenthic mussels to endobenthic is believed to vary sexually, temporally, by species, and age. Both bimodal (having two distinct epibenthic periods per annum) and unimodal, (having one continuous epibenthic period per annum) vertical migration patterns have been observed among species sharing similar reproductive seasons, and even brief temporary emigration has been recorded within species (Amyot and Downing 1997; Watters et al. 2001). Thus, multiple samples will improve the probability of detection, and if specific reproductive habits are ambiguous or unknown collecting samples through time will presumably increase the likelihood that sampling is conducted during the time when the mussels are most likely at the surface.

Factors Influencing Mussel Distribution and Community Structure

By understanding the distribution and structure of mussel communities, greater sampling effort can be focused on areas that are more likely to contain targeted species. I hypothesize that

species presence within a given area is based upon scale-specific hierarchy of determinants or 'constraints' (Figure 1). At the upper level (largest spatial extent), mussel distribution is influenced by geomorphic history. For example, mussel assemblages in the Altamaha and Apalachicola Rivers contain 16 and 31 species respectively. Although both are coastal rivers with basins in Georgia, the Altamaha is an Atlantic slope drainage whereas the Apalachicola drains in to the Gulf of Mexico; hence they have entirely different species pools. Further, I hypothesize that mussels are distributed through a spatially nested system of constraints from large to small scales, and the development of efficient and cost-effective sampling designs requires an understanding of each constraint.

At the next level, sub-units of the river network, defined here as a reach, contain additional factors that may influence mussel distribution. As previously stated, the location that juvenile mussels settle is hypothesized to be related to the specific habitat use of their host fish and if they are able to survive given the environmental conditions where they drop off the host (Vaughn and Taylor 2000). This requires knowledge of the factors influencing the distribution and structure of fish communities. At the reach level, stream size and channel gradient influence the physical habitat structure and environmental stability of a stream section, which in turn influences the structure of the resident fish community (Vannote et al. 1980; Junk et al. 1989).

Mussel distribution may be related to specific habitat types or meso-habitat channel units (e.g., pools, riffles). Although highly variable, factors such as sediment composition (van Cleave 1940; Harman 1972; Vannote and Minshall 1982; Stern 1983), current velocity (Salmon and Green 1982; DiMaio and Corkum 1995; Hornbach et al. 1996), juvenile mussel distribution (Morales et al. 2006), and depth (Salmon and Green 1982; Stern 1983; Hornbach et al. 1996) may be useful for determining mussel distribution and community structure. Host fish habitat

use may also influence mussel distribution within a reach since they are attached during the parasitic glochidic stage (Haag and Warren 1998; Vaughn and Taylor 2000). Like mussels, fish also relate to various habitats depending upon preferences and tolerances. Under these assumptions, an aggregated or clumped mussel distribution may be due, in part, to the characteristics that influence fish communities for each particular host (van Cleave 1940; Strayer et al. 1994). When a mussel detaches from a host fish and settles to the streambed, a permeable substrate is required to keep from being re-suspended and displaced. Additionally, mussels require nutrients for reproduction, growth, and to sustain life, thus flow serves as a medium for transporting food. Therefore, mussel distribution within a reach depends on the suitability of the environment for mussels to live and host fish to be present. The lack of one or both criteria results in the absence of mussels for that area.

When developing stratum, one must be mindful that physical attributes of the classification units should be relatively homogeneous and predictable, and strata should accurately depict groupings of physical attributes that influence the distribution and abundance of target taxa (Hawkins 1993; Peterson and Rabeni 2001). Meso-scale factors such as sediment composition or current velocity are useful for predicting mussel occupancy or species composition, but are believed to be poor predictors of abundance (Lewis and Riebel 1984; Holland-Bartels 1990; Strayer 1993; Brim Box et al. 2002), which may limit their usefulness as strata. Alternatively, reach-scale factors such as stream size are better predictors of abundance, richness, and diversity (Strayer 1993), but has limited use as strata in large rivers with low variability in relative size. I hypothesize that hierarchical system in which meso-habitat types are nested within reaches (Figure 2) may be useful as sampling stratum with less variance than meso-scale factors alone (McRae et al. 2004).

Sampling Protocols

The purpose of mussel sampling protocols is to evaluate the population status within the environment. An effective protocol assists managers by helping them to determine the status of the population while minimizing costs and maximizing the ability to detect a change in status. However, there is a trade-off between accurate estimation and cost (MacKenzie et al. 2006). I define accuracy as a measure of precision and bias, where accuracy is proportional to precision and inversely related to bias. Precise estimates have relatively low variance associated with them. Therefore to improve precision, a larger sample size may be necessary to gain a less variable estimate; thus increasing the cost of the sampling design. Bias is a measure of "truth" where an unbiased estimate is a close representation to the actual population. Bias is a common factor when sampling mussel populations because of the inability to completely sample the entire population, and increases proportional to the difficulty associated with capture or detection due to rarity or elusiveness. For example, the greater the proportion of a mussels available for capture (i.e. at the surface) will yield an estimate that is closer to the actual population size. While bias is reduced through the use of statistical estimators, precision can be increased through increasing effort (number of samples) and through the sampling design.

Sampling techniques can be categorized into one of two types, index and estimation. An index is based on direct count of the number of species, individuals in a population, or number of locations occupied and often assumes a linear relationship to the true value (Strayer et al. 1997). Index sampling is a commonly adopted practice for freshwater mollusks, for example timed searches measure a catch per unit effort (CPUE), usually expressed as the number of individuals per hour. Index methods are preferred because they are easy and inexpensive to execute. However, index estimates are likely inaccurate because the detection of all individual and species

is usually not possible and the ability to detect (count) is often influenced by the same factors affecting mussel populations. For example, the endobenthic behavior of mussels will result in incomplete capture and bias the estimate of the true population by using indices from surface counts.

Estimation uses statistical models to estimate population parameters (i.e. abundance, occupancy, survival, etc.) based on the gathered data. Typically, such designs are more costly because of the time required for specific designs, whether taking spatial measurements within a site, equipment set-up (i.e. transects, quadrats), sampling techniques (i.e. excavation), spatial requirements (i.e. number sites and samples per site required), or temporal requirements (i.e. repeat visits). Estimation may be more costly, but careful planning of the design will result in clearly defined estimates based upon statistical analysis. Instead of assuming that individual counts within a sample follows a direct linear relationship of the population, the status is estimated based on a mean and variance gathered from samples with a probability of incomplete capture.

In Georgia there is currently no single standardized protocol for mussel sampling, resulting in a haphazard manner of determining sampling methods by each individual collector. The most common sampling strategies are timed searches where a crew searches a specified area for a given amount of time and catch is estimated as CPUE. This method is known to severely bias abundance and does not account for incomplete detection (Williams et al. 2002). Species presence estimates are also biased by index sampling because detection of a species depends on capture probabilities and abundance.

To account for these biases, previous mussel designs have used adaptive sampling, double sampling, stratified sampling, two-stage sampling, as well as model-based inference such

as distance sampling and mark-recapture models (Strayer and Smith 2003). A simple example of an estimation design is double sample, conducted through the use of excavations. By sampling along the surface within a site, then excavating a sub-sample of those units allows for a ratio of surface and sub-surface individuals to be applied to total surface count, resulting in a more precise estimate of density or abundance and reducing observation bias (Smith et al. 2001).

Unfortunately there are few mussel sampling designs that use estimation (Dorazio 1999; Smith et al. 2001; Brim Box et al. 2002; Villella et al. 2004). Moreover, the studies were applied to relatively shallow streams where sampling could be conducted by more convenient methods such as wading or snorkeling, thus their applicability is uncertain for larger and deeper systems such as the Altamaha River. Due to limited designs for mussels, it may be necessary to incorporate aspects from studies on animals that display similar characteristics. Vertical migration by terrestrial salamanders have been observed where the population available for sampling represents a subset of the total population inhabiting a given area (Bailey et al. 2004a), similar to freshwater mollusks. Additionally, crayfish also display similar characteristics by burrowing, thus rendering a portion of the population unsusceptible to capture at a given time (Rabeni et al. 1997).

CHAPTER 4

METHODS

Study Site

The Altamaha River Basin, located in the southeast region of the United States, is the largest drainage system in Georgia and one of the largest along the east coast, covering nearly 37,000 km^2. The river is formed by the confluence of the Ocmulgee and Oconee Rivers (Figure 3), in the Coastal Plain physiographic province (EPD 2003), and flows east 215 river-km (rkm) until it enters the Altamaha Sound and empties into the Atlantic Ocean. The mainstem Altamaha is unimpounded with the only impoundments within the upper watershed, located on the Oconee and Ocmulgee Rivers. The Altamaha River averages 50-70 m in width and 2-3 m in depth with some areas in excess of 5 m (Heidt and Gilbert 1978), with an average gradient of 0.13 m per km (EPD 2003) and average discharge of 381 m^3/s near Doctortown, GA (Rogers and Weber 1994). The streambed is comprised predominantly of sand with large woody debris distributed throughout the river via erosion and deposition. The Altamaha River also received large amounts of fine sediment from historic agriculture processes during the 1800s and early 1900s (EPD 2003).

I stratified potential sample sites along the Altamaha River from the confluence of the Oconee and Ocmulgee rivers downstream to the Altamaha Sound based on habitat type. Habitats were based on hydrogeomorphic channel units as defined as: slackwaters, glides, pools, and swiftwaters. Slackwater habitats are zones with low velocities and bedload deposition that

form along the shoreline (edgewater) or in areas sheltered from the main channel by shoreline outcroppings or islands (backwater, forewater, and side-channel; Peterson and Rabeni 2001). Glide habitats are areas with moderate current velocities and depth with respect to other hydraulic units. Glides can be associated with transition zones between pools and slackwaters. Pools form during high flows and occur: 1) in the main-channel and usually contains the thalweg, 2) on alluvial sediment at channel bends (lateral pools), or 3) with localized scouring around shoals or large woody debris (obstruction pools) (Peterson and Rabeni 2001). Swift water habitats are areas of relatively high current velocities with respect to other areas of the river. Swift water is formed when the river channel constricts or concentrates the flow of the water to a narrower path (runs, thalweg).

Demographic Parameters

Ultimately, mussel abundance and on occasion, survival are the specific parameters of interest in monitoring programs to be used by managers when evaluating the influence of past activities or predicting the effects of future decisions. Due to the longevity of mussels, useful annual survival estimates may take many years to estimate and due to time limitations, were not the main focus of this study. However, because not all mussels present are captured and counted during sampling, parameters such as capture probability (p), are needed to adjust for sample data for missed mussels. Moreover, an additional parameter is needed to account for the temporary endobenthic behavior of mussels, defined as temporary emigration (γ), which leads to an absolute non-capture (p=0) for mussels beneath the surface. To estimate these parameters, previous studies have conducted extensive excavation of substrate (e.g., Smith et al. 2001), or use a capture-recapture design (Villella et al. 2004) that included multiple visits to each site over time.

I conducted a preliminary study during 2005 in which I sampled mussels within multiple 0.25 m^2 quadrats using tactile methods followed by excavation of the quadrat according to methods suggested by Smith et al (2001). I found this approach impracticable in habitats that were deep or had moderate to swift current velocities. In addition, the approach was very time and work intensive which would have severely limited the number of evaluations that could have been conducted. Therefore, I decided to use a capture-recapture design to estimate demographic parameters.

Closed population estimators yield values of abundance and capture probability, but assume equal capture probabilities and no births, deaths, emigration, or immigration throughout the entire study (Pollock et al. 1990). Problems arise when mussels move vertically within the substrate between studies, and capture probabilities are not equal among endo- and epi-benthic mussels leading to biased estimates. Open population estimators allow for demographic change between studies and yield estimates of initial abundance, survival between periods, emigration, and capture probability. Although allowing for emigration, assumptions are such that all emigration is permanent; when a tagged mussel burrows and then returns to the surface, this assumption is violated, potentially biasing estimates of abundance (Pollock et al 1990). The Robust Design estimator (Pollock 1982) uses both open and closed-population estimators to relax assumptions about detection and emigration. Because of the burrowing behavior of mussels and the size and variation of habitat conditions on the Altamaha River, the Robust Design was the only method available to estimate the parameters of interest without violating assumptions.

The Robust Design estimates abundance, survival, capture probability, and emigration. Vertical migration patterns of burrowing mussels otherwise referred to as temporary emigration

can be estimated by relaxing permanent emigration assumptions (Pollock 1982). The design is based on repeated sampling occasions across secondary sampling periods nested within primary periods (Figure 4). A secondary period is a relatively short time interval between sampling occasions that assumes that the population is closed and no mortality or emigration occurs. Each primary period is a longer time interval containing a set of secondary periods and allows the population to be open to migration, mortality, and recruitment.

Sampling Procedure

Six sites were randomly selected (2 slackwater, 2 pool, and 2 swiftwater) in the mainstem Altamaha given that both *Lampsilis dolabraeformis* and *L. splendida* occur within the site (Figure 3, Appendix A). These initial species were selected because they are commonly found in all habitat types, but not so abundant that excessive time was spent on processing. Primary periods were defined as six-week intervals or as soon as feasible in the event of unsafe conditions (high discharge). Within each primary period, samples were collected during three secondary periods that ranged from 1-24h between sample periods. Systematic sampling should provide adequate spatial coverage and is useful for sampling clustered or rare populations (Smith et al. 2004; Thompson 2002). To ensure equal coverage, I divided the habitat area into three sub-units (upper, middle, lower) and assigned three random starting points in each sub-unit with respect to the origin (Figure 5) resulting in nine samples taken per secondary period. The starting point corresponded to the distance (in meters) upstream from the lower-most edge of the habitat. From each point, transects (length = 10 m, width = 1 m) were placed perpendicular to flow. Sampling was conducted as tactile searches along the sediment surface. In slackwater and shallow swiftwater habitats, mask and snorkels were used, whereas SCUBA equipment was used in areas with a depth greater than 1.5m, or where conditions were too hazardous to sample using

a mask and snorkel (pools and thalwegs). All captured mussels were placed in a mesh bag until sampling was completed. Temporal and spatial habitat factors such as: date, location (Global Positioning System), current velocity (Geopacks© flowmeter), and temperature also were recorded prior to or immediately following sampling.

Captured mussels were identified, shell length (posterior to anterior margin) measured to the nearest millimeter, and tagged or recorded as a recapture if a tag is already present. Tagging was conducted by affixing a Hallprint© shellfish tags to each valve using cyanoacrylate (Krazy Glue©). This method of tagging freshwater mussels provides a good long-term marking method (Lemarie et al. 2000). Both valves were tagged (double-tagging) to measure tag retention (following Reinert et al. 1998) and the probability of losing one (t_1) or both tags (t_2) was estimated as:

$$Pr[t_1] = l/N*(1-(l/N))$$

$$Pr[t_2] = (t_1)^2$$

where l is the number of mussels observed with tag loss and N is the total number of tagged mussels. Any recovered (dead) tagged shells encountered while sampling were collected and retained as vouchers. Determination of gravidity periods for species was not the main focus of this project, but I believe that reproductive behavior may influence the proportion at the surface. Therefore, I checked most individuals of all species for inflated gills (indicative of spawning or brooding females) while sampling and during tagging; however neither individual status nor total count were recorded. All collected mussels were then uniformly hand-placed back within the site, orienting anteriorly into the sediment.

Statistical Analysis

I constructed 16 Robust Design models for each species (Table 1), each model represented *a priori* hypotheses regarding the effects of habitat type on survival, seasonal changes on temporary emigration, and observer variation or habitat characteristics on detection. Due to the longevity of mussels (Strayer et al. 2004; Vaughn et al. 2004), survival was modeled as constant over all time periods, but differing by strata or remained constant over strata (Table 1; Table 2).

Models were constructed assuming random temporary emigration ($\gamma_i'' = \gamma_i'$) rather than Markovian emigration where *i* depends on the state (at or beneath the surface) of the mussel at time *i*-1 (Bailey et al. 2004a). Studies of migration have suggested that mussels respond to temperature, day-length, or both (Amyot and Downing 1997; Watters et al. 2001). Candidate emigration models consisted of constant and seasonal emigration alternatives (Table 1; Table 2). Water temperatures were used to define seasons *a priori* with emigration being modeled under a binary covariate corresponding to the respective season: Summer > 25ºC, 15ºC < Fall < 25ºC (with a negative change in temperature from previous time period), Winter < 15ºC, 15ºC < Spring < 25ºC (with a positive change in temperature from previous time period) (Table 2).

I constructed models of mussel capture probability assuming 1) constant capture probability among observers through time, 2) capture probability varying by habitat, 3) capture probability varying in relation to proportion of experienced observers, and 4) capture probability varying in relation to presence of large woody debris (LWD) (Table 1; Table 2). Experienced observers were defined as any participant who had >40h mussel sampling experience prior to the sampling occasion. Proportion of experience was calculated as the ratio of experienced observers to total observers for that sampling period. Models were based three levels of

proportion of experienced observers: low (<67%), mid (0.67-0.99%) or high (100%) (Table 2). Two sites (downstream pool, upstream swiftwater) contained large amounts of LWD (fallen trees; >0.75m diameter; encountered >0.3 of all transects) making it difficult to maneuver and thoroughly sample the area within each transect. Density of LWD was represented as a binary code with sites having LWD receiving a value of '1'. Based upon preliminary analysis with the data, all models assume that capture and recapture probabilities for those time periods were equal (i.e., no trap response).

Each of the 16 models was fit using Program MARK (White and Burnham 1999). If shells were recovered for a particular species, I included a recovery model (Barker 1997) known as Barker Robust Design to incorporate recovered shells (known mortality) into survival estimates. Recovery models include four additional parameters: the probability of recovering a dead shell (r), the probability that the mussel survives and is resighted alive between periods (R), the probability that a mussel is resighted alive between periods given that it died sometime before the following period and was never recovered (R'), and the probability that a mussel available to capture remains available to capture the following period (F). Therefore, to avoid unnecessary parameterization, I used the standard Robust Design if no shells were recovered for a particular species. For species with recovered shells I constructed models assuming R and R' constant and r varying by habitat because 1) the use of tactile and visual effort given to shallow habitats (slackwaters), and 2) the greater likelihood of displacement via greater current velocities in pools and swiftwaters. Fidelity (F) was assumed constant because estimates of temporary emigration (γ) accounted for capture availability.

I initially used Akaike's Information Criteria (AIC; Akaike 1973) to evaluate the relative fit of candidate models. During initial model fitting, I found that several of the candidate models

could not be fit using maximum likelihood methods; hence I had to fit the models using Monte-Carlo Markov Chain (MCMC) methods implemented in program MARK. This necessitated the use of another information theoretic approach known as Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002) in place of AIC. Although there are currently no available guidelines for evaluating DIC, I assessed model fit using DIC values and calculated weights w_i using the DIC values in place of AIC to compare models following Burnham and Anderson (2002). Borrowing Royall's (1997) $1/8^{th}$ rule, models with weights within $1/8^{th}$ of the value of the best fitting model (lowest DIC value) were considered as part of a confidence set of models. Therefore, influences on parameter estimates were reported only for those models within the confidence set. I based all inferences on parameter estimates from the best-fitting model and assessed precision by calculating 2.5% and 97.5% Bayesian credibility limits (BCL).

Using derived estimates of parameters, as described above, additional information was estimated that may have a greater effect on management actions. Since the capture probability ($\hat{p}$) given in program MARK, is conditional on mussels being present at the surface, an effective capture probability ($\hat{C}^{o}$) can be estimated to account for mussels not at the surface ($\hat{p} = 0$) following Bailey et al. (2004b) as:

$$\hat{C}_i^{o} = \hat{p}_i(1-\hat{\gamma}_i)$$

where $\hat{\gamma}_i$ is temporary emigration during primary period *i*. Estimates of $\hat{C}^{\circ}$ were then used to evaluate the efficacy of various sample designs, described below.

Estimated mussel abundance for each primary occasion is the estimated number of mussels at the surface during the sample period. To estimate the size of the total population (i.e., those at the surface and below), I assumed that differences in abundance between periods were due to the vertical orientation and that few if any mussels were displaced into or out of each

sample unit. Assuming that the temporary emigration (γ) estimates the proportion of mussels below the surface and (1-γ) represents the proportion of mussels at the surface, the total population ('superpopoulation'; $\hat{N}^{o}$) can be estimated following Bailey et al. (2004b) as:

$$\hat{N}^{\circ} = \frac{\hat{N}}{1 - \hat{\gamma}_i}$$

where ($\hat{N}$) is the surface abundance during the sixth primary period (summer) and ($\hat{\gamma}_i$) is temporary emigration during primary period *i* corresponding to the summer season. Superpopulation estimates were then used to evaluate the efficacy of various sample designs, described below.

Distribution and Detection

When operating over a large spatial scale such as an entire watershed, monitoring changes in population abundance or demographic parameters can be cost prohibitive. One useful alternative would be to monitor changes in the distribution of a species over time. The distribution of a species can be used to quantify the status and trends of populations. More specifically, the rates of change in distributions over time are important to managers when assessing population stability (MacKenzie et al. 2006). Temporal variations in distribution also are related to metapopulation dynamic processes (Hanski 1999), such as local extinction and colonization. Therefore, although abundance is not directly estimated, the status of a large-scale population (i.e., metapopulation) can be evaluated by estimating changes in distribution or metapopulation dynamic rates. For example, declines or increases in overall distribution would indicate changes in the status of the species. Trends or changes in distributions can be monitored by estimating occupancy through time.

One goal of this study was to develop sampling stratum. Stratification allows for biologists to allocate sampling effort efficiently. A useful stratum will group or stratify potential sample sites based on characteristics, such as the likelihood that a species occurs within the site. If the distribution and resource affinities of a species of interest are known, these specific variables can be used to define strata. However, this information was not available for mussels in the Altamaha. The Robust Design that was used to estimate demographic and capture probability parameters, however, required intensive sampling effort within a single site and was too labor and time intensive to use for estimating distribution and habitat affinities of mussels. Therefore, occupancy estimation also was used to evaluate mussel distribution in the Altamaha River.

Occupancy estimation is based on detection and non-detection of individuals within a site. When sampling mussels, three scenarios are possible (1) at least 1 individual was captured indicating that the sample site is occupied, (2) no individuals were captured and the site is unoccupied, or (3) no individuals were captured but the site is occupied, hence the importance for estimating detection. The proportion of area occupied or probability of occupancy is estimated as the ratio of the number of sites an individual is detected and the number of sites sampled given a probability of detection at the site. Detection is a function of the number of samples collected at a site, the probability of capturing a mussel, and the abundance of mussels at the surface within the site. Occupancy estimators assumptions include: 1) the population is closed to emigration/immigration and births/deaths, 2) detection is independent among sites, and 3) species are correctly identified (MacKenzie et al. 2006).

Sampling Procedure

Due to limited access along the river, sample reaches were chosen by randomly selecting boat launches and traveling upstream. Within each reach, sample sites were chosen by randomly selecting a habitat stratum and a random number between 1 and 3, corresponding to the order of encounter from the current location. For example if 'edgewater' and '3' were randomly chosen, the third edgewater from the boat ramp position would be sampled. Due to safety precautions, complete random selection of habitat stratum was not possible during each sampling occasion due to lack of equipment (e.g., SCUBA) or lack of trained personnel.

Within each sample site, systematic sampling should provide adequate spatial coverage and is useful for sampling clustered or rare populations (Smith et al. 2004; Thompson 2002). To ensure equal coverage, I divided the habitat area into three sub-units (upper, middle, lower) (Figure 5) and assigned nine random Cartesian coordinates in each sub-unit with respect to the origin. The origin, coordinate (0,0), was located in the habitat at the downstream end closest to the shoreline. Each coordinate corresponded to the distance (in meters) from the origin. For example a random coordinate of (5,6) indicated the point to be 5m upstream and 6m away from the edge of the origin. From each point, transects (10m X 1m) were placed perpendicular to flow. Mussel sampling was conducted as tactile searches along the sediment surface at each transect. In slackwater, glides, and shallow swiftwater habitats, mask and snorkels were used when depths were approximately between 0.7 and 1.5m, whereas SCUBA equipment was used in areas with a depth greater than 1.5m, or where conditions were too hazardous to sample using a mask and snorkel (pools and thalwegs). All captured mussels within each sample (transect) were counted, identified to species, and returned to the water within their respective capture location.

Each transect was treated as a sample within a site during occupancy estimation, therefore detection estimates are estimated per transect. To meet occupancy estimator assumptions, all transects were sampled within two hours at a site. Most sample sites were visited once, however a sub-set of sites were randomly selected and revisited again with an additional nine transects samples to determine if transect detection estimates varied between visits.

Prior to or immediately following mussel sampling, habitat characteristics were measured at each site. Spatial and temporal habitat measurements included date, location (Global Positioning System coordinates), total habitat area in meters, water temperature, and juxtaposition with respect to adjacent habitat hydrologic units. Physical habitat components were measured such as: depth of stream, current velocity (Geopacks flowmeter), and substrate classification. Substrate composition was visually and tactilely estimated and categorized according to particle diameter as follows: fines (0-0.5mm), sand (0.5-1mm), and coarse (>1mm). Sediment compactness was estimated using visual and tactile methods also and classified as either firm (compact) or not.

Statistical Analysis

I evaluated the relative plausibility of 28 occupancy models for each species (Table 3), each model represented *a priori* hypotheses regarding the effects of physical and spatial site-specific covariate effects on detection and occupancy. A 'global' model was developed consisting of all effects and interactions from site specific covariates corresponding to hypotheses described hereafter. Detection was modeled as constant among all sites, varying among sites due to the use of snorkels, or proportion of area sampled (area sampled/total habitat area) (Table 3; Table 4). I also modeled detection as varying between sample occasions at

revisited sites to test for temporal effects. Candidate models also were constructed based on site-specific covariate effects on occupancy (Table 3; Table 4). These models were based on previous studies and included occupancy as: constant; a function of depth, current velocity, and their interaction (Salmon and Green 1982; Stern 1983; DiMaio and Corkum 1995; Hornbach et al. 1996); influenced by sediment composition and compactness of fines or coarse substrate (van Cleave 1940; Harman 1972; Vannote and Minshall 1982; Stern 1983); or a function of the location of the habitat with respect to adjacent pool or sandbar habitats. Covariates of depth and current velocity were modeled on a continuous scale, whereas substrate and juxtaposition covariates were represented with a binary code that the site contained the variable (1) or not (0).

Candidate occupancy models were fit for each species using the occupancy estimator in Program MARK (White and Burnham 1999). I used an information theoretic approach (Burnham and Anderson 2002) and Akaike's Information Criteria (AIC; Akaike 1973) to evaluate the relative fit of candidate models to the global model and calculated Akaike weights (w_i) that range from 0 to 1, with the most plausible model having the greatest w_i (Burnham and Anderson 2002). Models with weights that were within $1/8^{th}$ of the value of the best fitting model were considered as a confidence set of candidate models (Royall 1997). Parameter estimates were reported only for those models within the confidence set. I based all inferences on parameter estimates from the best-fitting model and assessed precision by calculating 95% confidence intervals.

Alternative Sampling Designs

Designing a sampling protocol requires some measure to compare the efficacy of one design to another. By evaluating multiple designs, managers can choose the design that will provide them with the most useful information within a given budget. For example, given finite

sampling resources is it more beneficial to focus greater effort (i.e., number of transects) at fewer sample sites, or increase the number of sites with minimal effort? For managers to answer those types of questions and choose the most effective design, it is necessary to have: (1) a goal or scope for the project (i.e. what parameters need to be estimated), and (2) information on the trade-offs associated among potential designs. The objective of this section will focus on the latter by evaluating the efficacy of various design types in detecting changes in mussel populations.

I conducted two sets of simulations to examine the influence of sample design and metapopulation dynamics on the ability to detect changes in the population. In the first scenario, I assume that abundance declines gradually over time because of declining habitat conditions or decreased recruitment. Sampling success was evaluated on the ability to detect a population change in either: (1) abundance or (2) occupancy over time. Models began with a specified number of patches (a site with a finite area having specific habitat characteristics) to be sampled and randomly assigned mussel presence to each based on a specified habitat-specific initial occupancy rate. For unoccupied sites, all samples were assigned non-detection. The occupied sites (abundance ≥ 1) were assigned a specified initial abundance. Each site then was sampled as the random collection of nine samples (i.e. transects) per site for all simulations. To incorporate heterogeneity in capture probabilities among sample units within patches, an effective capture probability was randomly assigned for each patch using a beta distribution with specified mean of 0.1 for models during each sampling season (for two-season sampling, the mean effective capture probability for the second season was 0.2), with a coefficient of variation of one (100%). These values were based on empirical data from the demographic study. Sampling then occurred

at five year intervals for a duration of 20 years. For each time step, changes in the population were simulated as a simple linear function of time as:

$$P_t = P_0 - t*C$$

where P_0 is the initial population status rate (i.e. abundance) , P_t is the population status rate at sampling time t and C is the per year decrease in population status rate (i.e. abundance). Population for this study C was only simulated as a decline. Population changes were assessed on an annual basis having all sampling completed following the changes in population during the interval between sampling periods. I simulated combinations of initial population size (high, low), distribution of habitats occupied (generalist, specialist), and proportion of sites occupied (high, low) based on empirical data under two levels of population decline (high = 4%; low = 2%).

Alternative Population Decline

In the second scenario, populations within some sites rapidly become unoccupied because of rapidly changing environmental conditions (e.g., floods, droughts), while they remain more stable at other sites. Although uncertain to the support for either type of decline, I assume that both types of decline may be occurring within the overall mussel population, therefore the contrast of these two types of decline are studied. The second set of simulations modeled a constant decline in proportion of sites occupied rather than a constant decline in abundance over all sites using the same combinations of simulation scenarios defined above and under the same

rate of decline (4%, 2%). For each time step, changes in the population were simulated as a simple linear function of time as:

$$P_t = P_0 - t*C$$

where P_0 is the initial proportion of occupied sites, P_t is the proportion of occupied sites at sampling time t and C is the per year decline in occupancy. For example under the previous scenario, abundance within each site declined by a constant proportion until the site was unoccupied (abundance = 0), whereas under the alternative scenario an entire site became unoccupied while abundance at occupied sites remained unchanged. Again, sampling success was evaluated on the ability to detect a population change in abundance or occupancy over time. For clarification purposes, I will define these main simulation differences as: annual decline of abundance (AD) or occupancy (OD), and evaluate the ability to detect a change in abundance (EA) or occupancy (EO).

Sample Design

All simulations (AD, OD, EA, EO) used two basic designs, random sampling with replacement and a fixed set of sites. The random sampling with replacement design randomly selected sites with replacement at the start of each sampling event. Replacement assures that the probability of a site being selected is independent of previously selected sites, thus allowing for the potential for a site to be reselected during a later period. Alternatively, fixed sites were randomly selected for the first sampling period and revisited during each subsequent sampling period. For both sample designs, I evaluated the efficacy of incorporating strata in the sample design using two selection-weighting schemes: (1) samples are evenly distributed among strata (random sampling), (2) samples are unevenly distributed among strata (stratified sampling). For stratified sampling there were three scenarios of allocating effort: (1) most samples collected

from good quality stratum and least in the poor patch quality stratum, (2) most samples collected from moderate quality stratum, reduced effort at good quality patches, and least in the poor patch quality stratum, or (3) most samples collected from moderate quality stratum, reduced effort at poor quality patches, and least in the good quality patches. The quality of each patch (patch quality) was based on the likelihood of species occurrence in the patch determined by estimates from the occupancy study (see Distribution and Detection section). Good patches had high species occurrence whereas poor patches have low occurrence. Additionally, I used patch quality data to model initial proportion of area occupied as: (1) occupying a high proportion of area, or low, and (2) occupying an equal proportion of habitats (generalist) or selecting for specific habitat types (specialist).

I simulated two sampling frequencies for both designs: one sampling occasion per interval and two occasions per interval in different seasons, and two levels of effort: 30 and 60 sites with the total number of sites sampled over the entire sampling period. The total effort was evenly distributed among sample occasions. For example assuming 30 total sites, 30 sites and 15 sites per sampling occasion would be sampled when sampling frequency was one season per sampling interval and two seasons per sampling interval, respectively. All designs were based on the assumptions of: (1) two-person sampling crew, (2) habitats encountered on the Altamaha River, and (3) sampling conducted under safe streamflow conditions. The number of sites were based on what I defined as a realistic sample size obtained within a reasonable timeframe given the assumptions described above, and based on equivalent sampling efforts from empirical data (1 site~ 2-3 person hours).

Five hundred replicates were simulated for each combination of factors described above (total = 512). For each simulation, population dynamics were simulated in SAS while

occupancy models (EO) were fit via program MARK using time since initial occupancy sampling as a covariate (i.e., occupancy was modeled as a linear function of time); the MARK output was imported into SAS; and a one tailed p-value for the slope of the covariate was estimated using a t-statistic. Detection of a statistically significant effect was determined using the one-tailed p-value and two critical alpha-levels, 0.05 and 0.1. Multi-season Robust Design models (i.e. EO at fixed sites) were fit via program MARK and the occupancy rate (ψ) and colonization model. The occupancy growth rate (λ) also is estimated as a derived parameter. The MARK output was imported into SAS; and a one-tailed test that lambda was less than 1 (i.e., loss of occupancy) was estimated using a t-statistic. Detection of a statistically significant effect was determined using the one-tailed p-value and two critical alpha-levels, 0.05 and 0.1.

Statistical Analysis

Each design was evaluated on the power in the ability to detect changes in the population (EA, EO) for the simulated decline in either occupancy (OD) or abundance (AD) over time. I evaluated the influence of each factor on the ability to detect change using logistic regression, with detection of change as the event modeled. I included all-subsets of the simulation variables and two-way interactions for evaluation and selected the best fitting using Akaike's Information Criteria (Burnham and Anderson 2002).

CHAPTER 5

RESULTS

The discharge of the Altamaha River was relatively high at the initiation of the project (Figure 6) and prevented sampling until October 2005. Subsequent drought conditions caused below average water levels during the 12 month duration of the project (Figure 6), allowing safe sampling conditions during all periods other than the months from January through April 2007. Additionally, on October 29, 2005 nuclear power plant Hatch (near Baxley, GA) reported an oil spill into the Altamaha River, potentially affecting three sites downstream. No fish or mussel kills were reported for the Altamaha River throughout the study (Donald Harrison, GA DNR, personal communication), therefore I assume the effect of environmental stressors on mussels during this study were similar to stresses during any given year. Measured water temperatures ranged from 35 ^{0}C in slackwater habitats during July 2006 to 13 ^{0}C at all sites in December 2006. Although turbidity was not measured for this project, assessment of substrate visibility when snorkeling and diving was consistent among sites and sampling occasions (~23cm). However, sampling conducted in October 2006 had improved visibility (~1.5m).

Field observations included some proportion of *Lampsilils dolabraeformis* gravid during all sampling occasions (> 5%), with a markedly higher proportion of gravidity noticed during the spring for *L. splendida* (approximately 15%) and fall for *L. dolabraeformis* (approximately 20%). The only gravid *Alasmidonta arcula* was collected during preliminary sampling in November 2005, and no *Pyganodon gibbosa* were collected gravid.

Demographic Parameters

Sampling took place from July 2006 until June 2007 consisting of six primary periods having at least six-weeks between periods (Table 5). Each primary period contained three secondary periods with time between samples ranging from 0 to 24 hours. The location for sites included one site per stratum near the confluence of the Oconee and Ocmulgee rivers, and replicates near the confluence of Beard's Creek (Figure 3, Appendix A). The surface area was the same for all six sites (30m X 10m = 300m^2; Appendix A).

Only individuals of the species *Alasmidonta arcula, Lampsilis dolabraeformis, L. splendida,* and *Pyganodon gibbosa* captured within transects were tagged and used in the analysis because of their status as a state species of concern (Wisniewski et al. 2005) or relative abundance allowed for feasibility with respect to time spent tagging. Of those species, 1002 mussels were tagged and released (Table 6), with 520 individuals being recaptured alive at least once, and 43 (19 *L. dolabraeformis*, 24 *L. splendida*) recovered tagged shells (i.e., dead) over the entire study period. Therefore estimates for *A. arcula* and *P. gibbosa* were modeled using the standard Robust Design while estimates for *L. dolabraeformis* and *L. splendida* were modeled using the Barker Robust Design. Based on the observed loss of a single tag on eight mussels during the study (0.8 %), the estimated loss of two tags was 0.006%.

Temporal changes in sediment composition were observed at two sites. Shifty and loosely packed sand was present throughout the study area, except for the clay bank at the downstream swiftwater site (Appendix A) in 2006. Sampling during 2007, approximately five meters of compact sand was encountered outwards from the clay bank followed by shifty sand along the outermost end of the transects. Additionally, the upstream pool area (Appendix A) was

highly silted in 2006 (approximately 15cm fine silt), but only compact sand was encountered during sampling in 2007.

The best approximating Robust Design models differed slightly among species. Models where survival differed by habitat, seasonal temporary emigration, and constant capture probabilities were selected over other models for most species (Table 7). Exceptions were for *A. arcula* where the model with constant temporary emigration had a (0.501/ 0.301) 1.66 times more likely to be the best approximating compared to the second best approximating model containing seasonal emigration (Table 7). Similarly, the best approximating *L. dolabraeformis* model of habitat varying capture probabilities was 1.77 times more likely than the second best model representing the effect of observer experience on capture probabilities (Table 7). The best approximating model for *L. splendida* modeled capture probability as constant and was 3.7 times more likely than the second best approximating model where capture probability was function of large woody debris (Table 7). In contrast, there was relatively little support for the best approximating model over the second best model (1.11 times) for *P. gibbosa* as the differences in the weights for the model in the confidence set were small.

Models with survival that varied among habitat were 4.08 and 1.02 times more likely to be the best approximating models compared to models with survival constant among habitats for *L. dolabraefromis* and *P. gibbosa*, respectively. Models of constant survival were not contained in the confidence set for *L. splendida* with evidential ratios exceeding 100 times more support for the best fitting model (constant survival; Table 8). An exception was *A. arcula* that was only collected in a single habitat type (slackwater), limiting fitting of habitat-specific survival models. Therefore, survival estimates were limited to a single habitat type. Due to this study being conducted for a single year, survival is reported as the probability of surviving from one primary

period to the next (six-week survival), with primary periods being defined as six-week intervals. Survival estimates between primary periods were high with all studied species in all habitats having at least 0.95 six-week survival (Annual survival = $0.95^8 = 0.66$) contained within the 97.5 percentile of the estimate (Table 9) and survival being greatest in slackwater and lowest in swiftwater habitats. Additionally, *L. dolabraeformis* had higher survival among all habitats compared to other species (Table 9).

With the area of all sites being equal, capture probabilities were not modeled as a function of the proportion of area sampled unlike for the occupancy models. Constant capture probability models had 1.85 and 4.05 times more support than models that included proportion of experienced observers for *P. gibbosa* and *A. arcula,* respectively (Table 8). Models with constant capture probabilities were 3.62 times more likely than models accounting for the effect of large woody debris for *L. splendida* (Table 8). Mean capture probabilities among species ranged from 0.11 (*A. arcula*) to 0.12 (*L. splendida*) (Table 9). *L. dolabraeformis* was the only species for which best approximating model did not model capture probabilities as constant (i.e. varied by habitat), with estimates ranging from 0.13 in pools, 0.15 in swiftwaters, and 0.19 in slackwater habitats (Table 9). To further test for behavioral responses between secondary periods, I placed mussel replicas made from Plaster of Paris© within each site and compared capture probabilities between live mussels and replicas among periods (Appendix B). The ability to capture replicas (mean= 0.18; SE= 0.06) did not differ from that of live mussels (mean= 0.12; SE= 0.02) (Appendix B).

Temporary emigration was estimated for the second through sixth primary occasions with the second and sixth period representing the same season (summer) as determined by water temperature. Models of seasonal temporary emigration were included in confidence sets for all

species, although the best approximating model for *A. arcula* assumed constant emigration (Table 7). Models that allowed for seasonal temporary emigration exceeded 20, 100, and 1000 times more likely than models of constant emigration for *P. gibbosa*, *L. splendida*, and *L. dolabraeformis*, respectively (Table 8). The greatest estimated temporary emigration was for *P. gibbosa* during the winter months (0.92) and lowest for *L. splendida* during the summer (0.04) (Table 9). Estimated seasonal temporary emigration patterns varied among species, but some species exhibited similar patterns. For example, temporary emigration for *L. dolabraeformis* was least during the spring (0.11) and summer (0.08) seasons and greatest during the fall (0.4) and winter seasons (0.47), whereas temporary emigration was lowest in summer/fall and fall seasons for *L. splendida* (summer = 0.04; fall = 0.05) and *P. gibbosa* (0.35), respectively (Table 9).

Given estimates of conditional capture probabilities ($\hat{p}$) and temporary emigration ($\hat{\gamma}$), the captured proportion of the population, or effective capture probability ($\hat{C}^{o}$) was estimated for each season. Since the best fitting model for *A. arcula* was constant $\hat{\gamma}$ (0.64), $\hat{C}^{o}$ was constant (0.1) throughout seasons (Table 10). Mean estimates and Bayesian credibility limits were simulated (5000 replicates) from mean estimates of $\hat{p}$ and $\hat{\gamma}$ with respective standard deviations, assuming a normal distribution. Due to low capture and recaptures of *P. gibbosa*, $\hat{\gamma}$ estimates had a highly variable range within seasons (i.e. fall = 0.04-0.75) causing $\hat{C}^{o}$ to have wide BCL of 33% (Table 10). For the sake of convenience, I used the mean capture probability among habitats for *L. dolabraeformis*. For *Lampsiline* species, although conditional capture varied among seasons and slightly by species, approximately only 10% of the total population was captured during any given sampling period (Table 10).

Surface abundance estimates were greatest in the slackwater habitats and lowest at the downstream swiftwater site for all species although individual estimates differ markedly among species (Table 11). Because $\hat{\gamma}$ differed among species during the summer season, superpopulation estimates varied among species as a function of the specific $\hat{\gamma}$ and $\hat{N}$ estimates (Table 11). Again, mean estimates and Bayesian credibility limits were simulated (5000 replicates) from mean estimates of $\hat{\gamma}$ and $\hat{N}$ with respective standard deviations, assuming a normal distribution. Estimates were highest in slackwater sites for all species (Table 11). The upstream swiftwater site had higher abundances than pools for *L. dolabraeformis* and higher abundances than the downstream swiftwater or upstream pool for *L. splendida* (Table 11). *P. gibbosa* had roughly equal abundances (6-14) at the two sites it was captured in (upstream slackwater and downstream pool) (Table 11). The lower BCL for two species, *A. arcula* and *P. gibbosa*, underestimates a known number of mussels present. Although 33 *A. arcula* and 13 *P. gibbosa* were tagged (Table 6), the sum of the 2.5% BCL of the superpopulation across sites estimates 23 and seven individuals, respectively (Table 11). The variability between upper and lower BCL suggests that sparse data from relatively few captured individuals affected the precision of the estimates.

Distribution and Detection

Sixty-six different sites were sampled from June 2006 until June 2007 (Table 5) where 13,415 individuals were collected during occupancy estimation. I identified four main reaches each having a mean longitudinal distance of approximately 30 river kilometers (Figure 3). Location of sites ranged from the confluence on the Oconee and Ocmulgee Rivers downstream to Altamaha Park (Figure 3). Of the 19 known species within the basin (Jason Wisniewski, GA DNR, personal communication) at least 12 were collected (Table 12). Five of these species were

used for occupancy estimation including: *Alasmidonta arcula*, *Elliptio spinosa*, *Lampsilis splendida*, *L. dolabraeformis*, and *Pyganodon gibbosa*. The *Lampsiline* species were selected based on relative abundance throughout the river, whereas other species were selected because of their status as a federal or state species of concern (Wisniewski et al. 2005). I revisited approximately 25% of all sites (19 slackwaters, 6 glides, 1 swiftwater, 1 pool) during December 2006 or June 2007.

The best fitting occupancy models differed markedly among species. In most cases, models that included site specific covariates for modeling occupancy or detection comprised the majority of models in their respective confidence sets (Table 13). Only one model was reported for *E. spinosa* (constant model) because all other models had nonsensical occupancy estimates (mean = 0.0002 CI = 0-1), likely due to sparse data and low detection. The best fitting model for *A. arcula* modeled transect detection and occupancy as functions of proportion of area sampled and current velocity, respectively. The best approximating model had (0.308/0.108) 2.85 times more evidence supporting than the second approximating model that assumed constant detection regardless of proportion sampled (Table 14). Models that assumed constant detection but estimated occupancy as a function of depth for *L. dolabraeformis* fit 1.83 times better than the second best model (detection = constant, occupancy = coarse substrate) (Table 14). The best fitting model for *L. splendida* contained the relationship between current velocity measurements and occupancy and the influence of snorkel sampling on detection. The effects of current velocity on occupancy and snorkel sampling on detection was six times more likely to be the best approximating model than the model with the second best fit (Table 14). The model for constant detection and occupancy varying with current velocity was 1.97 times better than allowing detection to be a function of snorkel sites (2nd best fitting model) for *P. gibbosa* (Table 14).

There was no evidence of differences in detection per transect between visits for revisited sites for most species except *L. dolabraeformis*, where mean transect detection estimates decreased from 0.61 to 0.44 upon revisit (Table 15). Therefore, estimates of per transect detection were averaged for *L. dolabraeformis* (0.53). Factors affecting occupancy were species specific. For instance constant detection was selected 2.54 and 1.93 times more likely for *L. dolabraeformis* and *P. gibbosa* respectively over the second best detection predictor, whereas snorkel sites and proportion of area sampled had 7.78 and 2.63 times more evidence for *L. splendida* and *A. arcula* respectively (Table 14). Snorkel sampling at depths between 0.7 and 1.5 meters was 1.07 times more likely to detect *L. splendida* than sampling at alternative depths (Table 16). For every 10% increase in proportion of habitat area sampled, the probability of detection within a transect was (1/ 0.96) 1.04 times lower for *A. arcula* (Table 16).

When estimating occupancy, the best approximating models for *A. arcula*, *P. gibbosa,* and *L. splendida* included current velocity and were 5.3, 6.57, and 7.69 times more likely than the second best approximating models, respectively (Table 14). Models that contained depth as a predictor of *L. dolabraeformis* occupancy were 1.83 times more likely than coarse substrate (Table 14). I estimated for every 0.1 m/s increase in current velocity in a habitat, *A. arcula*, *L. splendida*, and *P. gibbosa* were 1.08, 1.08, 1.11 times less likely to occupy the habitat, respectively (Table 16); whereas *L. dolabraeformis* were 1.31 times more likely to occupy a habitat with each 0.3m increase in depth (Table 16).

Alternative Sampling Designs

Initial values for simulation inputs were generated from empirical data of the capture-recapture and occupancy study described in the previous sections (Table 17). Seasonal specific estimates (i.e. effective capture probability) were selected from the summer (single-season

sampling = 0.1) and fall (second-season sample = 0.2) based on the likelihood of safe sampling conditions (low flows) (Table 17).

Simulations took approximately 36 computer-days to complete. The slowest component of the simulation process was model fitting in program MARK. The program often stalled due to non-convergence during the fixed site simulations, which is likely to occur in real world applications.

When modeling unequal allocation of effort, there was consistently more power among all sample designs and rate decline dynamics when sampling the most at high occurrence patches and least at low occurrence patches (HIL). On average HIL had 6% higher power than both equal allocation and sampling the most at intermediate occurrence patches and least at low occurrence patches (IHL), and 17% more power than sampling mostly low and intermediate occurrence patches (ILH; Table 18). Therefore, comparisons of unequal allocation of effort among habitats hereafter were based on the scenario that consistently represented the highest power in detecting a population change (HIL).

An examination of the overdispersion parameter of the global logistic regression model of mussel sample design power indicated that that six of eight datasets were overdispersed (average c-hat > 1.43). Therefore I estimated quasi-likelihood logistic regression and adjusted AIC (QAIC) using estimated c-hat values for all data sets (Table 19).

For all simulation scenarios, the global model was the best fitting, but the effect of each factor simulated differed by scenario (Appendix C). However, I report those results according to the best predictors to detect a population change, thus facilitating management application. When modeling a decline in abundance through time, on average there was 48% more power to detect a decline in abundance (0.5) rather than occupancy (0.02). The factors that had the

greatest influence on detecting a change in abundance were growth rate and initial distribution (Table 20; Appendix C). In general, it was difficult to detect a population change if the change was subtle; when the rate of decline changed from 2% to 4%, power was 1.5 and 1.4 times greater at alpha levels 0.05 and 0.1 respectively (Table 20). Additionally, if the species were widely distributed there was 1.5 times greater times more likely to detect a change as opposed to occurring in fewer areas at both alpha levels (Table 20).

In contrast, when simulating a decline in occupied sites through time, average power to detect a change in the population via occupancy sampling was lower (mean = 11% range = 0-99%) than simulated declines of abundance. Fixed sites had the highest (negative) impact on power such that using fixed sites were (1/0.1 =) 10 times less likely to detect a change in the population than randomly selecting sites (Table 21; Appendix C). Seasonal sampling also had a negative effect of detecting a change being 4 times less likely than sampling during a single season (Table 21). Again, rate of decline had a positive effect having 2.86 times more power to detect a change at 4% than 2% decline (Table 21). Depending if the species were widely distributed, detecting a change was 2.72 times higher than if distribution was restricted (Table 21).

Given a scenario of a common generalist, a species widely distributed and found equally in various habitats, the ability to detect a population change was 1.63 times greater with fixed sites than with random selection of sites (Table 22) under a decline in abundance. Alternatively, if the population declines in occupied patches sampling during a single season was 33 times more likely to detect a change than sampling during two seasons (Table 22). Also, using fixed sites were (1/0.04 =) 25 times less likely to detect a change than randomly selecting sites (Table

22). By visiting 60 sites the ability to detect a change was 2.89 times greater than only visiting 30 sites (Table 22).

For common specialists, a species found in habitats with specific characteristics widely distributed throughout the system, the ability to detect a population change was 1.99 times greater with higher effort (60 sites) as opposed to 30 sites (Table 23) under a decline in abundance. Also, by focusing more effort at habitats likely to be occupied by the species increased the likelihood of detecting a change 1.54 times more than equal allocation of effort among sites (Table 23). Finally, using fixed sites was 1.56 times greater at detecting a change than using random selection (Table 23) under a decline in abundance. Alternatively, if the population declines in occupied patches, the ability to detect a change was 50 times greater by sampling during a single season instead of two-season sampling (Table 23). The same increase in power was obtained when selecting random sites instead of fixed sites (Table 23). By allocating more effort at sites with higher occurrences, the ability to detect a change was 1.73 times greater than equal allocation of effort (Table 23).

By using fixed sites, there is a 1.52 times greater chance of detecting a population change than using randomly selected sites for rare (low initial distribution) generalist species (Table 24). When effort is increased (60 sites), detecting a change is 1.48 times greater than lower (30 sites) effort (Table 24). Alternatively, if the population declines in occupied patches increased effort was 2.29 times more likely to detect a change than lower effort (Table 24). Single season sampling was 7.14 times greater at detecting a change than two-season sampling, and fixed sites were 11.1 times less likely to detect a change than using complete random selection (Table 24).

The ability to detect a population change for rare specialists was 1.36 times greater when more effort was used (60 instead of 30 sites), and 1.31 times greater when using fixed sites

instead of random sites (Table 25). Alternatively, if the population declines in occupied patches single season sampling was 12.5 times greater at detecting a change than two-season sampling, and fixed sites were 7.14 times less likely to detect a change than random selection (Table 25). Again, by increasing effort, the ability to detect a change was 1.95 times greater than reduced effort (Table 25).

CHAPTER 6

DISCUSSION

Mussel Demography and Behavior

Understanding the demography and behavior of mussels is crucial to developing effective and efficient conservation strategies. Recent studies have separately evaluated the effect of incomplete capture (Villella and Smith 2005) and seasonal vertical migration (Schwalb and Pusch 2007) on estimating mussel surface abundance and have estimated survival using open capture recapture estimators (Villella et al. 2004). To my knowledge, this is the first study to evaluate freshwater mussel seasonal behavior and estimate demographic parameters using the Robust Design (Pollock 1982) to gain a more comprehensive perspective of site-specific mussel populations. In addition, low flows throughout most of the study also provided the opportunity to study mussels during the winter months when streamflows are usually too high for safe sampling. Previous studies of mussels in smaller streams suggest that shallow water, low dissolved oxygen, and high temperatures caused by droughts alter behavioral responses of mussels and substantially lower survival (Golladay et al. 2004). However, droughts have a much smaller effect on dissolved oxygen levels and water temperatures in large rivers, such as the Altamaha River (Gordon et al. 1992) and I did not observe nor were there reported any acute adverse affects of the drought on the aquatic community in the Altamaha during this study (e.g., fish kills, mussel kills, or isolation of mussels in shallow pools). Therefore, I believe that my estimates and observations are an accurate reflection of the demography and behavior of freshwater mussels in the Altamaha River.

Survival is an important parameter to consider when making management decisions, for example certain habitats may have greater conservation value if habitat-specific survival was greater than others. Indeed, I found that mussel survival differed among habitats. Mussel survival is reportedly influenced by desiccation from emersion (Engel 1990), predation (Hanson et al. 1989), water pollution (Neves et al. 1997), impoundments (Strayer et al. 2004), and exploitation (Strayer et al. 2004). Of these, there are no impoundments and commercial mussel harvest on the Altamaha River, thus these factors are not considered. I also assume that the effect of point and non-point source water pollution on mussel survival occurs over larger spatial scales (e.g., stream segments) rather than the smaller mesohabitat scale due to the mixing that occurs in rivers (Gordon et al. 1992). At mesohabitat scales, I assume that mussel survival in influenced by the characteristics of the habitats. Slackwaters are shallow habitats located adjacent to the streambank with gently sloping bottom. As streamflows decrease, large portions of slackwater habitats are dewatered leaving large areas exposed to air, whereas other deeper habitat types remain watered. If slackwater-dwelling mussels were unable to escape receding water levels, they would have been stranded, leading to lower survival. Assuming that the ability of mammalian predators to locate mussel prey is negatively related to water depth (Neves and Odom 1989), the mussels in slackwater habitats should be more vulnerable to predation than in other habitat types. Furthermore, slackwaters are habitats where sediments are deposited during normal to low flow periods (Gordon et al. 1992). Sedimentation has been found to clog gills of mussels (Neves et al. 1997) and can reportedly kill large numbers of mussel within short time periods (Brim Box and Mossa 1999). Nonetheless, mussel survival in slackwater habitats was greater than other habitats for all species. I believe that the greater survival in slackwaters was that they served, in part, as high flow refugia (Strayer 1999; Waller et al. 1999). During high

streamflow events, pools and swiftwater habitats become areas of convergent flow and scour potentially dislodging resident mussels, whereas slackwaters are areas of divergent flow and deposition (Rabeni and Jacobson 1993). Identifying areas with high survival is critical for conservation decision-making. Although I cannot determine the exact mechanism responsible for the survival differences among habitats, the greater survival of mussels in slackwater suggests that be these might be critical habitats for mussel species in the Altamaha River.

Variation in survival among species or through time can be an important indicator of alterations to the environment that can affect species persistence. Six-week survival of mussels was, on average, relatively high (mean = 94%) and varied among species. When extrapolated, annual survival was lower (mean = 65%), but not dissimilar to, estimates reported for other *Lampsilines* (Villella et al. 2004). Survival may differ by species depending on habitat (stated above) or sensitivity to various environmental disturbances (Neves et al. 1997). If mussel response to changes in environmental conditions (e.g., temperature, dissolved oxygen) varied among species, I presume that species-specific survival would differ assuming habitat-specific factors were held constant. There was little difference in estimated survival among the species studied within slackwaters, but *L. dolabraeformis* had higher survival than other species in pool (92%) and swiftwater (78%) habitats. I believe that the differences are due to the degree of resource specialization among species. Some species may be able to survive in a broader range of habitats (generalist), whereas some species can only survive in specific habitats (specialist) (Johnson 1970; Parmalee and Bogan 1998). *L. dolabraeformis* is considered a generalist species that uses many habitats, but I found occupancy was positively related with water depth, suggesting that the species was more of a pool-dwelling specialist. Likewise, *L. dolabraeformis* had higher survival in pool habitats than other species (*L. splendida* or *P. gibbosa*). Therefore, I

believe that differences in survival among species are related to their degree of habitat specialization. To further test these assumptions, future studies can implement long-term monitoring allowing survival to vary temporally, potentially identifying differences in survival among species and habitat given temporal changes (i.e. receding water levels, floods).

Aside from mortality, violations of model assumptions can affect survival estimates. One factor potentially influencing (biasing) my survival estimates is emigration because the probability that an individual leaves the superpopulation (permanent emigration) is confounded within the survival estimate (Williams et al. 2002). This may be the reason my estimates are lower than those reported by Villela (2004) who used an open population design over multiple years to estimate survival for *L. cariosa*. Open population estimators assume that all emigration is permanent, thus any return to the site is a violation of the assumption than can bias the estimates (Pollock et al. 1990). This violation is probably the reason annual survival estimates of Villela (2004) increased through time for the 3 year study. That is, the individuals that temporally emigrated in year 1 were considered lost (dead) biasing the survival low. A portion of these individuals were available for capture in year 2, reducing the bias. In contrast, the Robust Design allows for individuals to leave and return to the site (temporary emigration); moreover, the Barker Robust Design allows for the incorporation of recovered shells (known mortality) when applicable, therefore utilizing all possible data rather than censoring recoveries under other sample designs, although permanent emigration is still confounded with survival. Horizontal movement can be upwards to two meters per day (Amyot and Downing 1997) whereas mussels can bury themselves within a day (Schwalb and Pusch 2007). Therefore, I believe that permanent emigration may have incorporated some bias within my estimates. To evaluate this potential source of bias, I suggest that future studies include searching areas adjacent to the study

areas to account for displacement and perhaps use multistrata models to estimate and incorporate mussel movement.

A common assessment of mussel populations is based on changes in abundance over time (Strayer and Smith 2003). Surface abundance varied spatially with greater abundance in slackwaters for all focal species and seasonally at a location with differences among species. Studies have proposed various factors that affect mussel abundance, such as sediment composition (van Cleave 1940; Harman 1972; Vannote and Minshall 1982; Stern 1983), current velocity (Salmon and Green 1982; DiMaio and Corkum 1995; Hornbach et al. 1996), depth (Salmon and Green 1982; Stern 1983; Hornbach et al. 1996), and local host fish habitat use (Haag and Warren 1998; Vaughn and Taylor 2000). However, the effect of these factors is highly variable and seldom replicated (Strayer et al. 2004). I believe that species presence within a given area is based upon scale-specific hierarchy of determinants or 'constraints' (Figure 1) for both the mussel and host-fish. At a basic level, both mussel and host must be present within the system. Although the host fishes of most of the focal unionid species is currently unknown, both *Lampilines* were observed with modified mantle flaps resembling small minnows (personal observation). Previous studies of other mussel fish hosts indicated that the host fishes of mussels with similar lures tend to be picivorous and are often species in the family Centrarchidae (Etnier and Starnes 1993). Next, the host should frequent habitats where mussels are, and remain in habitats that juveniles can persist in once they drop off. Most species of juvenile centrarchidae (i.e., sunfishes, black basses) generally use shallow, slow current velocity habitats (Etnier and Starnes 1993). Although, fish can develop an immune response to glochidia infestation (Kirk and Layzer 1997; Bauer and Vogel 1987; Meyers et al. 1980), juvenile or short-lived fishes would be more susceptible to infestation, suggesting a greater likelihood that new recruits drop

off the host fish in (shallow) slackwater habitats than other habitats. Once juvenile mussels drop off the host fish, they must be able to survive at that particular location. Although I was unable to detect juvenile mussels due to small size (< 1mm; Jones et al. 2005), I assume that factors influencing juvenile survival are similar to those influencing adult survival. The greater survival of mussels in slackwater habitats and lower survival in swiftwater habitats also suggests that slackwaters should have greater abundance of mussels. Thus, I hypothesize that mussel abundance within a habitat is influenced, in part, by the habitat preferences of host-fishes and the survival of mussels after they detach from a host fish. To evaluate for support of one factor over the other requires knowledge of host fish and a laboratory setting where juvenile mussels can be monitored. Assuming that mussel abundance in a mesohabitat is related to host fish abundance and habitat use, mesohabitat-specific mussel abundance also may be useful for identifying potential host fish for future host fish identification studies.

Many freshwater mussel surveys are based on searching for mussels on the sediment surface. The likelihood of detecting an animal is positively related to the number available for capture (Williams at al. 2002); therefore when mussels migrate to and from the surface, the detectability of species changes. Seasonal mussel migration behavior in the Altamaha River was similar to previous studies (Watters et al. 2001, Amyot and Downing 1997; Schwalb and Pusch 2007) and was related to water temperature, although other environmental cues for migration may exist. I assume that mussels would likely be on the surface at any given time, only migrating to escape lethal thermal limits (Waller et al. 1999) or emersion (Waller et al. 1995). The relatively low river discharge throughout the study (Figure 6) and especially during the summer months suggests that mussels were at greater risk of emersion during the summer. Furthermore, water temperatures were greatest from May to November when upper thermal

limits would likely be exceeded. Nonetheless, I observed the highest proportion at the surface during this time for most species. Thus, I believe that emersion and high temperatures did not influence migration. Albeit, migration can be both vertical and horizontal and the design could not differentiate between mussels moving horizontally out of the area and vertically into the substrate. Future studies can implement methods that can differentiate between types of migration such as excavation for buried mussels or looking outside of the study area for horizontally migrated individuals, but for this study I assume that most migration is due to vertical migration.

Mussels need to be on the surface for successful reproduction. Incurrent and excurrent apperatures are used to transfer gametes, and the glochidia are released into the water column or retained by the female at the surface using an attractor device for host fish (Watters et al. 2001). Reproductive strategies, such as brooding season and fertilization, can vary among species (Ortmann 1911), including bradytictal and tachytictal reproductive strategies that are analogous to 'bet hedging' strategies by other wildlife species (Winemiller and Rose 1992). Bradytictal species have a long-term brooding season (Ortmann 1911), suggesting that there are a proportion of gravid females of these species at the surface at all times. In contrast, tachytictic mussels are believed to be short-term brooders (Ortmann 1911), suggesting that these species would exhibit definitive peaks in proportion at the surface through time. Although the life histories of the focal species are unknown, bradytictic species such as *L. cariosa* and *L. radiata* (Ortmann 1919) are believed to be closely related to *L. dolabraeformis* and *L. splendida* respectively (Johnson 1970). Assuming migration is related to reproductive state, my observations of large proportions of *L. dolabraeformis* and *L. splendida* at the surface throughout the study is consistent with the hypothesis of bradyticticity. *Pyganodon gibbosa,* however, had relative large proportions at the

surface during the fall suggesting that they may be tachytictic. In addition, irregular breeding patterns (Moles and Layzer 2008) may cause seasonal emigration to vary from year to year, possibly accounting for lack of support for seasonal effects in *A. arcula*. Thus, I hypothesize that the species-specific seasonal movement patterns are related to reproductive activity with greater proportion of mussels at the surface corresponding to times when both sexes were at the surface during fertilization. Future research is needed to evaluate the reproductive strategies to confirm or reject this hypothesis. Knowledge of temporal variation in migration is important irregardless of the mechanism, because managers can plan surveys according to the surface population when detection is highest.

Mussel Occupancy and Detection

Occupancy of mussels in the Altamaha River was related to mesohabitat characteristics. Previous studies have found that mussel presence at small (microhabitat, $\geq$1 m^2) scales was related to sediment composition (van Cleave 1940; Harman 1972; Vannote and Minshall 1982; Stern 1983), current velocity (Salmon and Green 1982; DiMaio and Corkum 1995; Hornbach et al. 1996), water depth (Salmon and Green 1982; Stern 1983; Hornbach et al. 1996), and local host fish habitat use (Haag and Warren 1998; Vaughn and Taylor 2000). However, other studies suggest that microhabitat characteristics are poor predictors of mussel distribution (Layzer and Madison 1995; McRae et al. 2004). I believe that these discrepancies were due in part to the relatively sedentary behavior of mussels and the dynamic nature of rivers. Mussel presence at a location is influenced by multiple factors that vary through time. Mussels are distributed by their host fish (Vaughn and Taylor 2000), but once they drop off the host, mussels must be able to persist by burrowing into the substrate and not being scoured out (Strayer 1999). Similarly, the

characteristics of a given location in a stream change with changing discharge. For example, pool habitats become areas of convergent flow and scour during high discharge, whereas they are depositional areas during base or low discharge. The physical characteristics of the location at which a mussel was captured (e.g., depth, velocity) may not reflect the factors that led to the mussel being located at that spot, particularly at microhabitat scales. In contrast, my sample unit was a mesohabitat that were at least 30 times larger than microhabitats. Mesohabitats are formed as a result of fluvial dynamic processes and thus, mussels in a particular mesohabitat type will experience similar process through time (e.g., scour, deposition). They also have relatively unique physical characteristics at base to low flows and unique fish assemblages that are potential fish hosts (Peterson and Rabeni 2001). Mesohabitats incorporate many of the factors influencing mussel presence. By using mesohabitats as my sample unit, I likely incorporated the effect of these factors in my occupancy model. This is probably the reason why I detected relationships between physical habitat characteristics and mussel occupancy, whereas other studies did not. Additionally, this suggests that mesohabitats are useful for defining mussel habitats.

Mussel distribution also is influenced by large-scale (reach scale) factors (Strayer 1993; McRae et al. 2004). Although I did not compare effects of longitudinal changes on occupancy, I believe that reach-scale effects might have influenced mussel distribution in the Altamaha. I sampled mussels in mesohabitats in four reaches Altamaha River based on river access points (boat launches). The size of the stream increased from the upstream to the downstream reach, but the characteristics of most of the reaches were similar with one exception. The water at the downstream reach (Figure 3), beginning near Jesup, GA and flowing downstream to Altamaha Park, GA had noticeably more tannic coloration. Detection of occupied habitats was noticeably

lower within this reach for all mussel species (naïve estimates of sites occupied by *L. dolabraeformis* or *L. splendida* upstream = 0.88; downstream = 0.23). This could have been due to changes in water (i.e., greater amounts of blackwater, or salinity), stream size, municipal effluent, or potential fish host community. Given that this is only one river, it is unlikely that additional statistical analysis of my data will provide a way to identify the likely causes. Therefore, I suggest that future studies focus efforts on determining the life histories (e.g., host fish) of Altamaha River mussel species.

Mussel distribution varied among species, with the greatest occupancy rates for *L. dolabraeformis*. I believe that species presence within a given area is based upon scale-specific hierarchy of determinants or 'constraints' (Figure 1) for both the mussel and host-fish. At a basic level, both mussel and host must be present within the system. The host should then frequent habitats where mussels are to increase the likelihood of being infested with glochidia. Once juvenile mussels drop off the host fish, they must be able to persist at that particular location, suggesting the range of habitats frequented by host fish should be adequate for attached mussels because their survival is dependant upon the habitat where they fall off. Certain mussel species can occupy a wide variety of habitats (Parmalee and Bogan 1998), called generalists, whereas other species are restricted to specific habitats (Parmalee and Bogan 1998), referred to as specialists. I assume that generalist species occupy a large proportion of available habitats, whereas specialists are restricted to fewer. Occupancy was greatest for *L. dolabraeformis* and *L. splendida*, suggesting these species were generalists. Although they used a greater number of available habitats, occupancy was related to habitat characteristics for both species. Occupancy for *L. dolabraeformis* was positively related to water depth, although assuming a constant probability of occupancy (equal use) among habitats is included in the confidence set of models;

whereas, *L. splendida* occupancy was negatively related to current velocity, suggesting *L. splendida* prefers slow flowing habitats but can inhabit other types. In contrast, *A. arcula* and *P. gibbosa* occupied a much smaller proportion of habitats and only those with low current velocities and are likely specialist species. Johnson (1970) and Sickel (1980) similarly observed both *A. arcula* and *P. gibbosa* in habitats with low current velocities (slackwaters). I was unable to identify any factors relating to *E. spinos*a occupancy suggesting an equal likelihood of occupancy in all habitats. However, *E. spinos*a data were sparse with only six invividuals being collected on only four occasions within two sites, thus the likely cause for the lack of relationship between occupancy and habitat factors. Other studies report an association between *E. spinosa* and the protected area of sand bars (Clench 1962; Thomas and Scott 1965; Johnson 1970), in medium to coarse sand without silt (Sickel 1980), and in swift water (Johnson 1970). The distribution of *E. spinosa* is believed to be greatly restricted to specific habitat types (Johnson 1970). I also observed that sites where *E. spinosa* were found is areas with firm, silt-free substrate and moderate current velocities as suggested by Sickel (1980) and Johnson (1970). I suggest that future studies incorporate metrics, such as embeddedness, that provide a more detailed explanation of the sediment structure than composition alone, when relating habitat characteristics to *E. spinosa* occupancy. Nevertheless, even without habitat specific predictors for estimating occupancy, my estimates of detection and occupancy can be useful for managers and if incorporated into an adaptive framework, can be updated as more information is collected for *E. spinosa*.

Per transect detection and factors influencing detection varied among species. Many assessments of populations or communities (abundance, presence, species richness) are based on what species were physically observed, or detected (Strayer and Smith 2003); however, detection

is rarely perfect in wildlife surveys (MacKenzie et al. 2006). Detection is important because, if unaccounted for, occupancy or species richness will be underestimated (Williams et al. 2002). Factors influencing detection at a location are abundance, the number of samples collected, and ability to capture an individual (Williams et al. 2002). I hypothesized that transect detection would be influenced by: 1) intermediate depths (0.7 – 1.5 meters) when snorkels were used, assuming observers may lose contact with the substrate lowering capture and 2) differences in proportion of area sampled within a mesohabitat due to variability in total area among mesohabitats. Although the same number of transects (nine) were used at each mesohabitat the proportion of area sampled was negatively related to total area, thus assuming a decline in detection since nine transects may not adequately cover large areas due to the clumped nature of mussels (Smith et al. 2001). However, transect detection was greater at sites where snorkels were used (depth = 0.7-1.5 meters) for *L. splendida*, while transect detection increased as habitat area increased for *A. arcula*. Instead, factors that influence detection for *A. arcula* and *L. splendida* may be associated with abundance rather than ability to capture. The probability that a species will be detected is positively related to the number of that species available (Royle et al 2005). Relative abundance of species from the capture-recapture study correspond to transect detection estimates, with the more abundant species (*L. dolabraeformis* and *L. splendida*) having greater detection per transect (mean = 0.53 and 0.38 respectively) while less abundance species (*A. arcula* and *P. gibbosa*) have lower detection per transect (mean = 0.16 and 0.11 respectively). Furthermore, given the shallow (mean depth = 0.7 meters, excluding sandbars) gently sloping bottom of slackwaters creates large spatial area within the habitat. Therefore, I believe factors influencing transect detection for *A. arcula* and *L. splendida* are due to greater abundance in slackwaters. Consequently, *E. spinosa* had the lowest detection (0.04) suggesting previous

assumptions of low abundance are correct (Wisniewski et al. 2005). Therefore, detection can be used as a rough estimate of abundance, especially if the species is rare making direct abundance estimates difficult.

Detection of mussels was not perfect, with instances of detecting species during revisits not previously detected at that site. For instance, *A. arcula* was captured during revisits at two sites not previously detected, and no *E. spinosa* were captured during this study at a site with the highest known abundance (containing 18 previously tagged mussels; J. Wisniewski, GADNR, personal communication; personal observation). Although differences between initial and revisit detection (per transect) estimates were similar for most focal species, detection within a transect differed between visits for *L. dolabraeformis.* With detection being a function of capture and abundance, I assume differences of abundance between visits to be a likely factor rather than ability to capture because factors believed to influence capture (depth, habitat) did not change between visits. Abundance, specifically surface abundance, varies temporally and given differences between proportions at the surface was greater for *L. dolabraeformis* compared to *L. splendida* during revisits. Therefore, due to variability among species and temporally, accounting for detection is necessary because it allows for inferences to be made about what was captured and what was missed during decision making. More specifically, this information can be used by managers to make cost-effective decisions and minimize errors by assuming absence although the species is present but not detected (Peterson and Dunham, 2003). For example, given estimates for *E. spinosa* (probability of occupancy = 0.12; probability of detection within a transect given occupancy = 0.04), and using the same sampling techniques (nine transects), the probability of capturing *E. spinosa* in an occupied habitat is $1-(0.12*(1-(1-0.04)^{9})) = 3.7\%$. However, collecting additional transects within a mesohabitat or sampling more mesohabitats

within a river reach improves the probability of detection given presence in the reach, such that sampling 40 mesohabitats (nine transects each) has 1- $(1\text{-}0.037)^{40}$ = 78% probability of capturing *E. spinosa*. Therefore, managers can assess implications of actions based on risks associated with the management action and the probability of missing a species when it is present.

Being able to predict locations that species occupy is important when developing stratum for a monitoring plan. When operating over a large spatial scale such as an entire watershed, monitoring changes in population abundance using capture-recapture designs can be cost prohibitive without proper stratification (Christman 2000; Strayer and Smith 2003). Additionally, the status of a large-scale population (i.e., metapopulation) can be evaluated by estimating changes in distribution or metapopulation dynamic rates (Hanski 1999); especially useful when rare species may be reduced to a point that inhibits abundance estimation or when the resources required for population estimates are unavailable (MacKenzie et al. 2006). Tagging mussels in capture-recapture designs are time consuming (Strayer and Smith 2003), thus greatly limiting the number of samples; whereas sampling based on occupancy are relatively fast allowing more spatial coverage Information gathered about occupancy is useful for managers especially when working from a large spatial scale, such as a lowland river. The sample quality is important when managers rely on samples being a representation of the entire population, thus good spatial coverage reduces sampling bias (MacKenzie et al. 2006). I believe that there was adequate spatial coverage of the river and among habitats with distribution of species representative for the Altamaha River allowing for inferences about species distribution and factors that may affect the stratification of species among habitats, and to develop sampling stratum.

Suggested Sample Designs

High variance affects the ability to detect changes in the status of mussel populations (Strayer and Smith 2003). Sources of variability includes: clumped distribution (Smith et al. 2001), seasonal vertical migration (Schwalb and Pusch 2007), and incomplete capture (Smith 2006). Of these sources of variance, many can be incorporated into sample design. For example, using information from the Robust Design I was able to estimate seasonal migration, abundance, and incomplete capture, whereas occupancy estimates allowed inferences about the distribution of mussels. Therefore, this study may give mangers insight to account for spatial and temporal variability when developing sampling designs to account for mussels that were unavailable or missed. Capture-recapture designs are expensive and time consuming and may not be feasible at all sites; however, similar designs may be applied to a subset of sites to attain estimates that correct data at other sites via a double sampling approach. Furthermore, considering the lack of information available about specific life histories of mussels in the Altamaha, designs that provide demographic information (survival, abundance, seasonal migration) can be applied in a learning (adaptive management) framework to make decisions (e.g., habitat protection, potential relocation areas) and learn about mussel population dynamics as new information becomes available.

Increasing effort improved the ability to detect population changes. Increasing effort (number of samples) is known to reduce the amount of variance (Thompson 2002), thus supporting simulated scenarios. However, effort is related to cost (Strayer and Smith 2003) limiting the total effort allowed. Therefore, although power increases with effort, proper stratification of effort may be adjusted for species to optimize the allocation of effort. Optimal effort is determined by the manager based on the degree at which power is maximized given a

limited amount of effort. For instance, targeting easily detected species (e.g. *L. dolabraeformis*) could likely suffice with less effort, with more effort given to species with lower detection (*A. arcula, E. spinosa*). However, allocation of effort not only pertains to total number of samples, but rather to the number of samples per habitat. Focusing greater sampling effort in areas that contain suitable habitat helps to detect specialist species (Christman 2004) rather than randomly sampling habitats and encountering individuals that may be in a site based on stochastic events, such as capturing *L. splendida* in swiftwaters during the capture-recapture study. The relative number of samples collected per stratum also had a substantial influence on power, with greater power when most samples were collected from the higher occurrence patches, rather than from intermediate or lower occurrence patches. This suggests that optimal designs should expend a greater effort sampling higher occurrence patches. However, this does not mean that all samples should be collected from high occurrence patches; some samples should be collected from what are perceived as lesser quality patches to avoid overestimation (Thompson 2002). Furthermore, if habitat preference (i.e. indicating areas with greater or lesser occurrence) is not well understood, equal sampling effort among sites should be implemented to avoid bias.

Temporary emigration explained much of the temporal variation in surface abundance at a location. This suggests that count indices, such as catch-per-unit-effort, are biased by species specific life histories and environmental factors that can effect mussel populations. For example, if sampling during a single season, the proportion captured with respect to total population size will be different for each species, potentially missing some species altogether. Additionally, if samples are taken during multiple seasons, the proportion captured within a given amount of time not only differs by species, but differs by season as well. Without accounting for missed species, occupancy is underestimated. However simply acknowledging that species are missed,

does not allow for any inferences unless detection is estimated. Temporary emigration is a special case in which there is no possibility of capture if the individual is below the surface. Robust Design allows for estimates of the probability that an individual will be at the surface and the probability of capturing an individual once at the surface. Therefore, not only can populations be estimated with less bias by accounting for incomplete capture, but seasonal migration patterns of mussels can be differentiated from observer effects. I would suggest that sampling be conducted during a period of highest possible detection (greater proportion at the surface) under safe conditions.

Another way to minimize variance is to choose a proper estimator and sample design. Estimators provide managers with information on mussel population status with less bias by accounting for incomplete detection (Strayer and Smith 2003). Because detection varied among mussel species, it is critical to account for missed mussels. Aside from the importance of using the proper estimator, I found that designs that randomly selected sites and revisited them through time detected trends in mussel populations better. Fixed sites also allow for additional estimation of demographic parameters (i.e. survival, recruitment) in conjunction with abundance estimates using the same design by incorporating capture-recapture designs at a sub-set of sites (double-sampling). Therefore, I believe that the best sample design for monitoring mussels in the Altamaha River is a design that estimates abundance within fixed sites, during a single season (presumably corresponding to greater surface abundance), with as much effort as possible properly stratified focusing more effort in areas with greater occurrence. However, if factors such as effort limit the number of sites that can be sampled, the ability to detect changes may be compromised. In contrast, if the population declines solely by site occupancy (i.e., no change in abundance until entire site becomes unoccupied), fixed sites have poor ability to detect changes

and occupancy estimation is suggested; given such circumstances, sampling to detect a change in occupancy and randomly selecting sites during each occasion would be a better protocol. Currently, the factors that affect population change in the Altamaha River are unknown, and likely differ by section or the river (i.e. sedimentation, chemical toxicity) and among species. I simulated two types of population decline (abundance, occupancy) based on how I believe the system may function. The plausibility that both scenarios may affect the population at the same time is a valid hypothesis. Future research may yield evidence towards population dynamics of mussels. Additionally, the development of a 'hybrid' simulation may need to be constructed to model both a reduction in patch abundance and patch occupancy simultaneously. With regard to uncertainty of system dynamics, the models from this study are useful in developing the framework of an adaptive management context, facilitating learning. Consequently, I believe that the current simulations are useful for evaluating the relative merits of various sample designs.

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Table 1. List of models created for each species analyzed with Program MARK using capture-recapture data.

Survival		Emigration		Capture probability			
constant	stratum	constant	stratum	constant	habitat	wood density	observer
x		x		x			
x		x			x		
x		x				x	
x		x					x
x			x	x			
x			x		x		
x			x			x	
x			x				x
	x	x		x			
	x	x			x		
	x	x				x	
	x	x					x
	x		x	x			
	x		x		x		
	x		x			x	
	x		x				x

Table 2. List of parameters of capture-recapture study and variations of models constructed with biological definitions as an explanation for constructing the model.

Parameter	Definition/Hypothesis
Survival 'S'	
Constant	Survival is constant among habitat.
Stratum	Survival varies among habitats.
Emigration 'G'	Temporary emigration is constant through time and among habitats.
Constant	
Seasonal	Temporary emigration varies among seasons, delineated by water temperatures.
Capture probability 'C'	The probability of capturing an individual was constant during each sampling period
Constant	
Habitat	The probability of capturing an individual varied by habitat type.
Large woody debris	Capture probabilities vary among habitats due to the presence of large woody debris (>0.75m diameter) encountered at least in 30% of transects per visit. More specifically downstream pool and upstream swiftwater sites had large woody debris making it difficult to sample around and underneath crevices.
Proportion of observer experience	Detection varies between sampling periods depending on the ratio of experienced (>40h prior mussel experience) observers to total observers for each sampling occasion.

Table 3. List of models created for each species analyzed with Program MARK for estimating occupancy.

Detection			Occupancy								
							substrate			juxtaposition	
constant	depth	area	constant	depth	current velocity	interaction	fine	coarse	compact	pool	sandbar
x			x								
x				x							
x					x						
x						x					
x							x				
x								x			
x									x		
x										x	
x											x
	x		x								
	x			x							
	x				x						
	x					x					
	x						x				
	x							x			
	x								x		

Table 3. continued.

Detection			Occupancy								
							substrate			juxtaposition	
constant	depth	area	constant	depth	current velocity	interaction	fine	coarse	compact	pool	sandbar
	x									x	
	x										x
		x	x								
		x		x							
		x			x						
		x				x					
		x					x				
		x						x			
		x							x		
		x								x	
		x									x
	x	x		x	x	x	x	x	x	x	x

Table 4. Mean, standard deviation (SD) and range of parameters of occupancy study and variations of models using site-specific covariates with biological definitions as an explanation for constructing the model.

		Site-Specific Covariates		
Parameter	Definition/Hypothesis	% Sites	Mean (SD)	Range
Detection				
Constant	Detection was modeled constant among all sites.			
Snorkel sites	Detection could differ among sites depending on depth and method. Samples were grouped as either a snorkel (0.7m<depth<1.5m) or non-snorkel (depth<0.7m or 1.5m<depth) sites.	48		
Proportion of Area Sampled	Detection was modeled as a function of proportion of area sampled (area sampled/total habitat area).		0.17 (0.1)	0.02 – 0.6
Occupancy				
Constant	Occupancy was constant across sites.			
Depth	Occupancy was dependant upon water depth in meters.		0.79 (0.37)	0.2 – 2.5
Current velocity	Occupancy depended upon current velocity in meters per second.		0.17 (0.1)	0-0.5
Depth*Current velocity	Occupancy was modeled as a function of the interaction of depth with respect to current velocity			
Fine particle substrate	Models were constructed based on areas containing large proportions of fine particulates (0-0.5mm)	14		

Table 4. continued.

Parameter	Definition/Hypothesis	Site-Specific Covariates % Sites	Mean (SD)	Range
Occupancy				
Large particle substrate	Models were constructed based on areas where coarse particulates (>1mm) deposit after high flow events.	18		
Compact substrate	Models were constructed based on areas with compact substrate.	68		
Adjacent to pool	Occupancy modeled as a function of a sites adjacency to pools.	36		
Adjacent to sandbar	Occupancy modeled as a function of a sites adjacency to sandbars.	38		

Table 5. Date and location (upper or lower river sites) for secondary sampling within six primary periods for capture-recapture sites and number of sites sampled per strata for occupancy sites.

	Capture-Recapture		Occupancy			
Sampling period	Upper	Lower	Slackwater	Pool	Glide	Swiftwater
6/20/2006 - 7/12/2006			7	1	2	1
7/19/2006 - 7/21/2006	X					
7/26/2006 - 7/28/2006		X				
8/1/2006 – 8/4/2006			11		1	1
8/29/2006 – 8/31/2006	X		4			
9/6/2006 – 9/8/2006		X		1		1
9/23/2006			9			
10/13/2006 – 10/15/2006	X					
10/19/2006 – 10/21/2006		X				
12/14/2006 – 12/16/2006		X	2		1	
12/17/2006 – 12/19/2006	X		3			
5/1/2007 – 5/3/2007	X	X				
5/8/2007*	X					
5/9/2007 – 6/15/2007			14	3	7	3
6/20/2007		X				
6/21/2007	X					
6/22/2007 – 6/29/2007			14	1	5	1

* one of the three upper sites was not sampled during 5/1-5/3/2007 due to unsafe conditions and instead was sampled on 5/8/2007.

Table 6. Total initial captures of individuals by species and primary period during 2006-2007 sampling period on the Altamaha River.

	Primary Period						
	1	2	3	4	5	6	Totals
Lampsilis splendida	180	95	82	34	74	60	525
L. dolabraeformis	112	96	61	31	72	59	431
Alasmidonta arcula	9	12	6	3	3	0	33
Pyganodon gibbosa	3	2	4	3	1	0	13
Totals	304	205	153	71	150	119	1002

Table 7. Deviance information criteria (DIC) and weights (w_i) for the confidence set of Robust Design models for estimating mussel survival, temporary emigration, and capture probability by species.

Model				
Survival	Temporary emigration	Capture probability	DIC	w_i
Alasmidonta arcula				
constant[1]	constant	constant	256.38	0.501
constant[1]	seasonal	constant	257.40	0.301
constant[1]	constant	observer experience	259.25	0.119
constant[1]	seasonal	observer experience	260.08	0.079
Lampsilis dolabraeformis				
habitat	seasonal	habitat	-1350.26	0.478
habitat	seasonal	observer experience	-1349.11	0.269
constant	seasonal	habitat	-1348.34	0.183
L. splendida				
habitat	seasonal	constant	-451.25	0.588
habitat	seasonal	large woody debris	-448.63	0.159
habitat	seasonal	habitat	-448.43	0.144
habitat	seasonal	observer experience	-447.65	0.097
Pyganodon gibbosa				
habitat	seasonal	constant	118.11	0.249
constant	seasonal	constant	118.31	0.225
habitat	seasonal	observer experience	119.38	0.132
constant	seasonal	habitat[2]	119.51	0.123
constant	seasonal	observer experience	119.53	0.122
habitat	seasonal	habitat[2]	119.89	0.102

[1] = *A. arcula* was only found in a single habitat, thus modeled as constant.

[2] = *P. gibbosa* was only found at two sites (1 pool, 1 slackwater). Large woody debris was present only at the pool site, thus model also represents large woody debris.

Table 8. Importance weights and evidential ratios for the first and second best predicting covariate regarding demographic parameters for selected species in the Altamaha River.

Hypothesis	Importance weight	Evidence ratio
Alasmidonta arcula		
Temp. Emigration		
Constant	0.620	1.63
Seasonal	0.380	
Capture/Recapture		
Constant	0.802	4.05
Observer experience	0.198	
Lampsilis dolabraeformis		
Survival		
Grouped by habitat	0.803	4.08
Constant	0.197	
Temporary Emigration		
Seasonal	0.999	>1000
Constant	<0.001	
Capture/Recapture		
Habitat	0.661	2.41
Observer experience	0.274	
L. splendida		
Survival		
Grouped by habitat	0.993	>100
Constant	0.005	
Temporary Emigration		
Seasonal	0.993	>100
Constant	0.005	
Capture/Recapture		
Constant	0.588	3.62
Woody debris	0.162	

Table 8. continued.

Hypothesis	Importance weight	Evidence ratio
Pyganodon gibbosa		
Survival		
Constant	0.494	
Grouped by habitat	0.506	1.02
Temporary Emigration		
Seasonal	0.953	20.11
Constant	0.047	
Capture/Recapture		
Constant	0.495	1.85
Observer experience	0.268	

Table 9. Parameter estimates, standard deviations (SD), and upper and lower 95% Bayesian confidence limits of six-week survival between primary periods, temporary emigration, and capture probabilities for selected mussel species. Mean annual survival calculated based on survival over a 12 month interval.

	Alasmidonta arcula		*Lampsilis dolabraeformis*		*L. splendida*		*Pyganodon gibbosa*	
Parameter	Mean (SD)	95% BCL	Mean (SD)	95% BCL	Mean (SD)	95% BCL	Mean (SD)	95% BCL
Six-Week Survival								
Slackwater	0.88 (0.07)	0.73-0.98	0.99 (0.02)	0.96-0.99	0.99 (0.01)	0.97-0.99	0.91 (0.10)	0.62-0.99
Pool			0.99 (0.04)	0.95-0.99	0.94 (0.04)	0.86-0.99	0.88 (0.10)	0.64-0.99
Swiftwater			0.97 (0.05)	0.86-0.99	0.89 (0.07)	0.75-0.99		
Annual Survival								
Slackwater	0.33	0.07-0.84	0.92	0.72-0.92	0.92	0.78-0.92	0.44	0.02-0.92
Pool			0.92	0.66-0.92	0.78	0.30-0.92	0.33	0.02-0.92
Swiftwater			0.78	0.3-0.92	0.39	0.01-0.92		
Temporary emigration								
Summer	0.64 (0.09)	0.43-0.79	0.08 (0.03)	0.03-0.15	0.04 (0.02)	0.01-0.09	0.80 (0.12)	0.50-0.96
Fall	0.64 (0.09)	0.43-0.79	0.4 (0.07)	0.26-0.52	0.05 (0.05)	0.01-0.17	0.35 (0.19)	0.04-0.75
Winter	0.64 (0.09)	0.43-0.79	0.47 (0.06)	0.35-0.58	0.34 (0.07)	0.21-0.46	0.92 (0.10)	0.64-0.99
Spring	0.64 (0.09)	0.43-0.79	0.11(0.07)	0.01-0.26	0.25 (0.07)	0.1-0.39	0.74 (0.17)	0.28-0.96
Capture probability								
Slackwater	0.29 (0.04)	0.21-0.37	0.19 (0.01)	0.17-0.21	0.12 (0.01)	0.11-0.13	0.26 (0.06)	0.16-0.39
Pool			0.13 (0.02)	0.1-0.16				
Swiftwater			0.15 (0.01)	0.12-0.18				

Table 10. Mean effective capture probabilities for each species by season with simulated 95% Bayesian credibility limits (BCL) based on temporary emigration and conditional capture probability estimates from the capture-recapture study.

	Estimate: Mean (95% BCL)			
Parameter	Summer[1]	Fall	Winter	Spring
Alasmidonta arcula				
Conditional Capture	0.29 (0.21-0.37)			
Temporary Emigration	0.64 (0.43-0.79)			
Effective Capture	0.1 (0.05-0.17)			
Lampsilis dolabraeformis				
Conditional Capture	0.16 (0.13-0.18)			
Temporary Emigration	0.08 (0.03-0.15)	0.4 (0.26-0.52)	0.47 (0.35-0.58)	0.11 (0.01-0.26)
Effective Capture	0.15 (0.11-0.17)	0.1 (0.06-0.13)	0.08 (0.05-0.12)	0.14 (0.1-0.18)
L. splendida				
Conditional Capture	0.12 (0.11-0.13)			
Temporary Emigration	0.04 (0.01-0.09)	0.05 (0.01-0.17)	0.34 (0.21-0.46)	0.25 (0.1-0.39)
Effective Capture	0.12 (0.1-0.13)	0.11 (0.09-0.13)	0.08 (0.06-0.1)	0.09 (0.07-0.12)
Pyganodon gibbosa				
Conditional Capture	0.26 (0.16-0.39)			
Temporary Emigration	0.8 (0.5-0.96)	0.35 (0.04-0.75)	0.92 (0.64-0.99)	0.74 (0.28-0.96)
Effective Capture	0.05 (0.01-0.13)	0.16 (0.06-0.31)	0.02 (<0.01-0.08)	0.07 (<0.01-0.17)

[1] : only shown once if modeled constant across seasons.

Table 11. Mean superpopulation estimates for each site by species with simulated 95% Bayesian credibility limits (BCL) based on temporary emigration and surface abundance estimates from the capture-recapture study.

	Estimate: Mean (95% BCL)					
	Slackwater		Pool		Swiftwater	
Parameter	Downstream	Upstream	Downstream	Upstream	Downstream	Upstream
Alasmidonta arcula						
Temporary						
Emigration	0.64 (0.43-0.79)	0.64 (0.43-0.79)				
Surface Abundance	11 (8-18)	7 (5-12)				
Superpopulation	31 (15-67)	20 (8-43)				
Lampsilis dolabraeformis						
Temporary						
Emigration	0.08 (0.03-0.15)	0.08 (0.03-0.15)	0.08 (0.03-0.15)	0.08 (0.03-0.15)	0.08 (0.03-0.15)	0.08 (0.03-0.15)
Surface Abundance	294 (253-341)	98 (78-122)	25 (13-44)	25 (13-43)	19 (11-33)	104 (79-138)
Superpopulation	320 (261-401)	107 (80-144)	27 (13-52)	27 (13-51)	21 (11-39)	113 (81-162)
L. splendida						
Temporary						
Emigration	0.04 (0.01-0.09)	0.04 (0.01-0.09)	0.04 (0.01-0.09)	0.04 (0.01-0.09)	0.04 (0.01-0.09)	0.04 (0.01-0.09)
Surface Abundance	544 (463-580)	279 (229-301)	65 (45-75)	16 (7-20)	4 (1-12)	29 (17-34)
Superpopulation	567 (468-637)	291 (231-331)	68 (45-82)	17 (7-22)	4 (1-13)	30 (17-37)

Table 11. continued.

	Estimate: Mean (95% BCL)					
	Slackwater		Pool		Swiftwater	
Parameter	Downstream	Upstream	Downstream	Upstream	Downstream	Upstream
Pyganodon gibbosa						
Temporary						
Emigration		0.80 (0.50-0.96)	0.80 (0.50-0.96)			
Surface Abundance		9 (6-10)	4 (3-5)			
Superpopulation		14 (5-37)	6 (2-16)			

Table 12. Names of the 12 species encountered and number of sites per stratum where they were encountered.

Species	Number of Sites			
	Slackwater	Pool	Glide	Swiftwater
Alasmidonta arcula	12	4	7	0
Elliptio dariensis	34	5	13	3
Elliptio hopetonensis	43	5	16	3
*Elliptio icterina**	24	4	13	2
Elliptio shpeardiania	34	5	16	2
Elliptio spinosa	2	0	2	0
Lampsilis dolabraeformis	37	5	15	6
Lampsilis splendida	36	3	13	1
Pyganodon gibbosa	12	2	1	0
Uniomerus carolinianus	2	1	1	0
Utterbackia imbecillis	13	0	1	0
Villosa delumbis	29	3	6	1

* Most mussels are *E. icterina* but may contain other described and undescribed species within the *E. complanata / icterina* complex.

Table 13. Confidence set of models compared to global model (w_i within $1/8^{th}$ of best fitting model) by species of the probability of detecting a species in a single sample and proportion of sites occupied. Models ranked and assigned a weight (w_i) based on respective AIC value given by program MARK.

Model		AIC	w_i
Alasmidonta arcula			
Probability of detection	**Probability of occupancy**		
proportion of area sampled	current velocity	391.15	0.308
constant	current velocity	393.25	0.108
snorkel sites	current velocity	394.20	0.067
proportion of area sampled	constant	394.71	0.052
proportion of area sampled	adjacent to pool	394.96	0.046
proportion of area sampled	coarse substrate	395.26	0.039
proportion of area sampled	water depth	395.28	0.039
proportion of area sampled + snorkel sites	current velocity + water depth + depth*current velocity + fine particle substrate + coarse substrate + compact substrate + adjacent to pool + adjacent to sandbar	395.36	0.038
Elliptio spinosa			
Probability of detection	**Probability of occupancy**		
constant *	constant*	78.36	0.49
proportion of area sampled + snorkel sites	current velocity + water depth + depth*current velocity + fine particle substrate + coarse substrate + compact substrate + adjacent to pool + adjacent to sandbar	88.61	0.000

Table 13. continued.

Model		AIC	w_i
Lampsilis dolabraeformis			
Probability of detection	**Probability of occupancy**		
constant	water depth	976.35	0.236
constant	coarse substrate	977.55	0.129
proportion of area sampled	water depth	977.94	0.07
snorkel sites	water depth	978.58	0.076
proportion of area sampled	coarse substrate	979.14	0.059
constant	compact substrate	979.31	0.054
constant	constant	979.62	0.046
snorkel sites	coarse substrate	979.78	0.043
constant	adjacent to sandbar	980.59	0.028
	current velocity + water depth + depth*current velocity + fine particle substrate + coarse substrate + compact substrate + adjacent to pool + adjacent to sandbar		
proportion of area sampled + snorkel sites		990.23	0.001

Table 13 continued.

L. splendida			
Probability of detection	**Probability of occupancy**		
snorkel sites	current velocity	894.63	0.545
constant	current velocity	898.22	0.091
snorkel sites	coarse substrate	898.62	0.074
	current velocity + water depth + depth*current velocity + fine particle substrate + coarse substrate + compact substrate + adjacent to pool + adjacent to sandbar		
proportion of area sampled + snorkel sites		901.83	0.015

Table 13. continued.

Model		AIC	w_i
Pyganodon gibbosa			
Probability of detection	**Probability of occupancy**		
constant	current velocity	216.95	0.337
snorkel sites	current velocity	218.30	0.171
proportion of area sampled	current velocity	219.09	0.116
constant	water depth	220.69	0.052
proportion of area sampled + snorkel sites	current velocity + water depth + depth*current velocity + small particle substrate + coarse substrate + compact substrate + adjacent to pool + adjacent to sandbar	233.33	0.000

*Only model within set to contain estimatable parameters.

Table 14. Akaike importance weights and evidential ratio for the first and second best predicting covariate regarding detection and occupancy for selected species in the Altamaha River.

Hypothesis	Importance weight	Evidence ratio
Alasmidonta arcula		
Detection		
Constant	0.571	
Area	0.217	2.63
Occupancy		
Constant	0.089	
Current Velocity	0.472	5.30
Lampsilis dolabraeformis		
Detection		
Constant	0.559	2.54
Area	0.22	
Occupancy		
Depth	0.42	1.83
Coarse substrate	0.23	

Table 14. continued.

Hypothesis	Importance weight	Evidence ratio
L. splendida		
Detection		
Snorkel sites	0.801	7.78
Constant	0.103	
Occupancy		
Current Velocity	0.669	7.69
Coarse substrate	0.087	
Pyganodon gibbosa		
Detection		
Constant	0.511	1.93
Snorkel sites	0.265	
Occupancy		
Current Velocity	0.624	6.57
Depth	0.095	

Table 15. Variation of transect detection estimates, with standard error (SE) and 95% confidence intervals, for selected sites revisited during occupancy sampling.

	Visit			Re-Visit		
Species	Estimate	SE	95% CI	Estimate	SE	95% CI
Alasmidonta arcula	0.17	0.03	(0.11, 0.23)	0.16	0.03	(0.11, 0.24)
Elliptio spinosa	0.04	0.03	(0.01, 0.16)	0.09	0.05	(0.03, 0.25)
Lampsilis dolabraeformis	0.61	0.02	(0.56, 0.65)	0.44	0.04	(0.38, 0.52)
L. splendida	0.38	0.03	(0.33, 0.43)	0.32	0.03	(0.26, 0.39)
Pyganodon gibbosa	0.12	0.03	(0.07, 0.20)	0.09	0.04	(0.04, 0.20)

Table 16. Parameter estimates, standard errors (SE), and upper and lower 95% confidence intervals (CI) of detection per transect and occupancy with covariate effects of the best fitting model for each species.

Parameter	Estimate	SE	95% CI	Unit Change	Scaled odds ratio (95% Unit Change)
Alasmidonta arcula					
Detection					
Intercept	-1.63	0.21	(-2.03, -1.22)		
Proportion of area sampled	-0.38	0.19	(-0.75, -0.01)	0.1	0.96 (0.93-0.99)
Occupancy					
Intercept	-0.66	0.31	(-1.26, -0.05)		
Current Velocity	-0.76	0.35	(-1.43, -0.08)	0.1	0.93 (0.87-0.99)
Elliptio spinosa					
Detection					
Intercept	-3.26	0.81	(-4.85, -1.66)		
Occupancy					
Intercept	-1.95	0.71	(-3.35, -0.55)		
Lampsilis dolabraeformis					
Detection					
Intercept	0.44	0.1	0.25, 0.63)		
Occupancy					
Intercept	1.03	0.3	(0.45, 1.61)		
Depth	0.89	0.45	(0.01, 1.76)	0.3	1.31 (1-1.7)
L. splendida					
Detection					
Intercept	-0.50	0.11	(-0.71, -0.29)		
Snorkel Depth	0.21	0.09	(0.04, 0.38)		1.07 (1.01-1.12)
Occupancy					
Intercept	0.60	0.27	(0.07, 1.12)		
Current Velocity	-0.73	0.28	(-1.28, -0.18)	0.1	0.93 (0.88-0.98)

Table 16. continued.

Parameter	Estimate	SE	95% CI	Unit Change	Scaled odds ratio (95% Unit Change)
Pyganodon gibbosa					
Detection					
Intercept	-2.01	0.30	(-2.60, -1.41)		
Occupancy					
Intercept	-1.36	0.43	(-2.20, -0.52)		
Current Velocity	-1.06	0.47	(-1.98, -0.14)	0.1	0.9 (0.82-0.99)

Table 17. List of scenarios with respective values used in simulations. Simulations ran all possible combinations of the following scenarios under various designs (ability to detect a change in abundance/occupancy) and population dynamics (decline in abundance/occupied sites)

Parameter	Values
Population Decline	4% ; 2%
Sites per Occasion	60 ; 30
Allocation of Effort	Equal Unequal -1 (slackwater = 53%, pool = 33%, swiftwater = 4%) Unequal -2 (pool = 53%, slackwater = 33%, swiftwater = 4%) Unequal -3 (pool = 53%, swiftwater = 33%, slackwater = 4%)
Distribution (percent occupied habitat)	Wide & Equal (0.5) Wide& Unequal (slackwater = 0.75, pool = 0.5, swiftwater = 0.25) Low & Equal (0.2) Low & Unequal (slackwater = 0.4, pool = 0.15, swiftwater = 0.05)
Initial Population (Individuals per occupied site)	High (slackwater = 300, pool = 150, swiftwater = 50) Low (slackwater = 60, pool = 30, swiftwater = 10)
Samples per Occasion (with respective capture probabilities)	1-Season (Summer = 0.1) 2-Seasons (Summer = 0.1 + Fall = 0.2)
Site Selection	Fixed Sites Complete Random with Replacement

Table 18. Mean power to detect population change among sampling design given different allocation of effort. Alpha level = 0.05.

	Decline in mussel density		Decline in occupied sites	
Allocation of effort	Complete replacement	Fixed sites	Complete replacement	Fixed sites
Equal	0.425	0.520	0.253	0.004
Most at high and least at low occurrence	0.487	0.581	0.283	0.005
Most at intermediate and least at low occurrence	0.438	0.554	0.268	0.004
Most at intermediate and least at high occurrence	0.310	0.412	0.118	0.004

Table 19. Overdispersion (c-hat) estimates for data sets. Values are represented according to the type of simulated population decline and method for evaluating the population, listed given alpha level 0.05 and 0.1 separated by " | ".

	Simulated Population Decline	
Method of Evaluation of Sampling	Abundance	Occupied Patches
Abundance	6.89 | 5.95	1.67 | 1.43
Occupancy	0.52 | 0.56	2.81 | 2.98

Table 20. Parameter estimates and standard error in parentheses from best fitting logistic regression models relating the rate of power to detect changes in density at alpha levels of 0.05 and 0.1 during simulation of decline in abundance.

	Alpha = 0.05		Alpha = 0.1	
Parameter	Estimate	Scaled Odds	Estimate	Scaled Odds
Intercept	-1.22 (0.09)		-0.82 (0.09)	
Rate of decline	0.41 (0.09)	**1.51**	0.33 (0.09)	**1.39**
Sites sampled per occasion	0.27 (0.09)	**1.31**	0.18 (0.09)	1.20
Stratified effort	-0.07 (0.09)	0.93	0.01 (0.09)	1.01
Wide distribution	0.42 (0.09)	**1.53**	0.39 (0.09)	**1.48**
Equal distribution	0.01 (0.09)	1.01	-0.01 (0.09)	0.99
Initial population size	0.86 (0.10)	1.09	-0.12 (0.09)	0.89
2-Season sampling	-0.10 (0.10)	0.91	-0.12 (0.09)	0.89
Fixed sites	-0.02 (0.09)	0.98	0.01 (0.09)	1.01
Rate of decline* Sites sampled	0.45 (0.07)	**1.57**	0.51 (0.06)	**1.67**
Rate of decline* Stratified effort	0.32 (0.07)	**1.37**	0.23 (0.06)	1.25
Rate of decline* Wide distribution	0.64 (0.07)	**1.90**	0.71 (0.06)	**2.04**
Rate of decline* Equal distribution	0.11 (0.07)	1.12	0.23 (0.06)	1.26
Rate of decline* Initial population	0.02 (0.07)	1.02	0.11 (0.06)	1.12
Rate of decline* 2-Season sampling	-0.07 (0.07)	0.93	-0.15 (0.06)	0.86
Rate of decline* Fixed sites	0.38 (0.07)	**1.46**	0.38 (0.06)	**1.46**
Number of sites sampled*Stratified effort	0.08 (0.0.7)	1.09	0.09 (0.06)	1.10
Number of sites sampled*Wide distribution	0.28 (0.07)	**1.32**	0.31 (0.06)	**1.36**
Number of sites sampled* Equal distribution	0.06 (0.06)	1.07	0.05 (0.06)	1.05

Table 20. continued.

Parameter	Alpha = 0.05 Estimate	Alpha = 0.05 Scaled Odds	Alpha = 0.1 Estimate	Alpha = 0.1 Scaled Odds
Number of sites sampled* Initial population	-0.13 (0.06)	0.88	-0.04 (0.06)	0.96
Number of sites sampled* 2-Season sampling	-0.11 (0.06)	0.90	-0.01 (0.06)	0.99
Number of sites sampled* Fixed sites	0.23 (0.06)	1.25	0.23 (0.06)	1.26
Stratified effort* Wide distribution	0.13 (0.07)	1.14	0.10 (0.06)	1.10
Stratified effort* Equal distribution	0.25 (0.06)	1.29	0.22 (0.06)	1.25
Stratified effort * Initial population	-0.01 (0.06)	0.99	-0.02 (0.06)	0.98
Stratified effort * 2-Seasonsampling	-0.05 (0.06)	0.95	-0.05 (0.06)	0.95
Stratified effort * Fixed sites	0.05 (0.06)	1.05	0.08 (0.06)	1.09
Wide*Equal distribution	0.04 (0.06)	1.04	0.08 (0.06)	1.09
Wide distribution* Init. population	0.06 (0.06)	1.06	0.06 (0.06)	1.06
Wide distribution * 2-Season sampling	-0.03 (0.06)	0.97	-0.02 (0.06)	0.98
High distribution * Fixed sites	0.14 (0.07)	1.15	0.10 (0.06)	1.11
Equal distribution* Initial population	0.00 (0.06)	1.00	0.01 (0.06)	1.01
Equal distribution* 2-Season sampling	0.13 (0.06)	1.14	0.03 (0.06)	1.03
Equal distribution* Fixed sites	-0.09 (0.06)	0.91	-0.08 (0.06)	0.92
Initial population* 2- Season sampling	-0.05 (0.06)	0.95	0.09 (0.06)	1.10
Initial population*Fixed sites	0.11 (0.06)	1.12	0.16 (0.06)	1.17
2-Season sampling*Fixed sites	0.16 (0.06)	1.18	0.13 (0.06)	1.14

Table 21. Parameter estimates and standard error in parentheses from best fitting logistic regression models relating the rate of power to detect changes in occupancy at alpha levels of 0.05 and 0.1 during simulation of decline in proportion of occupied sites.

	Alpha = 0.05		Alpha = 0.1	
Parameter	Estimate	Scaled Odds	Estimate	Scaled Odds
Intercept	-2.61 (0.2)		-1.88 (0.18)	
Rate of decline	1.11 (0.18)	**3.03**	1.05 (0.17)	**2.86**
Sites sampled per occasion	0.74 (0.18)	**2.10**	0.65 (0.17)	**1.92**
Stratified effort	0.06 (0.18)	1.06	0.11 (0.17)	1.11
Wide distribution	1.13 (0.18)	**3.10**	1.00 (0.17)	**2.72**
Equal distribution	0.4 (0.18)	**1.49**	0.35 (0.17)	**1.42**
Initial population size	0.43 (0.18)	**1.54**	0.40 (0.17)	**1.49**
2-Season sampling	-1.64 (0.27)	**0.19**	-1.37 (0.22)	**0.25**
Fixed sites	-1.59 (0.26)	**0.20**	-2.26 (0.24)	**0.10**
Rate of decline* Sites sampled	0.17 (0.13)	1.19	0.16 (0.13)	1.17
Rate of decline* Stratified effort	0.08 (0.13)	1.08	0.08 (0.13)	1.08
Rate of decline* Wide distribution	0.37 (0.13)	**1.45**	0.35 (0.13)	**1.42**
Rate of decline* Equal distribution	0.03 (0.13)	1.03	0.02 (0.13)	1.02
Rate of decline* Initial population	-0.07 (0.13)	0.93	-0.09 (0.13)	0.91
Rate of decline* 2-Season sampling	-0.88 (0.19)	**0.41**	-0.86 (0.16)	**0.42**
Rate of decline* Fixed sites	-1.12 (0.18)	**0.33**	-1.04 (0.17)	**0.35**
Number of sites sampled*Stratified effort	-0.02 (0.13)	0.98	-0.01 (0.13)	0.99
Number of sites sampled*Wide distribution	0.34 (0.13)	**1.40**	0.33 (0.13)	**1.39**
Number of sites sampled* Equal distribution	-0.13 (0.13)	0.88	-0.09 (0.13)	0.91

Table 21. continued.

Parameter	Alpha = 0.05 Estimate	Alpha = 0.05 Scaled Odds	Alpha = 0.1 Estimate	Alpha = 0.1 Scaled Odds
Number of sites sampled* Initial population	-0.04 (0.13)	0.96	-0.07 (0.13)	0.93
Number of sites sampled* 2-Season sampling	-0.63 (0.19)	**0.53**	-0.67 (0.15)	**0.51**
Number of sites sampled* Fixed sites	-0.36 (0.18)	**0.70**	-0.24 (0.17)	0.79
Stratified effort* Wide distribution	0.13 (0.13)	1.14	0.11 (0.13)	1.12
Stratified effort* Equal distribution	0.31 (0.31)	**1.36**	0.21 (0.13)	1.23
Stratified effort * Initial population	-0.01 (0.13)	0.99	-0.06 (0.13)	0.94
Stratified effort * 2-Seasonsampling	-0.18 (0.18)	0.84	-0.24 (0.15)	0.79
Stratified effort * Fixed sites	-0.38 (0.18)	**0.68**	-0.23 (0.16)	0.79
Wide*Equal distribution	-0.05 (0.13)	0.95	-0.05 (0.13)	0.95
Wide distribution* Initial population	0.02 (0.13)	1.02	0.10 (0.13)	1.11
Wide distribution * 2-Season sampling	-1.22 (0.19)	**0.30**	-1.14 (0.16)	**0.32**
Wide distribution * Fixed sites	-0.68 (0.19)	**0.51**	-0.48 (0.17)	**0.62**
Equal distribution* Initial population	-0.13 (0.13)	0.88	-0.03 (0.13)	0.97
Equal distribution* 2-Season sampling	-0.34 (0.18)	**0.71**	-0.29 (0.15)	**0.75**
Equal distribution* Fixed sites	-0.35 (0.18)	**0.70**	-0.21 (0.16)	0.81
Initial population* 2- Season sampling	-0.15 (0.18)	0.86	-0.28 (0.15)	0.76
Initial population*Fixed sites	-0.43 (0.18)	**0.65**	-0.22 (0.16)	0.80
2-Season sampling*Fixed sites	2.89 (0.21)	**17.99**	2.91 (0.18)	**18.36**

Table 22. Parameter estimates and standard error in parentheses from best fitting logistic regression models relating the rate of power to detect changes in density for common generalist species at alpha levels of 0.05 during simulations of decline in both abundance and occupancy over time.

	Decline in Abundance		Decline in Occupancy	
Parameter	Estimate	Scaled Odds	Estimate	Scaled Odds
Intercept	-0.36 (0.34)		-0.46 (0.24)	
More sites sampled per occasion	0.54 (0.41)	**1.71**	1.06 (0.33)	**2.89**
Stratified effort	0.20 (0.41)	1.22	0.26 (0.33)	1.30
1-Season sampling	0.15 (0.41)	1.16	3.50 (0.66)	**33.00**
Fixed sites	0.49 (0.41)	**1.63**	-3.34 (0.63)	**0.04**
More sites sampled*Stratified effort	0.03 (0.41)	1.03	-0.23 (0.44)	0.79
More sites sampled*1-Season sampling	0.06 (0.41)	1.07	0.67 (0.68)	**1.96**
More sites sampled* Fixed sites	0.12 (0.41)	1.12	0.09 (0.63)	1.09
Stratified effort*1-Season sampling	0.03 (0.41)	1.03	0.17 (0.66)	1.19
Stratified effort* Fixed sites	-0.02 (0.41)	0.98	-0.23 (0.60)	0.79
1-Season sampling*Fixed sites	-0.08 (0.41)	0.93	3.12 (0.70)	**22.65**

Table 23. Parameter estimates and standard error in parentheses from best fitting logistic regression models relating the rate of power to detect changes in density for common specialist species at alpha levels of 0.05 during simulations of decline in both abundance and occupancy over time.

	Decline in Abundance		Decline in Occupancy	
Parameter	Estimate	Scaled Odds	Estimate	Scaled Odds
Intercept	-0.21 (0.35)		-0.17 (0.23)	
More sites sampled per occasion	0.69 (0.43)	**1.99**	0.76 (0.32)	**2.14**
Stratified effort	0.43 (0.43)	**1.54**	0.55 (0.32)	**1.73**
1-Season sampling	0.18 (0.43)	1.20	3.91 (0.65)	**50.00**
Fixed sites	0.45 (0.43)	**1.56**	-3.88 (0.67)	**0.02**
More sites sampled*Stratified effort	-0.03 (0.44)	0.97	0.15 (0.44)	1.16
More sites sampled*1-Season sampling	0.04 (0.44)	1.04	0.53 (0.67)	**1.69**
More sites sampled* Fixed sites	0.07 (0.44)	1.07	0.28 (0.67)	1.32
Stratified effort*1-Season sampling	-0.10 (0.44)	0.90	0.37 (0.65)	**1.45**
Stratified effort* Fixed sites	0.01 (0.44)	1.01	-0.76 (0.63)	**0.47**
1-Season sampling*Fixed sites	-0.24 (0.44)	0.79	3.85 (0.69)	**46.99**

Table 24. Parameter estimates and standard error in parentheses from best fitting logistic regression models relating the rate of power to detect changes in density for rare generalist species at alpha levels of 0.05 during simulations of decline in both abundance and occupancy over time.

	Decline in Abundance		Decline in Occupancy	
Parameter	Estimate	Scaled Odds	Estimate	Scaled Odds
Intercept	-1.11 (0.28)		-1.76 (0.20)	
More sites sampled per occasion	0.39 (0.33)	**1.48**	0.83 (0.25)	**2.29**
Stratified effort	0.15 (0.33)	1.16	0.04 (0.27)	1.04
1-Season sampling	0.01 (0.33)	1.01	1.97 (0.41)	**7.14**
Fixed sites	0.42 (0.33)	**1.52**	-2.39 (0.47)	**0.09**
More sites sampled*Stratified effort	-0.07 (0.32)	0.93	0.02 (0.33)	1.02
More sites sampled*1-Season sampling	0.16 (0.32)	1.17	0.78 (0.44)	**2.17**
More sites sampled* Fixed sites	0.24 (0.32)	1.27	-0.55 (0.47)	**0.58**
Stratified effort*1-Season sampling	0.17 (0.32)	1.19	-0.03 (0.44)	0.97
Stratified effort* Fixed sites	-0.18 (0.32)	0.84	-0.03 (0.47)	0.97
1-Season sampling*Fixed sites	-0.08 (0.32)	0.93	2.34 (0.48)	**10.38**

Table 25. Parameter estimates and standard error in parentheses from best fitting logistic regression models relating the rate of power to detect changes in density for rare specialist species at alpha levels of 0.05 during simulations of decline in both abundance and occupancy over time.

	Decline in Abundance		Decline in Occupancy	
Parameter	Estimate	Scaled Odds	Estimate	Scaled Odds
Intercept	-0.85 (0.27)		-1.41 (0.23)	
More sites sampled per occasion	0.31 (0.32)	**1.36**	0.67 (0.29)	**1.95**
Stratified effort	0.13 (0.32)	1.14	0.28 (0.30)	1.32
1-Season sampling	0.07 (0.32)	1.07	2.53 (0.53)	**12.50**
Fixed sites	0.24 (0.32)	1.31	-1.99 (0.47)	**0.14**
More sites sampled*Stratified effort	0.20 (0.31)	1.23	0.10 (0.37)	1.11
More sites sampled*1-Season sampling	0.08 (0.31)	1.08	0.39 (0.55)	**1.47**
More sites sampled* Fixed sites	0.18 (0.31)	1.20	-1.21 (0.55)	**0.30**
Stratified effort*1-Season sampling	0.06 (0.31)	1.06	0.17 (0.54)	1.19
Stratified effort* Fixed sites	0.22 (0.31)	1.24	-0.32 (0.54)	**0.73**
1-Season sampling*Fixed sites	-0.23 (0.31)	0.80	2.07 (0.61)	**7.92**

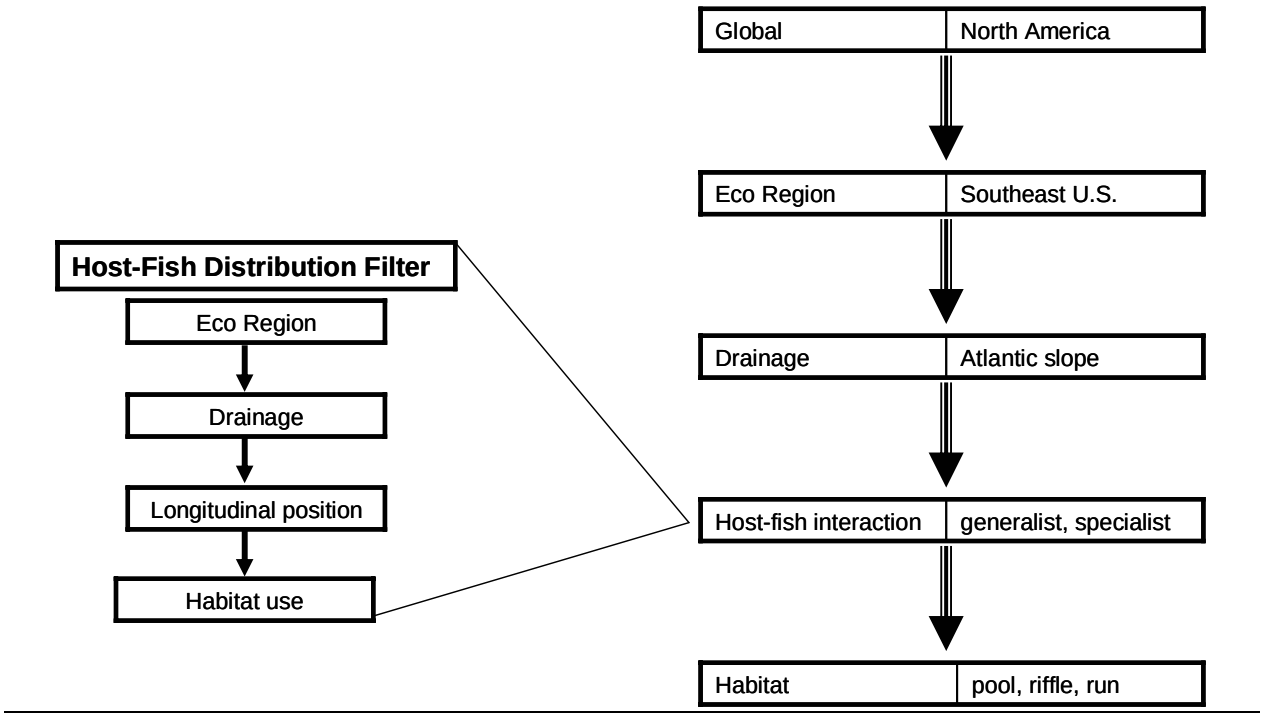

Figure 1. Distribution filter for freshwater mussels.

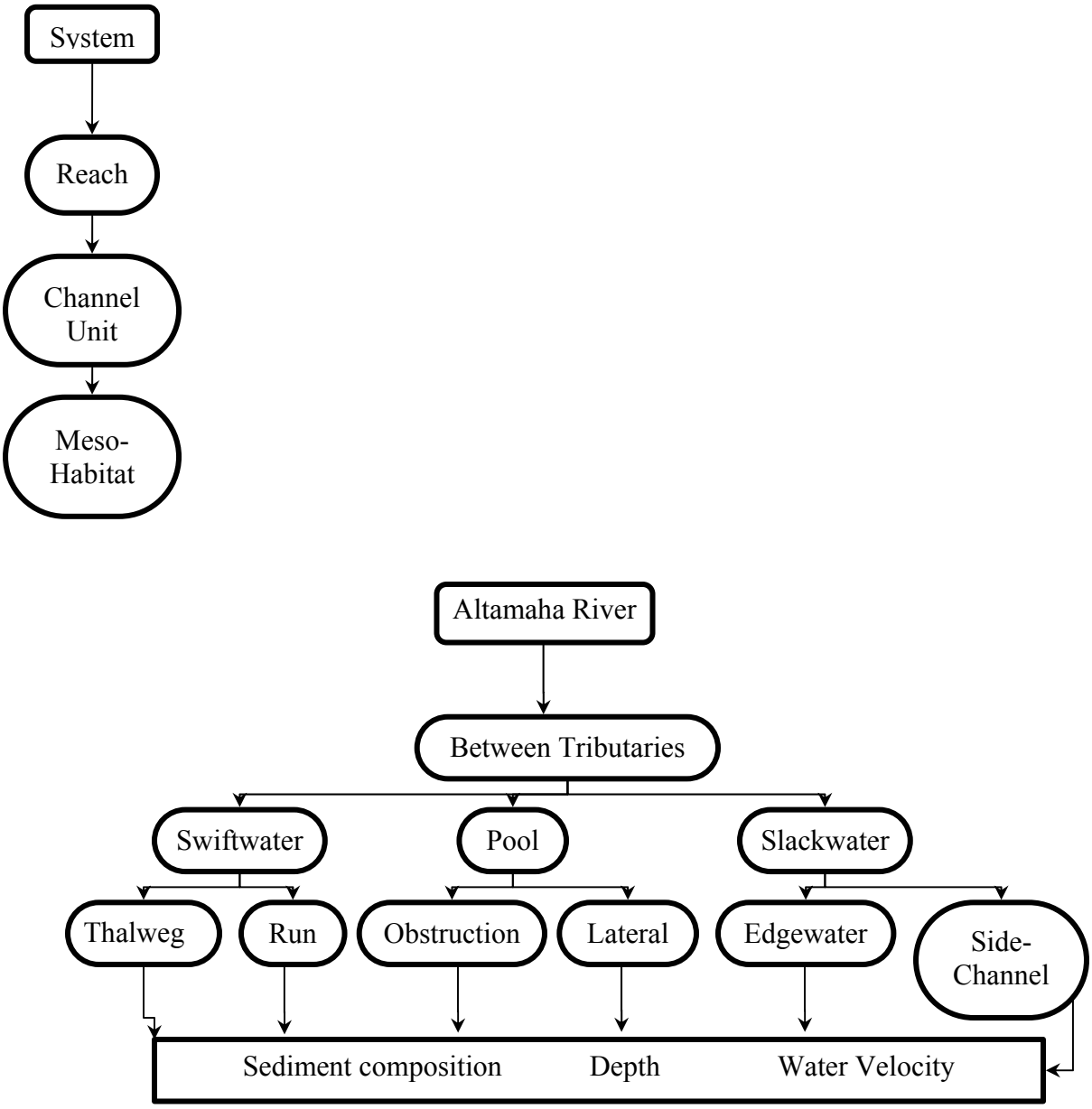

Figure 2. Hierarchal units of distribution scales.

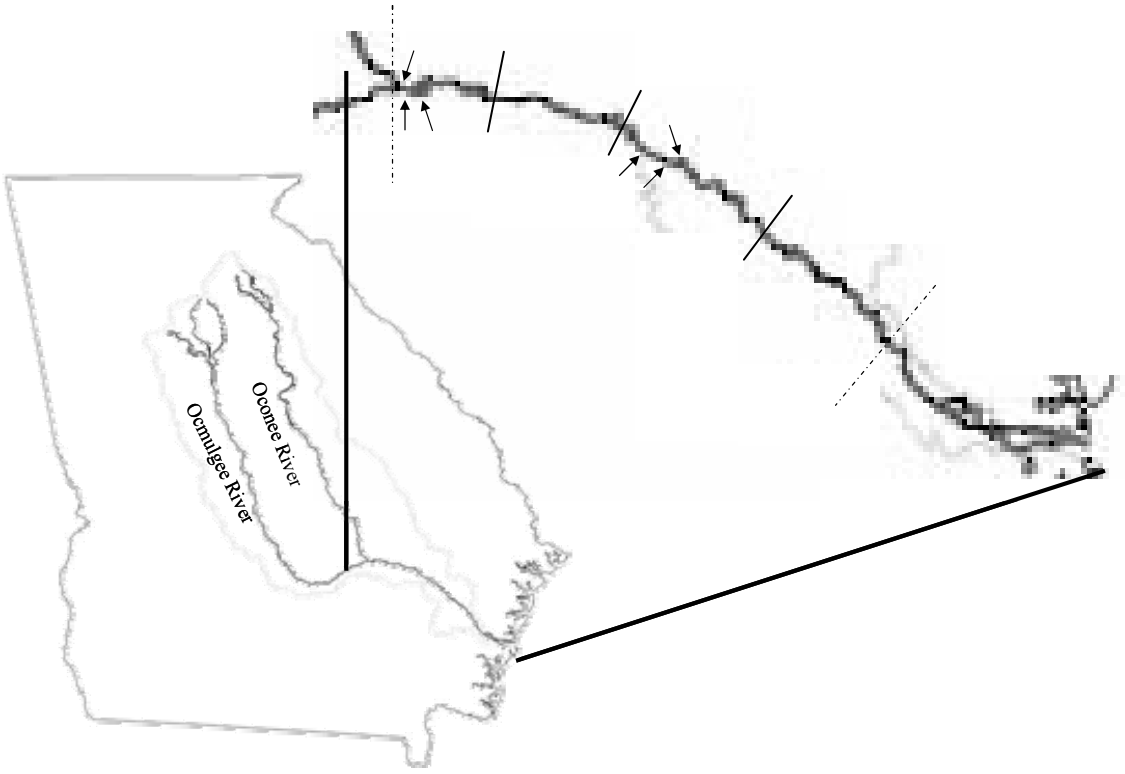

Figure 3. Altamaha River basin with major rivers, inset displays Altamaha River from confluence of Oconee and Ocmulgee rivers to the Altamaha Sound. Dashed lines represent upstream and downstream-most location sampled for occupancy analysis, solid lines representing reaches based on boat launches, and pointers indicating approximate location for capture-recapture study.

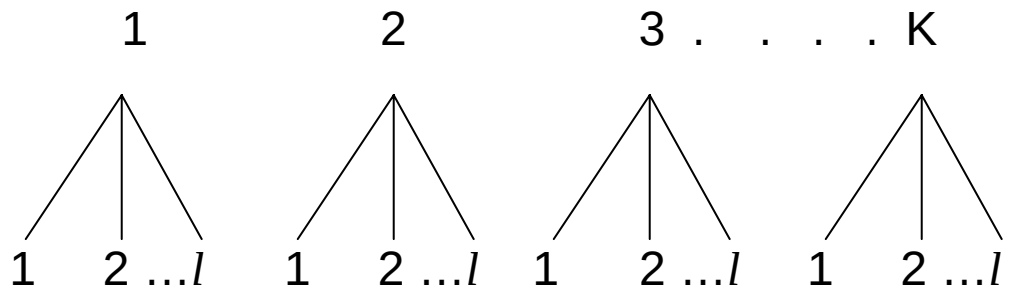

Figure 4. Diagram of Pollock's (1982) Robust Design with K primary periods assuming open population, each with *l* closely-spaced secondary periods assuming a closed population.

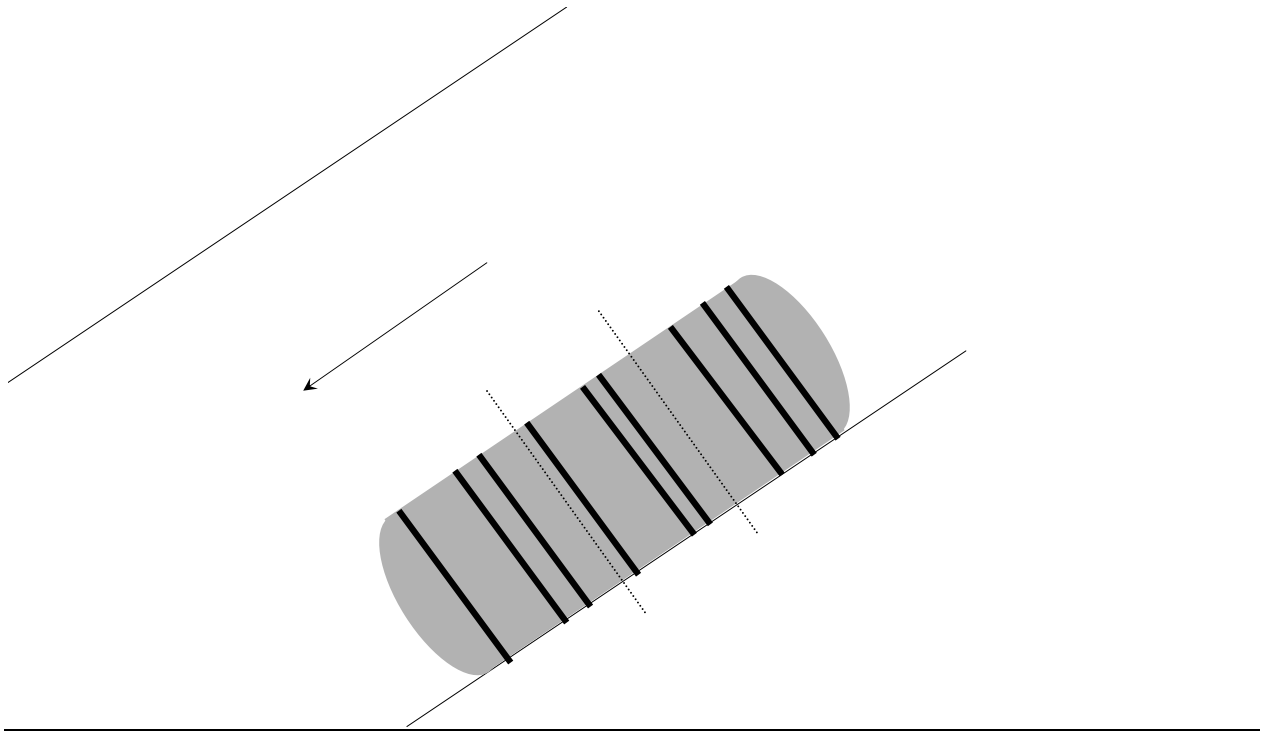

Figure 5. Example of randomly placed transects (dark lines) within a defined habitat (shaded) within a river (light lines with arrow representing direction of flow). Light dashed lines separate the lower, middle, and upper thirds of the area.

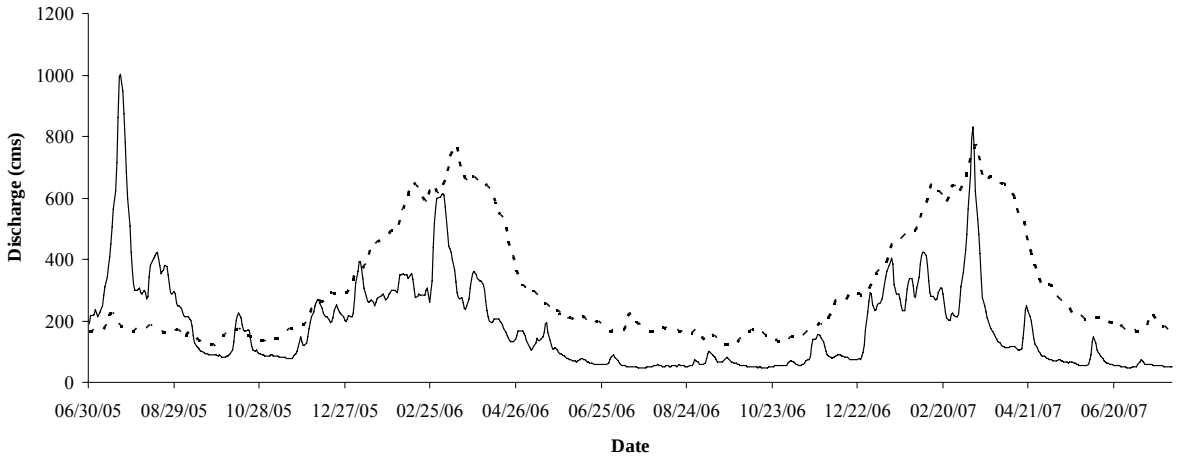

Figure 6. Estimated discharge (cubic meters per second) for the Altamaha River, Georgia for the duration of this study (solid line) in comparison to mean estimated discharge (dashed line) based on 75 years of data.

APPENDIX A

Appendix A. Longitudinal direction, habitat type, area in meters, and geographic coordinate location in decimal degrees (North, West) of sites sampled on the Altamaha River using the Robust Design during 2006-2007.

Direction	Habitat Type	Length	Width	Location
Downstream	Slackwater/Backwater	30	10	31.79461, 81.99996
Upstream	Slackwater/Edgewater	30	10	31.95863, 82.52971
Downstream	Pool/Lateral	30	10	31.78998, 81.96323
Upstream	Pool/Lateral	30	10	31.95751, 82.52205
Downstream	Swiftwater/Run	30	10	31.78673, 81.98708
Upstream	Swiftwater/Thalweg	30	10	31.95668, 82.53711

APPENDIX B

THE USE OF SURROGATES FOR EVALUATING FRESHWATER MUSSEL SURVEYS

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Introduction

Complete capture and enumeration of all individuals when sampling wildlife is usually not possible and mussel sampling is no exception. The proportion of mussels captured (i.e., capture efficiency) is influenced by substrate, water temperature, experience of observers, and sampling technique (Strayer and Smith 2003). Presence/absence surveys are affected by incomplete capture because the probability of detecting a species is a function of its probability of capture and its abundance (Bayley and Peterson 2001), both of which are influenced by habitat features that vary in space (e.g., stream to stream) and through time. Mussel distribution and population status also are influenced by aquatic habitat characteristics such as substrate, current velocity, depth, and habitat stability (van Cleave 1940; Harman 1972; Salmon and Green 1982; Vannote and Minshall 1982; Stern 1983; DiMaio and Corkum 1995; Hornbach et al. 1996). Therefore, the variables that influence mussel populations can be the same factors that affect the ability to capture mussels and reliance on biased estimates of mussel population size and distribution could lead to poor resource management decisions.

Several approaches have been developed to account for incomplete capture of individuals or detection of mussel species during sampling. Double sampling techniques involve sampling with a relatively quick and simple method (e.g., visual counting) and more intensive sampling (e.g., excavation) in a proportion of sample units to estimate the proportion of individuals detected (Strayer and Smith 2003). Alternatively, unbiased or minimally biased estimates of population size and species distribution can be obtained using statistical estimators (Williams et al. 2002). All of these approaches require that specific assumptions be met to obtain population size (or distribution) estimates with minimal bias. For example, closed population capture-recapture estimators require the assumption that there are no births/deaths, or emigration. Endo- and epi-benthic migration patterns of mussels vary seasonally (Amyot and Downing 1997,

Schwalb and Pusch 2007) which may bias estimates by violating closure assumptions. In addition, many of these techniques require greater sampling effort when compared to simple surveys and can be time consuming and potentially cost-prohibitive.

Unbiased estimates of population size and distribution can only be assured by evaluating potential violations of assumptions under typical sampling conditions and by comparing estimates to known values. The true number of animals in a given area, however, is rarely known with certainty. Previous evaluations have used animal surrogates (e.g., animal replicas, decoys) to evaluate wildlife sampling protocols (Smith et al. 1995; Frederick et al. 2003). For surrogates to be useful and effective, consideration must be given to pertinent aspects such as cost, realism, durability, and disposability. For example, a surrogate that cannot mimic authentic sampling characteristics of the target taxa may bias estimates, whereas cost can influence the number that be deployed. Surrogates also should withstand exposure to environmental conditions for the duration of the study, but should also be inert and degradable in the likely event that some are not recaptured during the study.

Our objectives were to describe the construction of morphometric replicates of native bivalves (i.e., surrogates), evaluate the durability and characteristics of the surrogates under actual sampling situations, and compare capture efficiency estimates of the surrogates to those of native bivalves in a large lowland river.

Methods

Study site

The Altamaha River Basin, located in the southeast region of the United States, is the largest drainage system in Georgia and one of the largest along the east coast, covering nearly 37,000 km^2. The river is formed at the confluence of the Ocmulgee and Oconee Rivers, in the Coastal Plain physiographic province (EPD 2003), flowing east 215 river-km (rkm) until it enters the Altamaha Sound and empties into the Atlantic Ocean. The river is unimpounded with the only impoundments within the upper watershed, located on the Oconee and Ocmulgee Rivers. The Altamaha River averages 50-70 m in width and 2-3 m in depth with some areas in excess of 5 m (Heidt and Gilbert 1978), with an average gradient of 0.13 m per km (EPD 2003) with an average discharge of 381 m^3/s (Rogers and Weber 1994). The streambed is comprised predominantly of sand. The Altamaha River also received large amounts of fine sediment from historic agriculture processes during the 1800s and early 1900s (EPD 2003).

Currently, 19 species of freshwater mussels are recognized from the Altamaha River (Jason Wisneiwski, GADNR, personal communication) three of which are believed to be imperiled. The Altamaha spinymussel (*Elliptio spinosa*; Lea 1836) is listed by the state of Georgia as endangered and recognized as a candidate for federal listing under the U.S. ESA. The Savannah lilliput (*Toxolasma pullus*; Conrad 1838) is classified as a federal species of concern because of its global rarity and critically imperiled in Georgia due to extreme rarity within the state borders. The Altamaha arcmussel (*Alasmidonta arcula*; Lea 1838) is listed as rare, both globally and state wide (GADNR).

Mark-Recapture study

The Robust Design estimates abundance, survival, capture probability, and emigration. Vertical migration patterns of burrowing mussels otherwise referred to as temporary emigration

can be estimated by relaxing permanent emigration assumptions (Pollock 1982). The design is based on repeat sampling occasions during primary and secondary sampling periods to a site. Secondary sampling periods are nested within primary sampling periods. A secondary period is a relatively short time interval between sampling occasions that assumes that the population is closed and no mortality or emigration occurs. Each primary period is a longer time interval containing a set of secondary periods and allows the population to be open to migration, mortality, and recruitment.

Six sites were randomly selected (2 slackwater, 2 pool, and 2 swiftwater) in the mainstem Altamaha based on information that both *Lampsilis dolabraeformis* and *L. splendida* occur within the site. Primary periods were defined as six week intervals or as soon as feasible in the event of unsafe conditions. Within each primary period, samples were collected during three secondary periods that ranged from 1-24h between sample periods. Systematic sampling should provide adequate spatial coverage and is useful for sampling clustered or rare populations (Smith et al. 2004; Thompson 2002). To ensure equal coverage, we divided the habitat area into three sub-units (upper, middle, lower) and assigned three random starting points in each sub-unit with respect to the origin (Figure B1) resulting in nine samples taken per secondary period. The starting point corresponded to the distance (in meters) upstream from the lower-most edge of the habitat. From each point, transects (length = 10 m, width= 1 m) were placed perpendicular to flow. Sampling was conducted as tactile searches along the sediment surface. In slackwater and shallow swiftwater habitats, mask and snorkels were used, whereas SCUBA equipment was used in areas with a depth greater than 1.5m, or where conditions were too hazardous to sample using a mask and snorkel (pools and thalwegs). All captured mussels were placed in a mesh bag until sampling was completed. Captured mussels were identified, measured for shell length, and

tagged (using Hallprint ® shellfish tags) or recorded as a recapture if a tag is already present. All collected mussels were then uniformly hand-placed back within the site, orienting anteriorly into the sediment.

Surrogate study

Intact mussel shells of *Lampsilis dolabraeformis* and *L. splendida* were collected from the Altamaha and valves were separated at the hinge line. Each valve was pressed into soft modeling clay to create a mold. Mussel surrogates were constructed by pouring plaster (made by mixing Plaster of Paris® with water) into the mussel molds. Upon sufficient drying of the plaster (plaster was firm to the touch), the casts were removed from the clay and allowed to dry for at least 24h. Right and left valves were matched according to the specific shell from which they were cast. Interior surfaces were sanded if needed, coated with a waterproof adhesive (Amazing Goop®), and joined together aligned by umbo position. Exterior surfaces were painted with a waterproof primer followed by walnut colored enamel.

One hundred twenty surrogates were created in approximately 18 person-hours (one person at 18 hours) although efficiency improved dramatically over time. The combined cost of materials (plaster, clay, adhesive, paint) combined to slightly less than $0.30 per surrogate. Each surrogate was inspected by hand to ensure the best quality of manufacturing and free of defects. The weight of the surrogates, although unquantified, was perceived as a similar match to actual live mussels of the same species.

Sampling was conducted during May 2007 corresponding to the three secondary periods within the fifth primary period for the mark-recapture study (see thesis). Water temperatures were approximately constant at 25ºC for the duration of the surrogate study. Twenty surrogates

were deployed within each site by hand placing each surrogate into the substrate anteriorly >70% of the length at uniform intervals.

Surrogates were placed in mesh dive bags by observers as they were encountered along with live mussels (see mark-recapture study above). Upon completion of all transects, collected surrogates and live mussels were recorded and returned uniformly within the area. Sites were then revisited two more times for a total of three samples (27 transects) per site.

Statistical Analysis

Capture-recapture data for both species among all primary periods (includes all tagged mussels) were combined and a model was constructed based on survival varying by habitat and temporary emigration varying seasonally (see thesis). However for the sake of this study, capture probabilities (p) were allowed to vary by habitat, and differ between secondary periods (for primary period 5) allowing comparisons to be made between live mussels and surrogates. Estimates of p for mussels at the surface were reported for each habitat using the Robust Design (Pollock et al. 1990) in Program MARK (White and Burnham 1999).

Surrogate p's were estimated for each sample occasion by dividing the number of surrogates recaptured per sample by the known "population" (20 surrogates per site). Again, p at a sub-unit were combined across occasions and similar habitats to get an average $\hat{p}$ for the particular habitat type. Surrogate estimates were compared to capture-recapture estimates to measure the plausibility of plaster mussels having realistic qualities of live mussels.

Results

Each site had been sampled 18 times (six primary periods) from July 2006 until June 2007 using the mark-recapture design for live mussels. The fifth primary period visit for live mussels and surrogate study was conducted May 1-3 2007 for five sites. One swiftwater site was

sampled during May 8, 2007 due to prior unsafe conditions. Intervals ranged from 1-24 hours between consecutive samples within an area. SCUBA equipment was used for both pool habitats and one of the swiftwater sites.

Twenty surrogates were deployed in each site. Capture histories of live mussels (slackwater = 515, pool = 187, swiftwater = 214) were read though program MARK. Detectable mussel (epibenthic) estimates during surrogate sampling, with standard error in parentheses, were slackwater = 423 (37), pools = 187 (53), and swiftwater = 249 (64). Mean capture probabilities from surrogates ranged from 0.20 to 0.23 in slackwater, 0.13 to 0.20 in pools, and 0.13 to 0.23 in swiftwater. Similarly, detection estimates from the mark-recapture study ranged from 0.18 to 0.20 in slackwater, 0.09 to 0.10 in pools, and 0.07 to 0.10 in swiftwater (Figure B2).

During sampling, no differences were noticed between live and surrogate mussels. Upon close inspection while sampling surveyors may observe differences, but many instances samplers were unaware that surrogates were captured until mesh bags were examined along the bank. During the three sampling occasions all captured surrogates showed minimal (<10%) to zero erosion. However, 20 surrogates were deployed at a swiftwater site May 1, 2007 prior to deeming sampling unsafe. Although discharge was constantly receding, upon revisiting the site six days later severe surrogate erosion was observed (>90%). Conversely, surrogates captured in swiftwater and pool sites revisited during the sixth primary period (six weeks later) showed moderate erosion (25-75%).

Discussion

Our method allows surveyors to quantify their ability to capture individuals in conjunction with their method of sampling. Moreover, detection can be evaluated for individual

observers or various sampling protocols. Furthermore, model-based assumptions (i.e. closure) can be tested for violations, allowing the user to evaluate the robustness of the estimator.

For this study we assumed no displacement of the surrogates since they were >70% buried in the sediment. However, detection was higher for surrogates compared to tagged mussels in some swiftwater and pool samples. A possible explanation for this could be that surrogates are in a "fixed location" when placed in the substrate. For example, live mussels were given at least six weeks to migrate or settle into suitable locations between the three consecutive secondary samples (see Pollock et al. 1990) and were recaptured throughout the sampling area. For the slackwater habitat, the entire area was available to random seeding whereas surrogates were randomly placed within three meters from the bank at pool (and one swiftwater) habitats due to depth constraints. Additionally, large amounts of woody debris were present at a single site from a pool and swiftwater habitat. While tagged mussels were found in crevices in and around large woody debris, surrogates may have been placed in more open areas. However, another possible explanation for the variance in detection for some samples could simply be a random event.

Like many large coastal rivers, most sites consisted mostly of sand, with some silt and clay present in areas with lower velocity. Due to low visibility tactile methods were preferred; therefore surrogates were constructed to have the texture and weight of a mussel and thus may exclude applicability to visual surveys. Moreover, coarser substrates such as gravel and cobble may limit the depth at which surrogates can be buried by hand. All sampling within each site was conducted in three days or less. Surrogates were found in-tact at the conclusion of the sample. However, long-term exposure to flow will begin to erode. Surrogates recovered six days after deployment at a swiftwater site were severely eroded, while recoveries in a slackwater

site six weeks following had moderate erosion. The maximum current velocity measured at any site was 0.4 m/s. Although erosion rates were not tested, flow and water chemistry may effect the duration of surrogates in the water; therefore shorter time periods, more sealant, or abrasion resistant materials may be necessary for use in other waters.

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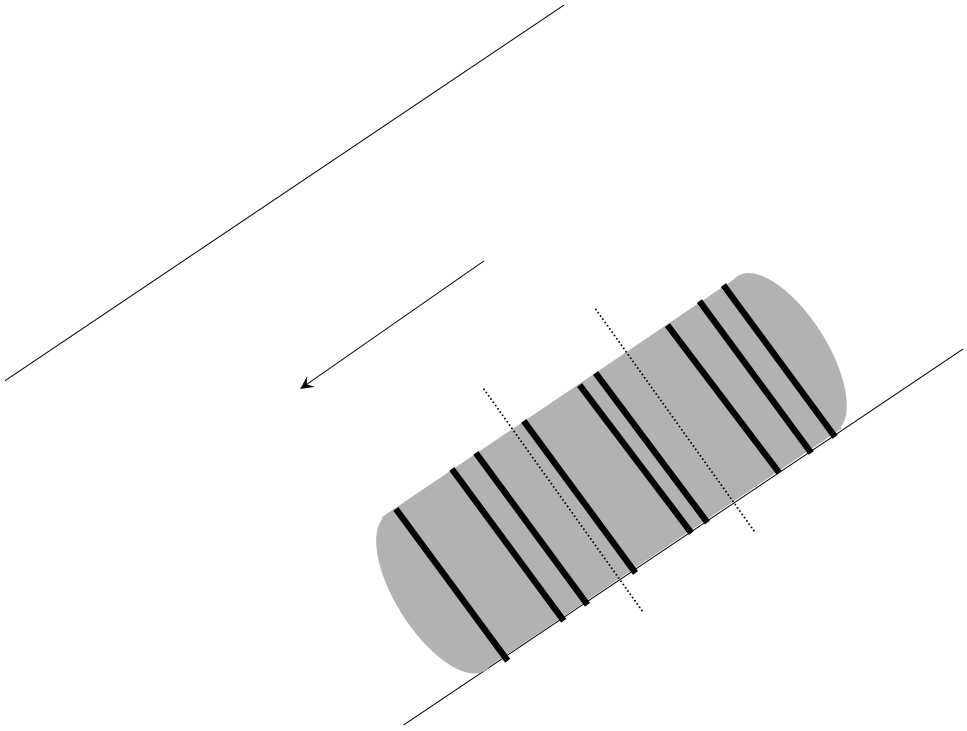

Figure B1. Example of randomly placed transects (dark lines) within a defined habitat (shaded) within a river (light lines with arrow representing direction of flow). Light dashed lines separate the lower, middle, and upper thirds of the area.

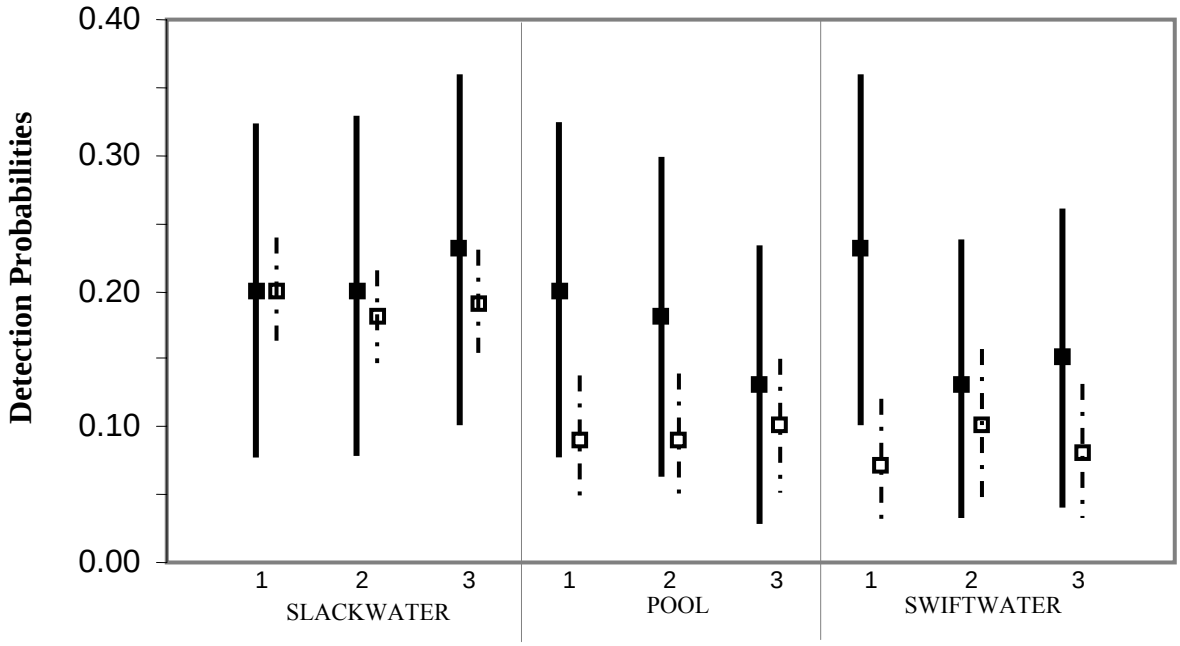

Figure B2. Mean, with 95% CI, detection probabilities for surrogates and live, epibenthic mussels (closed-square/solid line and open-square/dashed line respectively) sampled concurrently within the same location. X-axis corresponds to the stratum and sample interval which each estimate was taken.

APPENDIX C

Table C1. QAIC values for simulation models of decline in population abundance and abundance sampling with alpha levels of 0.05 and 0.1.

	Alpha = 0.05		Alpha = 0.1	
Model	QAIC	w_i	QAIC	w_i
Global	3318	1	4375	1
Lambda*High distribution	3453	0	4584	0
Lambda	3524	0	4673	0
Lambda*High effort	3548	0	4694	0
Lambda*Fixed sites	3590	0	4751	0
Wide distribution	3614	0	4779	0
High effort* distribution	3614	0	4783	0
Lambda*Stratified effort	3618	0	4795	0
Lambda*Stratified distribution	3636	0	4804	0
Wide distribution* Fixed sites	3652	0	4832	0
Lambda* Initial population	3661	0	4840	0
Stratified effort * Wide distribution	3670	0	4854	0
Wide * Stratified Distribution	3677	0	4862	0
Lambda* Season	3684	0	4866	0
High effort* Fixed sites	3686	0	4871	0
High effort	3689	0	4876	0
Wide distribution* Initial population	3691	0	4884	0
High*Stratified Effort	3705	0	4893	0
High effort * Stratified distribution	3708	0	4901	0
Wide distribution* Season	3709	0	4901	0

Table C1. continued.

Model	Alpha = 0.05		Alpha = 0.1	
	QAIC	w_i	QAIC	w_i
Fixed site	3720	0	4912	0
Stratified effort * Fixed sites	3722	0	4914	0
High effort * initial population	3725	0	4920	0
Stratified Effort * Distribution	3727	0	4925	0
Stratified distribution * Fixed sites	3727	0	4925	0
Initial population * Fixed sites	3730	0	4928	0
High effort * Season	3733	0	4928	0
Stratified effort	3734	0	4933	0
Season* Fixed site	3736	0	4936	0
Stratified distribution	3736	0	4938	0
Stratified effort* Initial population	3739	0	4941	0
Stratified distribution* Initial population	3740	0	4942	0
Stratified distribution* Season	3742	0	4945	0
Stratified effort* Season	3743	0	4945	0
Season	3743	0	4946	0
Initial population	3743	0	4946	0
Initial population * Season	3744	0	4947	0

Table C2. QAIC values for simulation models of decline in population abundance and occupancy sampling with alpha levels of 0.05 and 0.1.

	Alpha = 0.05		Alpha = 0.1	
Model	QAIC	w_i	QAIC	w_i
Global	86086	1	114441	1
Fixed site	91170	0	119779	0
Lambda*Fixed sites	100570	0	134559	0
High effort* Fixed sites	100570	0	134559	0
Stratified effort * Fixed sites	100570	0	134559	0
Wide distribution* Fixed sites	100570	0	134559	0
Stratified distribution * Fixed sites	100570	0	134559	0
Initial population * Fixed sites	100570	0	134559	0
Season* Fixed site	100570	0	134559	0
Season	105558	0	143300	0
Initial population	105902	0	143466	0
Lambda* Wide distribution	106118	0	143806	0
Initial population * Season	106179	0	143732	0
Lambda	106368	0	144244	0
Lambda*High effort	106427	0	144297	0
Stratified distribution* Season	106494	0	144230	0
Stratified effort* Season	106636	0	144354	0
Stratified distribution* Initial population	106698	0	144375	0
Stratified effort* Initial population	106714	0	144360	0
Wide distribution	106722	0	144416	0
High effort * Season	106759	0	144463	0
Wide distribution* Season	106799	0	144527	0

Table C2. continued.

Model	Alpha = 0.05		Alpha = 0.1	
	QAIC	w_i	QAIC	w_i
High effort* Distribution	106812	0	144466	0
High effort * Initial population	106834	0	144544	0
Lambda* Season	106879	0	144583	0
Lambda*Stratified effort	106911	0	144710	0
Lambda* Initial population	106941	0	144680	0
Wide distribution* Initial population	106955	0	144630	0
Lambda*Stratified distribution	107045	0	144750	0
High effort	107059	0	144782	0
Stratified effort * Wide distribution	107083	0	144821	0
Wide * Stratified Distribution	107085	0	144777	0
High* Stratified Effort	107163	0	144886	0
High effort * Stratified distribution	107172	0	144888	0
Stratified distribution	107194	0	144929	0
Stratified effort * Distribution	107197	0	144931	0
Stratified effort	107198	0	144931	0

Table C3. QAIC values for simulation models of decline in proportion of occupied sites sampling to detect a decline in abundance with alpha levels of 0.05 and 0.1.

	Alpha = 0.05		Alpha = 0.1	
Model	QAIC	w_i	QAIC	w_i
Global	35250	1	35057	1
Fixed site	41335	0	41084	0
Lambda*Fixed sites	48964	0	49631	0
Season* Fixed site	48969	0	49627	0
Stratified effort * Fixed sites	49045	0	49695	0
Initial population * Fixed sites	49066	0	49734	0
Stratified distribution * Fixed sites	49090	0	49734	0
High effort* Fixed sites	49094	0	49764	0
Wide distribution* Fixed sites	49127	0	49798	0
Season	50475	0	51825	0
Lambda* Season	52757	0	54041	0
Initial population * Season	52772	0	54063	0
Stratified effort* Season	52805	0	54092	0
High effort * Season	52824	0	54118	0
Stratified distribution* Season	52827	0	54128	0
Wide distribution* Season	52835	0	54129	0
Lambda* Wide distribution	53586	0	54913	0
Lambda*High effort	53723	0	55041	0
Lambda	53731	0	55029	0
High effort* Distribution	53789	0	55075	0
Wide distribution	53817	0	55100	0
Lambda*Stratified effort	53903	0	55181	0
Stratified effort * Wide distribution	53921	0	55197	0

Table C3. continued.

Model	Alpha = 0.05		Alpha = 0.1	
	QAIC	w_i	QAIC	w_i
Lambda*Stratified distribution	53932	0	55187	0
High effort	53985	0	55243	0
Wide * Stratified Distribution	53988	0	55237	0
Lambda* Initial population	53989	0	55243	0
Wide distribution* Initial population	54015	0	55266	0
High* Stratified Effort	54020	0	55271	0
High effort * Stratified distribution	54055	0	55294	0
High effort * Initial population	54072	0	55315	0
Stratified effort * Distribution	54098	0	55335	0
Stratified effort	54104	0	55341	0
Stratified effort* Initial population	54113	0	55350	0
Stratified distribution	54124	0	55351	0
Stratified distribution* Initial population	54128	0	55359	0
Initial population	54135	0	55365	0

Table C4. QAIC values for simulation models of decline in proportion of occupied sites sampling to detect a decline in abundance with alpha levels of 0.05 and 0.1.

	Alpha = 0.05		Alpha = 0.1	
Model	QAIC	w_i	QAIC	w_i
Global	5772	1	5999	1
Fixed site	8922	0	9024	0
Season	9517	0	10106	0
Lambda*Fixed sites	10357	0	10749	0
Season* Fixed site	10368	0	10756	0
Initial population * Fixed sites	10372	0	10768	0
Stratified distribution * Fixed sites	10384	0	10775	0
Stratified effort * Fixed sites	10386	0	10773	0
Wide distribution* Fixed sites	10404	0	10799	0
High effort* Fixed sites	10406	0	10794	0
Stratified distribution* Season	10639	0	11239	0
Wide distribution* Season	10642	0	11232	0
Initial population * Season	10644	0	11229	0
Lambda* Season	10644	0	11234	0
Stratified effort* Season	10650	0	11230	0
High effort * Season	10659	0	11228	0
Lambda* Wide distribution	11005	0	11704	0
Wide distribution	11099	0	11754	0
High effort* Distribution	11139	0	11789	0
Lambda	11154	0	11784	0
Lambda*High effort	11163	0	11802	0
Stratified effort * Wide distribution	11237	0	11849	0

Table C4. continued.

Model	Alpha = 0.05		Alpha = 0.1	
	QAIC	w_i	QAIC	w_i
Wide * Stratified Distribution	11238	0	11850	0
Wide distribution* Initial population	11247	0	11848	0
Lambda*Stratified distribution	11257	0	11858	0
Lambda*Stratified effort	11260	0	11862	0
Lambda* Initial population	11277	0	11871	0
High effort	11283	0	11882	0
High* Stratified Effort	11317	0	11903	0
High effort * Stratified distribution	11317	0	11903	0
High effort * Initial population	11323	0	11906	0
Stratified effort * Distribution	11342	0	11918	0
Stratified distribution	11354	0	11924	0
Stratified effort* Initial population	11357	0	11928	0
Stratified distribution* Initial population	11358	0	11925	0
Stratified effort	11359	0	11930	0
Initial population	11361	0	11928	0