WATER RESOURCE MANAGEMENT UNDER UNCERTAINTY: APPROACHES FOR THE MANAGEMENT AND CONSERVATION OF FRESHWATER MUSSEL SPECIES IN THE LOWER FLINT RIVER BASIN, GEORGIA

by

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(Under the Direction of James T. Peterson)

ABSTRACT

This study investigates methods for approaching the management and conservation of freshwater mussel species in the lower Flint River Basin (LFRB), Georgia. The research focused on developing predictive models of the status, distribution, and dynamics of freshwater mussel species in relation to site-, watershed-, and species-level characteristics. The objectives were to: (1) develop methods for correcting mussel collection data for biases associated with incomplete detection and misidentification of species; (2) develop predictive models of mussel species occurrence that accounted for detection and misidentification biases; (3) develop dynamic multi-state, multi-species occupancy models to estimate metapopulation dynamic rates and improve understanding of the factors contributing to changes in the status and distribution of mussel species; and (4) synthesize knowledge gained from objectives 1-3 into a comprehensive framework useful for developing a decision tool that predicts the response of mussel populations to alternative water resource management actions. Research methods involved field data collection combined with existing mussel collection data from sites located throughout the

LFRB. The results indicated generally low species detection probabilities and a substantial risk of misidentification for many LFRB mussel species. Additionally, although misidentification rates generally declined with observer experience, the risk of misidentification varied substantially among observers with identical experience. Models also suggested that mussel species presence was strongly and negatively related to the presence of impoundments and climatic drought, although the effects of drought and reach isolation were largely restricted to small- and mid-order tributaries. Models of mussel species meta-demographic rates indicated an elevated risk of local population extinction in the presence of short-term summer floods, generally low rates of colonization, and reduced local recruitment to existing populations in the presence of below-average low winter flow conditions. Results from this dissertation add to a growing body of literature regarding the influence of natural and anthropogenic factors on the status and dynamics of freshwater mussel populations and species. This knowledge could be useful in the development of management and conservation strategies aimed at balancing human and ecological water resource requirements, particularly if used in conjunction with ongoing monitoring activities under an Adaptive Resource Management framework.

INDEX WORDS: Unionids, Occupancy Modeling, Metapopulations, Species Misidentification, Stream Ecology, Flow-Ecology Relationships

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In 2003, I came to in Athens in pursuit of a Master's degree to work with streamfishes in the Flint River, Georgia. My only exposure to the Flint River Basin beforehand was while working in Gainesville, Florida two years earlier. This was during one of the most severe droughts in recent memory in the southeastern United States – the effects of which I witnessed first-hand while surveying lakes throughout Florida. Back then, I heard of a project that involved SCUBA diving for freshwater mussels in the Apalachicola River, but I had little knowledge of the issues surrounding freshwater mussels and water use in the ACF basin. It sounded interesting back then, and I even applied for the position, but I ended up snorkeling and electrofishing for bull trout in Washington State with Jim Peterson's first graduate student. Unbeknownst to me, I would be working with Jim for quite a while and would eventually enter a doctoral program working with freshwater mussels in the Flint River Basin. During this time, I have continually grown as an individual and as a scientist, and I owe much of what I know to Jim, who has (patiently) schooled me in the ways of science, statistics, and ecology. I thank him for providing me the opportunity to pursue my goals here in Athens and beyond.

This project would have been much more difficult without the support of many people. I was extremely fortunate to have Jason Wisniewski's expertise and friendship throughout the course of this study and have rarely met an individual so keenly devoted to the conservation of freshwater mussels. Jason's good nature and strong work ethic were particularly helpful during long hours tagging mussels on the stream bank, and I look forward to working with him for many years into the future. Field work was an important component of this project, and it would not have been nearly as enjoyable and productive without the tremendous effort put forth by a number people, including: Sandy Abbott, Paul Benton, Ben Carswell, Andrea Crownhart, Justin Dycus, Jason Emmel, Ryan Harrell, Karen Herrington, Jason Meador, Katie Owers, Will Pruitt, Brittany Trushel, and Deb Weiler. I also thank Jacob LaFontaine, who was instrumental in the development of hydrologic models for the Flint River Basin that were critically important for the metapopulation modeling conducted in Chapter 4. I would also like to thank Krishna Pacifici and Pete Hazelton for good discussions of all things modeling and estimation (among other things, of course) and look forward to continuing those discussions into the future. Jim Williams, Nate Johnson, and Jayne Brim Box also were valuable resources who willingly shared their tremendous knowledge of freshwater mussel ecology and biology. My committee members, Brett Albanese, Mike Conroy, and Mary Freeman also provided critical input throughout the course of this project.

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BACKGROUND AND CHAPTER ORGANIZATION

INTRODUCTION

As human populations continue to expand, so does demand for water resources. Water resource development activities, including the construction of water supply reservoirs and the extraction of surface and groundwater, are essential components of water resource management plans (Poff et al. 2003, Fitzhugh and Richter 2004). These activities, however, can substantially modify the physical, hydrological, and ecological characteristics of stream systems (Richter et al. 2003). In recent decades, many aquatic species throughout North America have experienced substantial population declines that have been attributed to the effects of water resource development activities (Richter et al. 1997a, Richter et al. 2003). As such, managers are increasingly required to consider the potential effects of these activities on aquatic biota when developing water resource management plans. The development of effective management plans requires knowledge of the resources (e.g., habitat, streamflow) important to stream biota, combined with an understanding of the factors influencing population- and community-level processes (Arthington et al. 2006). This knowledge is currently lacking for many aquatic organisms, which impedes the ability of resource managers to develop plans that protect at-risk species.

A resource is defined as a source of supply, support, or aid that can be readily drawn upon when needed. To stream biota (e.g., insects, crayfish, mussels, fish), the most important available resource is flowing water, which provides a template for the availability of other resources (e.g., food and habitat) that are necessary to fulfill basic life history requirements, such as growth, survival, and reproduction (Junk et al. 1989, Schlosser 1990). In this sense, the ability of stream biota to persist in their environment is dependent the availability of water resources that meet or exceed their critical requirements.

Identifying the critical resource requirements of stream biota, coupled with an understanding of the factors influencing population and community-level processes, is critical for the development of effective water resource management strategies (Arthington et al. 2006). With this knowledge, managers and biologists would be better able to: (1) restore at-risk species by identifying the factors and mechanisms responsible for population declines; (2) protect at-risk species by predicting the effects of water resource development activities; and (3) enhance existing populations by developing water resource management strategies that meet the resource requirements of stream biota.

Assessing Critical Resource Requirements

Managers use techniques, often referred to as environmental flow assessments, to identify the physical (e.g., habitat) and hydrological (e.g., streamflow) resources important to stream biota (Richter et al. 1997b, Tharme 2003). Worldwide, more than 200 assessment techniques have been developed, most often for stream-dwelling fishes (Tharme 2003). The large number of assessment techniques reflects the wide array of stream environments and aquatic species that are subject to management efforts. Indeed, there is likely not a single assessment technique that is universally applicable. There are, however, several features that assessment techniques should possess to be useful for aiding in the development of effective water resource management strategies.

Environmental flow assessments should be conducted at spatial scales important to the activities of stream biota. For proper identification of the resources critical to aquatic organisms, assessments should be conducted at ecologically relevant spatial scales. Aquatic organisms often move throughout stream systems to fulfill various life history requirements (e.g., foraging or spawning habitat), although the extent to which organisms move varies among species and life history stages (Fausch et al. 2002). Highly mobile organisms such as fish can typically move throughout stream systems to seek out suitable resources in the event of disturbance (e.g., flow depletion) or to fulfill various life history requirements. In contrast, less mobile organisms such as mussels and crayfish are generally restricted to smaller spatial scales and cannot move as easily in response to environmental disturbances or to find suitable resources for fulfilling life history requirements. Therefore, failure to assess resource requirements at an ecologically relevant spatial scale may lead to inadequate understanding of critical resource requirements and ineffective management strategies.

Environmental flow assessments should be conducted at temporal scales important to stream biota. Species with a short life span (e.g., 2 or 3 years) tend to have relatively early reproductive maturity, high rates of reproduction, and populations that generally respond quickly to environmental disturbances (Schlosser 1990, Young et al. 2006). In contrast, long-lived species tend to have delayed reproduction and lower reproductive rates (e.g., every 5 or 10 years), potentially resulting in slower population recovery following a disturbance (Congdon et al. 1993, Musick 1999, Young et al. 2006). Long-lived species with low mobility may be particularly slow to respond to disturbance because of their limited ability to colonize via reproduction and dispersal (Strayer et al. 2004, Strayer 2008). Hence, the observed current population status and distribution of species may often be a function of historical environmental conditions, such as past land-use practices, the construction of impoundments, or drought, and in extreme cases the population-level effects of changing environmental conditions may only become apparent many years later (Tilman et al. 1994, Newton et al. 2008). In this sense, failure to assess critical resources at temporal scales important to stream biota may lead to inaccurate determination of critical resources and ineffective management strategies.

Current methods for assessing environmental flows are usually based on some measure of hydrology, physical habitat, or both (Tharme 2003, Petts 2009). A common technique is the establishment of minimum flow standards, which are metrics that are often derived from streamflow patterns based on historical stream gauge data (e.g., 30% of mean annual flow; Stalnaker 1981). More recently, hydrologic modeling approaches have been developed that use characteristics of the entire hydrograph to assess the level of a stream's impairment by comparing current to historical streamflow conditions (e.g., the Index of Hydrologic Alteration, IHA; Richter et al. 1997b). Hydraulic-habitat modeling approaches combine hydrologic models with detailed habitat models to quantify the amount of physical habitat available to target species over a range of streamflow conditions (e.g., Instream Incremental Flow Methodology, IFIM; Bovee 1982). Although these techniques differ in their complexity, data requirements, and ease of implementation, they possess certain advantages and disadvantages that should be considered prior to their implementation in a management setting.

One disadvantage of most existing assessment techniques is that they rarely explicitly estimate ecological responses to changes in resource availability. This is primarily because such information can be difficult and resource intensive to collect (Richter et al. 1997b). When ecological responses are estimated, they often are restricted to target species or species guilds (Stalnaker 1995). As a result, the interrelationships between changes in resource availability and population- or community-level responses are often poorly understood (Stalnaker 1981, Richter et al. 1997b, Arthington et al. 2006). Management strategies based on limited knowledge of flow-ecology relationships are likely not protective for all populations and species (Arthington et al. 2006, Huckstorf et al. 2008, Petts 2009). Nevertheless, managers are often forced to implicitly assume that meeting prescribed resource assessment criteria such as established minimum flow standards will fulfill the resource requirements of aquatic biota, thereby protecting target species or communities.

Another disadvantage is that most assessment techniques are conducted at limited spatial scales (Petts 2009) and may be resistant to changing scales (Conroy and Noon 1996, Fausch et al. 2002). The spatial scale of resource assessment techniques in stream systems can be limited either because (1) locations are limited to sites where long-term stream discharge data are available (i.e., USGS gauge sites) or (2) the cost of conducting the resource assessment at multiple locations is prohibitive. However, hydrological and physical processes vary longitudinally and laterally throughout stream systems and greatly influence the structure and composition of aquatic communities (Vannote et al. 1980, Junk et al. 1989). As such, species that are distributed throughout stream systems may have different resource requirements depending on the physical and hydrological characteristics of the surrounding environment (Schlosser 1982). Thus, the observed resource use for a given species at one location may not adequately describe its critical resource requirements at other locations.

Most assessment techniques also tend to ignore the dynamic nature of ecological and hydrological processes in stream systems (Petts 2009). Aquatic organisms are continually responding to changing conditions in their environment, perhaps on a seasonal or annual basis, or as they progress through different life history stages (Fausch et al. 2002). As such, the observed resource use by a species (i.e., what is observed during the time of data collection) may not adequately reflect the true resource requirements critical to that species. Similarly, the comparison of current hydrological conditions to historical conditions is based on the assumption that there exists a single natural flow regime for a given stream. However, there is increasing support for the notion that flow regimes are themselves dynamic, particularly with respect to global climate change, and that viewing flow regimes as static may not be sufficient for managing water resources into the future (Milly et al. 2008).

Despite these challenges, environmental flow assessments have been successfully applied to a variety of stream systems and species throughout the world (Tharme 2003, Richter 2009). Indeed, provided the disadvantages of a given assessment technique (e.g., limited spatial or temporal extent) are acknowledged and properly matched with management objectives, the development of effective water resource management strategies is possible. In general, where little conflict exists between potential user groups or where risk to aquatic biota is minimal, the simplest and most cost-effective techniques are likely the most practical ones. In contrast, where conflict exists between user groups or where aquatic species face substantial risk of imperilment, the use of more informative and widely applicable resource assessment techniques is likely merited (Arthington et al. 2006). In such cases, the most useful techniques would (1) be cost effective (time and money); (2) allow for determination of resource requirements at spatial and temporal scales relevant to stream biota; (3) increase understanding of the factors driving population and community-level processes; and (4) allow for the incorporation of new information regarding the factors driving population and community-level processes.

Freshwater Mussel Diversity and Population Declines

North America is the world center of freshwater mussel diversity with approximately 300 known species, the majority of which belong to the family Unionidae (Williams et al. 1993, Turgeon et al. 1998, Bogan and Roe 2008). Mussels in the eastern United States account for approximately 90% of North American mussel species (Neves et al. 1997), and they are especially diverse in the southeastern states of Alabama, Georgia, and Tennessee (Parmalee and Bogan 1998, Williams et al. 2008). Many mussel species have experienced substantial population declines in recent decades (Bogan 1993, Bogan 1996, Ricciardi and Rasmussen 1999, Bogan and Roe 2008), but only during the past 30 years has the magnitude and severity of these declines been widely recognized (Williams et al. 2008). As such, freshwater mussels also are among the most imperiled organisms in North America, and the southeastern United States harbors approximately 95% of imperiled species (Strayer 2008, Williams et al. 2008). Presently, 70 mussel species in the United States are federally protected, many more are species of special concern, and approximately 10% are presumed extinct (Williams et al. 2008).

Mussel population declines have been attributed to a variety of factors, including excessive erosion and sedimentation (Bogan 1996, Brim Box and Mossa 1999), stream impoundment and channelization (Vaughn and Taylor 1999, Layzer and Scott 2006), habitat fragmentation (Watters 1999), water quality degradation (Augspurger et al. 2003); drought (Lake 2003, Golladay et al. 2004, Haag and Warren 2008), reductions in host fish populations (Smith 1985, Haag and Warren 2003), and invasive species introductions (Ricciardi and Rasmussen 1999, Strayer and Malcolm 2006). Despite the wide range of attributed factors, their relative influence on observed mussel population declines remains unclear (Strayer et al. 2004, Strayer 2008, Williams et al. 2008, Downing et al. 2010), and the underlying mechanisms responsible for population declines, such as reproductive failure and low adult survival, are poorly understood for many species (Bogan 1993, Strayer et al. 2004). Much of this uncertainty stems from the long life span, complex life history, and cryptic behavior of mussels, all of which contribute challenges to research and management.

Management and Conservation Challenges

Freshwater mussels are long-lived organisms, with maximum age varying among species but generally ranging from tens to one hundred years or more (Bauer 1992, Bogan 1993, Bauer and Wächtler 2001). In contrast, most mussel studies are typically conducted over relatively short time periods. As such, observation of important population- and community-level processes (e.g., birth, mortality, immigration) is difficult because they occur at time intervals that exceed most studies (Strayer 2008). As a result, long-term datasets are often unavailable for many species, resulting in a lack of data regarding basic ecology, life history, and dynamics in distribution and abundance. The potentially slow response time of mussel species to disturbance causes additional uncertainty surrounding the factors responsible for population declines (Strayer 2008). Similarly, mussel populations are potentially slow to respond to management and conservation efforts, resulting in additional uncertainty surrounding the effectiveness of management activities for protecting at-risk species.

Larval and juvenile mussels are largely unobservable in a field setting, which further complicates the observation of important population and community-level processes. Larval mussels (glochidia) for almost all unionids are obligate external parasites of frequently unknown freshwater fish hosts. Many species have a narrow range of suitable host fish species, whereas other species have much more generalized host fish requirements (Barnhart et al. 2008). Glochidia generally develop in modified gill compartments (marsupia) of female mussels over weeks (short-term brooders) to months (long-term brooders; O'Brien and Williams 2002, Haag and Warren 2003). Upon contact with a host-fish, glochidia are expelled from marsupia and attach to gills, scales, and fins of host fish (Haag and Staton 2003), where they encyst and undergo metamorphosis to the juvenile stage (Rogers-Lowery and Dimock 2006, Barnhart et al. 2008). This largely unobservable parasitic phase is the primary mechanism by which mussel species disperse throughout stream systems (Strayer et al. 2008). In response to cues not fully understood, juveniles drop from the fish host to begin life as free-living mussels. Juvenile mussels are known to burrow into the stream substrate, where they can remain buried for several years (Strayer et al. 2004). Hence, because of the small size, complex life history, and cryptic behavior of glochidia and juvenile mussels, increasing knowledge of the critical resources required for population-level processes, such as recruitment, dispersal, survival, and growth, is usually very difficult to accomplish.

Potential Management Approaches

Unless effective management and conservation strategies are developed, mussel populations throughout North America will presumably continue to decline (Bogan and Roe 2008, Williams et al. 2008). Although existing environmental flow assessment techniques have been successfully applied for many organisms, they may not be useful for the development of effective management strategies for at-risk mussel species (Gore et al. 2001). Hence, there remains the need for management strategies that (1) are not prohibitively resource intensive; (2) allow for determination of the spatial and temporal resources relevant to mussels; (3) result in greater understanding of the factors influencing population and community-level processes; and (4) allow for managers to update knowledge of the factors influencing population and community-level processes.

Approaching the management of freshwater mussels within the context of metapopulation ecology may provide managers with the information required to develop effective strategies. The theory of metapopulation ecology was initially developed to model the dynamics of patchily-distributed agricultural insect pest populations (Levins 1969). Levins' view of metapopulations was as a collection of interacting populations (i.e., a population of populations), for which the state of a population at any given time could be summarized in one of two states: present or absent. These interacting populations exist in geographically isolated patches that are subject to processes of local extinction within a patch and colonization from neighboring patches from one time period to the next. Hence, metapopulation dynamics can be thought of as analogous to population-level dynamics (Hanski 1997). For example, the local colonization of a species in a metapopulation corresponds to the immigration of an individual into a population, whereas the local extinction of a species is analogous to the local mortality of an individual in a population. Metapopulation dynamics can be modeled as a function of patch-specific characteristics, such as patch-size, distance to neighboring patches, as well as environmental factors (Hanski 1997). Thus, metapopulation approaches are appealing from a management perspective because they are analytically tractable and allow for estimation of both metapopulation-level parameters (i.e., dynamic rates) and the influence of environmental factors on those processes.

Metapopulation dynamics can occur in several ways, and knowledge of how system dynamics operate can have important management implications. For example, non-equilibrium metapopulations are characterized by many small, isolated patches that are highly vulnerable to local extinction events because colonization events occur infrequently (Gotelli 2008). Classical metapopulations are characterized by populations that are small enough and close enough to each other that extinction events are balanced by frequent colonization of individuals from neighboring patches (Gotelli 2008). Island-mainland metapopulation dynamics describe a system that is a mixture of small and large patches, in which colonization occurs frequently to small, extinction prone patches from larger, extinction-resistant mainland patches (Hanski 1998). Hence, there are alternative hypotheses regarding how metapopulations function, and the relative belief in alternative explanations of system dynamics can be a source of great uncertainty in management settings.

Metapopulations may be an effective framework for approaching the management and conservation of mussel species. Mussels are thought to be dependent on specific environmental conditions (e.g., flow, substrate) and are frequently patchily-distributed throughout stream systems as a result (Strayer 1999, Strayer et al. 2004). Water resource development activities such as stream impoundment and habitat alteration have, in many cases, resulted in greater fragmentation of populations throughout stream systems (Strayer et al. 2004; Bogan and Roe 2008). Indeed, many mussel species once distributed over wide, contiguous spatial extents currently persist in patches of suitable habitat that are fragmented and isolated to varying degrees (Vaughn and Taylor 1999, Haag and Warren 2008). These small, isolated populations may be highly susceptible to local extinction events, either by chance or because of locally depressed population-level processes such as declines in reproduction, survival, or colonization (Haag and Warren 2008, Strayer 2008). Because of the extremely limited mobility of adult mussels, colonization of suitable habitats is limited to the dispersal of juvenile mussels attached to host-fish species. Thus, metapopulation ecology may be a useful framework for approaching the management and conservation of freshwater mussels.

Objectives and Chapter Organization

To improve understanding of the resources critical for the persistence of freshwater mussels and the factors contributing to population declines in the lower Flint River basin, Georgia, I addressed the following 4 objectives: (1) to develop methods for correcting historical and contemporary mussel collection data for biases associated with incomplete detection and misidentification of species; (2) to develop predictive models of mussel species occurrence that accounted for detection and misidentification biases to estimate the current status and distribution of LFRB mussel species; (3) to develop dynamic multi-state, multi-species occupancy models to estimate meta-population dynamic rates to improve understanding of the factors contributing to changes in the status and distribution of mussel species; and (4) to synthesize knowledge gained from objectives 1-3 into a comprehensive framework that can be used to develop a decision tool that models the response of mussel populations to potential water resource management actions.

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CHAPTER 2

MISIDENTIFICATION OF FRESHWATER MUSSEL SPECIES (BIVALVIA, UNIONIDAE): CONTRIBUTING FACTORS, MANAGEMENT IMPLICATIONS, AND POTENTIAL SOLUTIONS[1]

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[1] Shea, C. P., J. T. Peterson, J. M. Wisniewski, and N. A. Johnson. 2011. Misidentification of freshwater mussel species (Bivalvia: Unionidae): contributing factors, management implications, and potential solutions. Journal of the North American Benthological Society 30:446-458. Reprinted with permission of the publisher.

ABSTRACT

Surveys of freshwater mussel populations are used frequently to inform conservation decisions by providing information about the status and distribution of species. It is generally accepted that not all mussels or species are collected during surveys, and incomplete detection of individuals and species can bias data and can affect inferences. However, considerably less attention has been given to the potential effects of species misidentification. To evaluate the prevalence of and potential reasons for species misidentification, we conducted a laboratory-based identification exercise and quantified the relationships between mussel species characteristics, observer experience, and misidentification rate. We estimated that misidentification was fairly common, with rates averaging 27% across all species and ranging from 0 to 56%, and was related to mussel shell characteristics and observer experience. Most notably, species with shell texturing were 6.09× less likely than smooth-shelled species to be misidentified. Misidentification rates declined with observer experience, but for many species the risk of misidentification averaged >10% even for observers with moderate levels of experience (5–6 y). In addition, misidentification rates among observers showed substantial variability after controlling for experience. These results suggest that species misidentification may be common in field surveys of freshwater mussels and could potentially bias estimates of population status and trends. Misidentification rates possibly could be reduced through use of regional workshops, testing and certification programs, and the availability of archived specimens and tissue samples in museum collections.

INTRODUCTION

Surveys of mussel populations are used frequently to inform conservation decisions by providing information about the status and distribution of species. In general, not all mussels or species are collected during surveys (Green and Young 1993, Dorazio 1999, Metcalfe-Smith et al. 2000, Smith 2006), and incomplete detection of individuals and species can bias data and affect inferences (Williams et al. 2002). Factors that influence the ability to capture mussels (e.g., habitat complexity, species behaviors, and environmental conditions; Downing and Downing 1991, Strayer 1999) also influence mussel populations (Strayer 1993, Layzer and Madison 1995, Howard and Cuffey 2003) and could potentially confound ecological patterns (Yoccoz et al. 2001). Numerous sampling design and modeling approaches have been developed to minimize the effect of detection bias (MacKenzie et al. 2002, Williams et al. 2002, Tyre et al. 2003, Peterson and Bayley 2004). However, considerably less attention has been given to the potential effects of species misidentification. Most surveys of animal populations (and subsequent data analyses) are conducted under the assumption that species are identified perfectly, but in many cases, this assumption probably is untrue (Elphick 2008). Proper species identification can be hindered by non-distinctive morphology and coloration (Runge et al. 2007), as well as observer-level factors, such as experience (e.g., volunteer-based monitoring programs) (Sauer et al. 1994, Lotz and Allen 2007, Fitzpatrick et al. 2009).

Biologists often use morphological traits, such as shell size, color, form, and texture, to distinguish among mussel species during field surveys (Strayer and Smith 2003, Williams et al. 2008). Some mussel species present a relatively low risk of misidentification because they possess distinctive characteristics that are generally consistent among individuals (e.g., shell texturing; Mulvey et al. 1997). Other species may present a greater risk of misidentification because they are similar to other species or are highly variable among individuals (Williams and Mulvey 1994, Mulvey et al. 1997). In addition, ability to identify mussels often varies among people (Valledor de Lozoya and Araujo 2006), and the ability of a given individual may change over time as new skills are acquired. Consequently, survey data collected by different personnel over large spatial and temporal extents (e.g., long-term monitoring programs) may be confounded by misidentification. Confounding can obscure true ecological patterns, or worse, suggest false patterns (e.g., species may appear more widely distributed than they really are). For example, the Apalachicola–Chattahoochee–Flint Basin (ACF) in Alabama, Florida, and Georgia (USA), harbors a diverse and imperiled freshwater mussel assemblage (Brim Box and Williams 2000, Williams et al. 2008). During the past 20 y, substantial sampling effort has been expended in the basin to determine the status and distribution of mussel species (Brim Box and Williams 2000, Golladay et al. 2004, Williams et al. 2008). If mussel species have been misidentified during these surveys, information on the status, distribution, and temporal trends of mussel species in the ACF may be biased and could potentially inhibit the ability of managers and biologists to develop effective conservation and management strategies.

We evaluated the influence of species and observer-level factors on misidentification rates for 27 mussel species native to the ACF basin to assess the prominence of and factors contributing to species misidentification. We had the following objectives: 1) to estimate the probability of misidentifying mussel species, 2) to identify the species-level factors contributing to misidentification, and 3) to determine the relationship between observer experience and misidentification rate.

METHODS

Our primary interest was to assess the relationships among various species characteristics, observer experience, and identification errors during field surveys for mussel species in the ACF basin. However, a field evaluation of species misidentification rates would have been difficult to conduct because, without careful inspection, including sacrificing some individuals, the true identity of each specimen would have been uncertain. Thus, we evaluated species misidentification rates under controlled conditions. We conducted an identification exercise using the 27 extant freshwater mussel species native to the ACF Basin (Table 2.1) during the 2009 ACF Basin Freshwater Mussel Workshop, hosted by the Joseph W. Jones Ecological Research Center and Columbus State University. To ensure correct species identifications of the test specimens, 4 experienced regional mussel biologists (combined experience = 50 y) gathered ~1 mo before the workshop and compiled a potential test collection that consisted of multiple specimens (on average, 10 complete shells) for each of the 27 species (i.e., total ~250 shells). For each species, identification and suitability of specimens as 'representative' was made by consensus of the 4 experts. If the experts could not agree upon the identity of a specimen, it was not included in the potential test collection. Seventy-four specimens representing the 27 species were then selected from the potential test collection by one of the experts.

Eighteen workshop participants (hereafter, observers) were asked to identify the 74 test specimens. Specimens were randomly assigned to 1 of 25 test stations, each having 3 substations (labeled a, b, and c). To provide multiple opportunities to identify a given species, most species were represented 3 times throughout the test (Table 2.1). However, 3 species were represented only once and 1 species was represented twice because additional specimens were unavailable (Table 2.1). To minimize nomenclatural errors during the test, observers were provided with both a test sheet and an additional sheet containing species names (common and scientific) with numbers assigned to each of the 27 species. At each substation, observers recorded their specimen identification by matching the species number to the corresponding station and substation on the test sheet. During the exercise, observers were free to roam from station to station, with ~2 min allowed per station. Upon completion of the test, observers were given 10 min to revisit problem specimens. Observers also were asked to record their experience (e.g., days, months, or years) identifying mussels in the ACF basin.

The 18 observers who participated in the workshop had a wide range of experience identifying mussels in the ACF basin (mean = 3 y, range = 1 mo–20 y). Eleven observers had <6 mo of experience, 3 had 3 to 5 y of experience, 3 had 6 to 10 y of experience, and 1 had 20 y of experience. The observers included agency personnel, university students and faculty, and private consultants, many of whom had conducted mussel surveys throughout the ACF basin and were presumably a representative sample of experienced and inexperienced mussel researchers in the basin. Three of the 4 regional experts who compiled the potential test collection also participated in the test. Our rationale for allowing the 3 experts to take the test was: 1) the pool of experienced observers was extremely limited, 2) the potential test collection was compiled 1 mo before the test was conducted, and 3) the potential test collection consisted of multiple representative specimens of each species, but only a subset of these specimens (74) was eventually selected by the single expert who did not take the test. Hence, we assumed the risk of bias associated with the experts' memory of particular specimens would be low.

Statistical Analysis

We considered 2 types of incorrect responses: false negative and false positive errors (Table 2.1). False negative errors represented instances where observers failed to identify a specimen correctly, whereas false positive errors represented instances where a specimen was falsely declared to be a particular species. For example, consider an instance where mussel species A was misidentified as species B. This observation would count as a false negative error for species A and a false positive error for species B. We distinguished between these 2 error types because false negatives and false positives can corrupt survey data in different ways. False negatives artificially inflate the number of ‘0’ (i.e., absent) observations in a data set, whereas false positive errors artificially inflate the number of ‘1’ (i.e., present) observations. False negative identification errors tend to cause underestimation of population size and species presence in a manner similar to incomplete detection of individuals and species and can be accommodated by a variety of modeling approaches (MacKenzie et al. 2002, Williams et al. 2002, Tyre et al. 2003). In contrast, false positive errors tend to cause overestimation of population size and species presence, but relatively few modeling approaches have been developed to accommodate this source of bias in survey data (but see Royle and Link 2006, Runge et al. 2007). Thus, we focused our analysis on identifying how species characteristics and observer experience contributed to false positive errors.

We fitted logistic regression models (Agresti 2002) relating false positive identifications to mussel species and observer characteristics. The dependent variable was the individual species identifications made by each observer and was binary-coded as 1 for any instance where a species was falsely declared to be present and 0 otherwise. The misidentifications were modeled as a function of observer experience and traits belonging to the *predicted* species (i.e., the falsely identified species). This type of modeling enabled us to evaluate how species characteristics and observer experience contributed to misidentification. However, standard logistic regression cannot account for dependence (i.e., autocorrelation) among repeated samples, and we suspected that repeated identifications by observers of species were dependent (Sokal and Rohlf 1995). Hence, we fitted hierarchical logistic regression models to the species identification data to account for dependence among repeated species identifications by observers. Hierarchical models differ from more familiar regression techniques in that dependence among observations collected at lower-level units (here, the identification of individual specimens) within upper-level units (here, observers and species) is incorporated by including random effects for the lower-level intercept (Snijders and Bosker 1999). For our study, the log-odds of misidentification, η_{ijk}, was modeled as:

$$\eta_{ijk} = \beta_0 + u_{0k} + \beta_{\mathrm{Q}} \mathrm{X}_{\mathrm{Q}ijk} + u_{1j}$$

where β_0 was the intercept, β_{Q} was the effect of observer- (*k*) and species- (*j*) specific characteristics X_{Q} on misidentification, and u_{0k} and u_{1j} were the observer- and species-level random effects, respectively, that were assumed to be normally distributed with a mean of 0 and random effect-specific variance (Bryk and Raudenbush 2002). The random components u_{0k} and u_{1j} represented unique effects associated with observers and species, respectively, which were unexplained by observer experience and species-specific characteristics. To accommodate the complex model structure, we used Markov Chain Monte Carlo (MCMC) as implemented in WinBUGS software, version 1.4 (Spiegelhalter et al. 2006) to fit candidate hierarchical logistic regression models. All models were fitted using 200,000 iterations, 50,000 iteration burn-in (i.e., the first 50,000 MCMC iterations were dropped), and diffuse priors.

We used an information-theoretic approach (Spiegelhalter et al. 2002) to evaluate the relative fit of candidate models relating observer experience and species characteristics to misidentification. We developed 6 models representing hypothesized effects of observer experience and species characteristics on misidentification of mussels (Table 2.2). Observer experience was represented by only a single predictor variable (mo of experience identifying mussels in the ACF basin) in all models because we were interested in quantifying the relative influence of species characteristics on misidentification. The 6 candidate models contrasted the relative influence of the following 5 species-trait categories (i.e., predictor variables): 1) shell texture, 2) shell size, 3) shell color, 4) shell form, and 5) federal listing status (Table 2.2). The shell texture predictor variable included textured or the presence of texturing, such as corrugations, folds, plications, pustules, and wrinkles (species with smooth shells otherwise) on the shell. The shell size predictor included the size category of each species and represented the typical range of adult shell sizes as described by Brim Box and Williams (2000) and Williams et al. (2008), where small was ≤60 mm shell length, medium was >60 to 150 mm, and large was >150 mm. The shell color predictors included dark (species with a brown or black periostracum; yellow or green periostracum otherwise) and rayed (species with prominent rays on the periostracum; rays absent or faint otherwise). The shell form predictors included thin (thin-shelled species; moderately thick to thick otherwise) and inflated (moderately to greatly inflated species; moderately to greatly laterally compressed otherwise). The conservation status predictor included listed (species that were federally threatened or endangered; non-listed species otherwise). We also grouped species according to subfamily and tribe with classifications supported by molecular phylogenetics (Campbell et al. 2005) and averaged error rates across all species in each tribe to evaluate qualitatively differences in misidentification rate based on phylogeny. However, we excluded phylogenetic grouping as a predictor in hierarchical logistic regression models because shell characteristics show considerable convergent evolution among and within tribes (e.g., Watters 1994, Campbell et al. 2005). Prior to evaluating the fit of the candidate models, all species-level predictors were binary-coded as 0 (trait absent) or 1 (trait present) (Table 2.1).

Before fitting candidate models, we evaluated the relative fit of 4 different variance structures for the hierarchical model random effects using the global (all predictors) model by fitting models that contained several combinations of random effects for observers and species. The 4 variance structures included: 1) random effect associated with observer, 2) random effect associated with species, 3) observer and species random effects with covariance between the 2 random effects, and 4) observer and species random effects with no covariance. The best approximating variance structure was identified using the Deviance Information Criterion (DIC). DIC is a Bayesian measure of model fit or adequacy, and smaller DIC indicates a better approximating model (Spiegelhalter et al. 2002). We then evaluated the relative fit of the candidate models with DIC and calculated DIC weights following Link and Barker (2009). DIC weights range from 0 to 1, with the best approximating candidate model having the highest weight. We considered the most plausible models to be those with DIC weights that were ≥10% of the best-approximating model, which is similar to Royall’s general rule-of-thumb of ⅛ or 12% for evaluating strength of evidence (Royall 1997).

We assessed the precision of parameter estimates for each model by calculating 90% Bayesian credible intervals (Congdon 2001), which are analogous to 90% confidence intervals. To facilitate interpretation, we also calculated scaled odds ratios (SOR) for each fixed-effect observer and species-level predictor variable (Hosmer and Lemeshow 2000) and median odds ratios (MOR) for each random effect (Larsen et al. 2000). The odds-ratio scalar corresponded to what we thought were relevant unit changes in the observer experience predictor (Table 2.3). The random-effect MOR was a point estimate of the magnitude of the random effect in terms of odds and had the desirable property of being directly comparable to fixed effects. In the context of our model, the MOR associated with observer random effects were interpreted as the odds ratio between identical observers (with respect to predictors) with the highest and lowest probability of species misidentification (following Larsen et al. 2000). Goodness-of-fit (i.e., MCMC convergence) was assessed for each model in the confidence set with the diagnostics detailed by Gelman and Rubin (1992).

RESULTS

A total of 1217 species identifications was made by the 18 observers. This number was fewer than the total number of possible identifications (1332) because, in some cases, observers did not make a species identification. Of the 1217 species identifications, 323 were incorrect (Table 2.1). Across species, the false negative error rate averaged ~27% (i.e., ~27% of all identifications were incorrect) and ranged from 0% to ~67%, whereas the false positive error rate averaged ~27% across species (i.e., ~27% of species identifications were false positives) and ranged from 0% to ~56%. Only 1 species, *Alasmidonta triangulata*, had a false negative error rate of 0, and only 1 species, *Amblema neislerii*, had a false positive error rate of 0 (Table 2.1). Across tribes, the false negative error rate ranged from ~9% (Amblemini) to ~35% (Anodontini), and the false positive error rate ranged from 0% (Amblemini) to ~34% (Pleurobemini) (Table 2.1).

The best approximating variance structure in the hierarchical logistic regression models included both observer- and species-level random effects with no covariance. Hence, all candidate models included both random effects. The best approximating hierarchical logistic regression model relating false positive errors to species characteristics and observer experience was the mussel shell-size model that included observer experience, small and large mussel shell-size indicator variables, and a small shell size × observer experience interaction (Table 2.2). Based on DIC weights, the mussel shell-size model was only 1.05× more plausible than the next best-fitting model that included observer experience, textured shell, and a textured shell × observer experience interaction. DIC weights indicated the mussel shell-size model was 3.25, 5.57, 9.75, and 39× more likely than the mussel shell-form, federal listing-status, mussel shell-color, and global models, respectively (Table 2.2). Based on DIC weights, we concluded that support existed for models representing all 5 trait categories and reported parameter estimates for the confidence set of models (Table 2.3).

Parameter estimates based on the confidence set of models indicated that the probability of misidentification was strongly and negatively related to observer experience, federal listing status, the presence of shell texturing, and shell size (Fig. 1A–C; Table 2.3). SORs suggested that for every 1-y increase in experience, observers were 1.30× less likely to identify a species falsely (Table 2.3). SORs also suggested that species with textured shells were, on average, 6.09× less likely than smooth-shelled species to be identified falsely (Fig. 1B; Table 2.3). Similarly, federally listed species were, on average, 3.4× less likely to be falsely identified than non-listed species (Fig. 1A; Table 2.3). Parameter estimates for 2 interaction terms, small shell × observer experience and rayed shell × observer experience, indicated that the effect of shell size and the presence of rays decreased with observer experience. For every year increase in observer experience, small-shelled species were 1.98× less likely to be identified falsely, as opposed to 1.30× less likely for medium and large-shelled species (Fig. 1C; Table 2.3). Similarly, for every 1-y increase in observer experience, species with rayed shells were 1.64× less likely to be identified falsely, compared to 1.32× less likely for rayless species (Table 2.3). The parameter estimates also suggested that misidentification rates were, on average, lower for small-shelled species, large-shelled species, and mussels with inflated shells, and higher for mussels with rayed and thin shells. However, the parameter estimates were generally imprecise (Table 2.3).

Species-level random effects indicated that substantial heterogeneity remained among species after accounting for species-level characteristics (Table 2.3). Based on the best-fitting model (mussel shell size), the MOR for the species-level random effect suggested that for 2 species with identical characteristics, the more difficult-to-identify species was, on average, 2.24× more likely to be identified falsely than the less difficult species. Similarly, observer-level random effects suggested that substantial variability remained among observers' ability to identify mussels after accounting for experience (Fig. 1D; Table 2.3). Based on the best-fitting model (mussel shell size), the MOR for the observer-level random effect suggested that for 2 observers with identical experience, the less skilled person was, on average, 2.86× more likely than the person with greater skill to identify a species falsely (Table 2.3).

DISCUSSION

Relatively few studies have considered the potential for species misidentification during ecological surveys (but see Sauer et al. 1994, Bridges and Dorcas 2000, Royle and Link 2006, Runge et al. 2007, Fitzpatrick et al. 2009, McClintock et al. 2010), and we are unaware of any studies that have assessed species misidentification rates for freshwater mussels. Previous studies have shown that false negative error rates as low as 20% (Tyre et al. 2003) and false positive error rates as low as 5% (Royle and Link 2006) can bias species-presence models substantially. We found that false-positive species identifications of freshwater mussels can occur frequently, averaging >10% for observers with moderate levels of experience (5–6 y). We also found that misidentification rates were related to observer experience and species characteristics. No similar published studies are available for comparison, but we think that this study underestimated potential misidentification rates during actual field surveys in the ACF and possibly other basins. Participants in this study were provided with clean, archetypical shells from adult specimens and were allowed to use internal shell structures during identification. In contrast, mussel specimens encountered during field surveys are often heavily eroded, covered in organic deposits, or otherwise distorted because of local environmental conditions (Morris and Corkum 1999, Hornbach et al. 2010). These factors have the potential to make identification more difficult. Personnel also generally do not have access to internal structures, such as tooth structure and soft anatomy, both of which can be useful for distinguishing among species during field identifications. For example, in the ACF, *Anodontoides radiatus* and *Villosa vibex* can be difficult to separate during field surveys because they are similar-sized species that share several external characteristics (i.e., yellow-green periostracum with conspicuous rays). However, these species are easily separated by examination of lateral and pseudocardinal teeth, which are greatly reduced in *A. radiatus* compared to *V. vibex*. The mussel species in the ACF display a relatively wide range of shell characteristics and do not appear to be especially difficult to identify compared to species in other basins (J. Williams, Florida Museum of Natural History, personal communication). Thus, we think that the patterns and relationships revealed by this study should provide general insight into the factors contributing to misidentification of freshwater mussels, the species that present the greatest risk of misidentification, and the rationale for developing methods that minimize the risk of misidentification.

Identification errors were related to several species-level factors, most notably shell texturing and shell size. We think that species with shell texturing and large shells were rarely misidentified because these traits are highly visible and unambiguous. In contrast, species with smooth or medium-sized shells were misidentified considerably more often because distinguishing among these species is based on highly subjective traits, such as ray patterns, shell inflation, and shell coloration (Williams and Mulvey 1994, Mulvey et al. 1997). Indeed, misidentification error rates for smooth-shelled and medium-sized species often exceeded the 5% levels known to introduce substantial bias into survey data (Royle and Link 2006), and these species made up the majority of the ACF fauna (19 and 20 species, respectively). In addition, we found that error rates generally were highest for tribes containing the most speciose genera (e.g., *Utterbackia, Villosa,* and *Elliptio*), a pattern suggesting that misidentifications between closely related species were prevalent in this data set. Taxonomic difficulties in these genera have been documented previously, especially among members of *Elliptio* (Johnson 1970, Williams et al. 2008, Haag 2010). As such, misidentification is likely to have a greater effect on evaluations of the status and distribution of closely related mussel species that do not have highly distinctive and unambiguous traits.

The relatively high among-species variability in misidentification rates suggests that species-level factors other than our trait categories contributed to misidentification. We classified species broadly into trait categories (size, texture, color, form, and status) to determine their relative influence on misidentification and to generalize patterns of misidentification across a diverse group of species. However, some species may have possessed unmeasured characteristics that made them more or less difficult to identify relative to other species with the same general characteristics. For example, misidentification rates varied considerably (range = 0–30%) among the 7 ACF species that possess shell texturing. All of these species possessed shell texturing, but they differed in the location (e.g., posterior slope vs entire shell) and type of texturing (e.g., subtle plications vs prominent corrugations; Williams et al. 2008). These subtle differences may have contributed to the among-species variability in misidentification, represented by the species-level random effect that was unaccounted for by the shell-texturing predictor alone. The among-species variability potentially could be reduced by including additional trait categories. Alternatively, development of species-specific models would eliminate the need for species characteristics and species-level random effects. However, one of our primary objectives was to increase *general* understanding of how species-level factors contribute to misidentification of freshwater mussels, and we think that conducting species-specific analyses would have been a less effective approach for addressing this objective.

In studies of other taxa, species misidentification was presumed to decline rapidly with experience level and, therefore, was thought to bias survey data minimally (Tyre et al. 2003; see also Lotz and Allen 2007, Fitzpatrick et al. 2009). We found that observer experience reduced the probability of misidentification, but the effectiveness of experience in minimizing errors varied with species characteristics. For example, misidentification rates declined more rapidly with experience level for small-shelled species than for medium- and large-shelled species. Similarly, misidentification rates declined more rapidly with experience for rayed species than for rayless species. Federally listed species also were rarely misidentified, possibly because the significant management and conservation focus of these species resulted in their being among the first that observers learned to identify correctly. However, for non-listed, smooth-shelled species, misidentification rates often exceeded levels known to introduce substantial bias into survey data (>5%), even for observers with moderate levels of experience (5–6 y).

Substantial variability remained among observers after accounting for experience, suggesting that experience measured in time did not fully reflect the ability of observers to identify mussel specimens. One possible explanation is that observers in this study who listed identical experience differed in the proportion of time they had actually spent identifying mussels. For instance, one observer may have conducted monthly surveys, whereas another may have conducted bimonthly or even semi-annual surveys. More detailed descriptions of experience (e.g., nature and intensity of training) may have accounted for some of the remaining variability, but this information was unavailable. Another explanation is that some observers may be more skilled naturally than others regardless of experience. Thus, identification tests and possibly certification programs (e.g., similar to that offered by the Ecological Society of America and the North American Benthological Society), rather than experience measured in time, may be the most effective methods for determining identification ability.

This study suggests that misidentification of freshwater mussel species can occur at a rate sufficient to contribute bias to mussel survey data, particularly if identifications are made by a series of different observers. Historical mussel collections in the lower Flint River Basin (LFRB), Georgia, consist of field surveys of 24 mussel species collected over 20 y from >200 streams. Over this period, the LFRB has experienced 2 severe droughts (2000–2002 and 2006–2008; NCDC 2010), and 15 different groups have conducted surveys to evaluate changes in the status and distribution of mussel species. Individuals in each group probably differed in their ability to identify mussel species, potentially confounding ecological patterns with those introduced by misidentification errors (Yoccoz et al. 2001). Groups averaging 3 and 5.67 y of experience (sample-weighted average based on the most experienced crew member) conducted surveys before and after the 2000–2002 drought, respectively. *Villosa vibex* is a smooth-shelled, non-listed species that was collected from 47% (44/93) of pre-drought (1991–1999) and 28% (40/139) of post-drought (2000–2005) survey locations. These results suggest that *V. vibex* occurrence (i.e., the proportion of sites occupied) declined by ~19% following the drought. Using our best-fitting (mussel shell size) model, we predict that for groups with average identification ability, misidentification rates for *V. vibex* averaged 21% and 12% during the pre- and post-drought periods, respectively. Accounting for misidentification, the estimated decline in *V. vibex* occurrence is ~12%. Hence, the estimated effect of drought was 1.6× greater for the observed (biased) data compared to the adjusted data. We also predict that misidentification rates for *V. vibex* ranged from <1% to 31% across all survey locations. Therefore, when combined with the effects of incomplete detection of species during surveys, failure to account for species misidentification may further reduce our ability to assess the influence of temporal (e.g., drought) and spatial (e.g., land use and physiography) factors on the status and distribution of mussel species in the LFRB. Such assessments are complicated by the great variability in identification skill of observers with similar experience. However, estimates of likely misidentification rates gained from this and similar studies could be incorporated formally as prior knowledge into modeling procedures, potentially improving our ability to detect spatial and temporal trends in ecological patterns.

This study also suggests that efforts should be made to assess and improve the knowledge and identification ability of mussel biologists in the ACF and other river basins. We think that regional workshops provide an excellent forum for regional experts to teach identification skills and for people to examine the range of morphological variation present in most species. Over a 5-d period during the 2009 ACF workshop, attendees observed first-hand every species native to the ACF basin, either in a laboratory or field setting. This study also highlights the important role that natural history museums could play in reducing misidentification rates. The availability of accessible, archived voucher specimens from field collections could provide valuable information for biologists who wish to revisit past collections and evaluate questionable records. Indeed, even the most experienced specialists have made identification errors, and only the availability of archived voucher specimens (including tissue samples suitable for molecular analysis) allows evaluation of the accuracy of species identifications in historical data sets. This statement is true for other aquatic and terrestrial taxa prone to misidentification, such as amphibians (Lotz and Allen 2007), crayfishes (G. Schuster, East Kentucky University, personal communication), stream fishes (B. Albanese, Georgia Department of Natural Resources, personal communication), bats (MacSwiney et al. 2008), and birds (Alldredge et al. 2008).

Species misidentification appears to be pervasive in the ACF and possibly in many other river systems with diverse freshwater mussel assemblages. The combined use of regional workshops, identification tests, and museum archiving of specimens or tissue samples may reduce the risk of misidentification in survey data and provide managers and biologists with information to account for potential biases in historical collections. Bayesian modeling approaches could be used (e.g., Gelman and Hill 2007, Royle and Dorazio 2008, Link and Barker 2009) to include this a priori knowledge formally in modeling and estimation procedures to improve estimates from modeling approaches that accommodate species identification errors (Royle and Link 2006). Such approaches also could be extended to dynamic models that explore spatial and temporal species distribution patterns (Dorazio 2007, Royle and Kéry 2007, MacKenzie et al. 2009, McClintock et al. 2010). Continued efforts to reduce the biases associated with species misidentification should improve our ability to assess the status and trajectory of populations, which in turn, should improve our ability to make effective management and conservation decisions.

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Table 2.1. Subfamilies, tribes, and species included in the identification exercise, total number of possible correct identifications (*N*), species-specific false negative (FN) and false positive (FP) counts (total number of attempted identifications in parentheses) and percent error rates (%), trait categories, and species-specific traits (S=small, L=large, T=textured, R=rayed, D=dark, Th=thin, I=inflated, L=listed) used in hierarchical logistic regression models. Traits not listed (e.g., medium shell size) served as the statistical baseline for hierarchical logistic regression models.

		Error rate				Species trait categories and predictor variables								
		False negative		False positive		Size		Texture	Color		Form		Status
Subfamily, tribe, species	*N*	Count	%	Count	%	S	L	T	R	D	Th	I	L
Ambleminae, Amblemini	54	5 (53)	9.43	0 (48)	0.00								
Amblema neislerii	54	5 (53)	9.43	0 (48)	0.00	0	0	1	0	1	0	1	1
Ambleminae, Lampsilini	486	95 (411)	21.54	103 (449)	22.94								
Glebula rotundata	54	13 (45)	28.89	7 (39)	17.95	0	0	0	0	0	0	1	0
Hamiota subangulata	54	2 (54)	3.70	4 (58)	6.90	0	0	0	1	0	0	0	1
Lampsilis floridensis	54	4 (53)	7.55	11 (57)	19.30	0	1	0	0	0	0	0	0
Lampsilis straminea	54	8 (49)	16.33	15 (57)	26.32	0	0	0	0	0	0	1	0
Medionidus penicillatus	54	8 (51)	15.69	5 (48)	10.42	1	0	1	1	0	0	0	1

Toxolasma paulum	54	16 (49)	32.65	6 (39)	15.38	1	0	0	0	1	0	1	0
Villosa lienosa	54	10 (43)	23.26	15 (48)	31.25	0	0	0	1	0	0	0	0
Villosa vibex	54	13 (52)	25.00	22 (61)	36.07	0	0	0	1	0	0	0	0
Villosa villosa	54	21 (45)	46.67	18 (42)	42.86	0	0	0	1	1	0	1	0
Ambleminae, Pleurobemini	396	113 (356)	31.74	124 (367)	33.79								
Elliptio arctata	18	5 (18)	27.78	9 (22)	40.91	0	0	0	0	1	0	0	0
Elliptio chipolaensis	54	17 (46)	36.96	10 (39)	25.64	0	0	0	0	1	0	1	1
Elliptio crassidens	54	12 (51)	23.53	17 (56)	30.36	0	0	1	0	1	0	1	0
Elliptio fumata	54	23 (47)	48.94	15 (39)	38.46	0	0	0	1	1	0	0	0
Elliptio pullata	54	10 (47)	21.28	34 (71)	47.89	0	0	0	1	1	0	0	0
Elliptio purpurella	54	30 (45)	66.67	19 (34)	55.88	1	0	0	1	1	0	1	0
Elliptoideus sloatianus	54	3 (54)	5.56	2 (53)	3.77	0	1	1	0	1	0	0	1
Pleurobema pyriforme	54	13 (48)	27.08	18 (53)	33.96	1	0	0	0	1	0	0	1
Ambleminae, Quadrulini	144	28 (134)	20.90	26 (132)	19.70								
Megalonaias nervosa	36	1 (36)	2.78	8 (43)	18.60	0	1	1	0	1	0	0	0

Quadrula infucata	54	4 (49)	8.16	2 (47)	4.26	1	0	1	0	1	0	1	0
Uniomerus columbensis	54	23 (49)	46.94	16 (42)	38.10	0	0	0	0	1	0	0	0
Unioninae, Anodontini	252	82 (233)	35.19	70 (221)	31.67								
Alasmidonta triangulata	18	0 (18)	0.00	3 (21)	14.29	0	0	1	0	1	1	1	0
Anodonta heardi	54	19 (49)	38.78	15 (45)	33.33	0	0	0	0	0	1	1	0
Anodontoides radiatus	18	7 (16)	43.75	8 (17)	47.06	0	0	0	1	0	1	1	0
Pyganodon sp.[a]	54	18 (51)	35.29	10 (43)	23.26	0	1	0	0	1	1	1	0
Utterbackia imbecillis	54	15 (51)	29.41	16 (52)	30.77	0	0	0	1	0	1	0	0
Utterbackia peggyae	54	23 (48)	47.92	18 (43)	41.86	0	0	0	1	0	1	0	0
Total (across species)	1332	323 (1217)	26.54	323 (1217)	26.54								

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[a] Represented *P. cataracta* and *P. grandis* because these species are indistinguishable in the Apalachicola–Chattahoochee–Flint basin without genetic analysis.

Table 2.2. Model type, predictor variables, effective number of parameters (pD), Deviance Information Criteria (DIC), ΔDIC, and DIC weights (w_i) for the candidate set of hierarchical logistic regression models relating species characteristics and observer experience to false positive identification errors.

Model type	Candidate model	pD	DIC	ΔDIC	w_i
Shell size	Small shell, large shell, observer experience, small shell × observer experience	40.31	1016.61	0.00	0.39
Shell texture	Textured shell, observer experience, textured shell × observer experience	37.91	1016.73	0.12	0.37
Shell form	Thin shell, inflated shell, observer experience, thin shell × inflated shell, thin shell × observer experience	40.43	1019.01	2.40	0.12
Federal status	Federally listed, observer experience, federally listed × observer experience	38.88	1020.12	3.51	0.07
Shell color	Dark shell, rayed shell, observer experience, dark shell × rayed shell, dark shell × observer experience, rayed shell × observer experience	40.76	1020.92	4.31	0.04

Global	Small shell, large shell, textured shell, thin shell, inflated shell, dark shell, rayed shell, federally listed, observer experience, thin shell × inflated shell, dark shell × rayed shell, small shell × observer experience, textured shell × observer experience, thin shell × observer experience, federally listed × observer experience, dark shell × observer experience, rayed shell × observer experience	41.53	1023.91	7.30	0.01

Table 2.3. Parameter estimates, standard errors (SE), 90% credible intervals (CI), unit scalars (scalar), scaled odds ratios (SOR), median odds ratios (MOR), and 90% SOR credible intervals (SOR CI) based on the confidence set of hierarchical logistic regression models relating species characteristics and observer experience to false positive identification errors.

			90% CI			SOR/	90% SOR CI	
Model	Estimate	SE	Lower	Upper	Scalar	MOR	Lower	Upper
Shell size								
Fixed effects								
Intercept	–0.522	0.398	–1.187	0.119				
Small	–0.363	0.635	–1.411	0.669	1	0.692	0.244	1.951
Large	–0.977	0.671	–2.055	0.148	1	0.374	0.128	1.160
Experience	–0.022	0.005	–0.031	–0.013	12	0.768	0.689	0.856
Small × experience	–0.035	0.020	–0.072	–0.007	12	0.657	0.421	0.919
Random effects								
Intercept (observer)	1.224	0.504	0.559	2.168		2.860		

Intercept (species)	0.719	0.262	0.367	1.208		2.240		
Shell texture								
Fixed effects								
Intercept	–0.304	0.353	–0.889	0.270				
Textured	–1.804	0.478	–2.587	–1.02	1	0.164	0.075	0.361
Experience	–0.027	0.006	–0.037	–0.017	12	0.723	0.641	0.815
Textured × experience	0.013	0.007	0.001	0.027	12	1.169	1.012	1.383
Random effects								
Intercept (observer)	1.231	0.505	0.561	2.173		2.870		
Intercept (species)	1.184	0.421	0.612	1.963		2.810		
Shell form								
Fixed effects								
Intercept	–0.721	0.457	–1.478	0.022				
Thin	0.621	0.790	–0.681	1.920	1	1.861	0.506	6.794
Inflated	–0.353	0.545	–1.255	0.521	1	0.702	0.285	1.684

Thin × inflated	0.021	0.976	–1.583	1.644	1	1.021	0.205	5.160
Experience	–0.023	0.006	–0.033	–0.014	12	0.759	0.673	0.845
Thin × experience	–0.005	0.009	–0.021	0.008	12	0.942	0.777	1.101
Random effects								
Intercept (observer)	1.189	0.493	0.464	2.368		2.810		
Intercept (species)	0.636	0.227	0.290	1.168		2.130		
Federal status								
Fixed effects								
Intercept	–0.491	0.369	–1.232	0.226				
Listed	–1.226	0.549	–2.295	–0.134	1	0.292	0.040	2.180
Experience	–0.025	0.006	–0.036	–0.014	12	0.743	0.647	0.846
Listed × experience	0.003	0.009	–0.016	0.018	12	1.039	0.827	1.242
Random effects								
Intercept (observer)	1.222	0.504	0.477	2.423		2.860		
Intercept (species)	0.881	0.313	0.404	1.615		2.440		

Shell color								
Fixed effects								
Intercept	–0.888	0.562	–1.996	0.221				
Dark	–0.072	0.578	–1.233	1.040	1	0.926	0.120	7.241
Rayed	0.487	0.629	–0.766	1.719	1	1.619	0.210	12.664
Dark × rayed	0.886	0.951	–1.029	2.706	1	2.413	0.312	18.874
Experience	–0.026	0.009	–0.046	–0.010	12	0.733	0.577	0.888
Dark × experience	0.006	0.008	–0.009	0.024	12	1.074	0.900	1.337
Rayed × experience	–0.015	0.007	–0.035	–0.001	12	0.831	0.659	0.988
Random effects								
Intercept (observer)	1.279	0.523	0.503	2.530		2.930		
Intercept (species)	0.764	0.286	0.336	1.436		2.224		

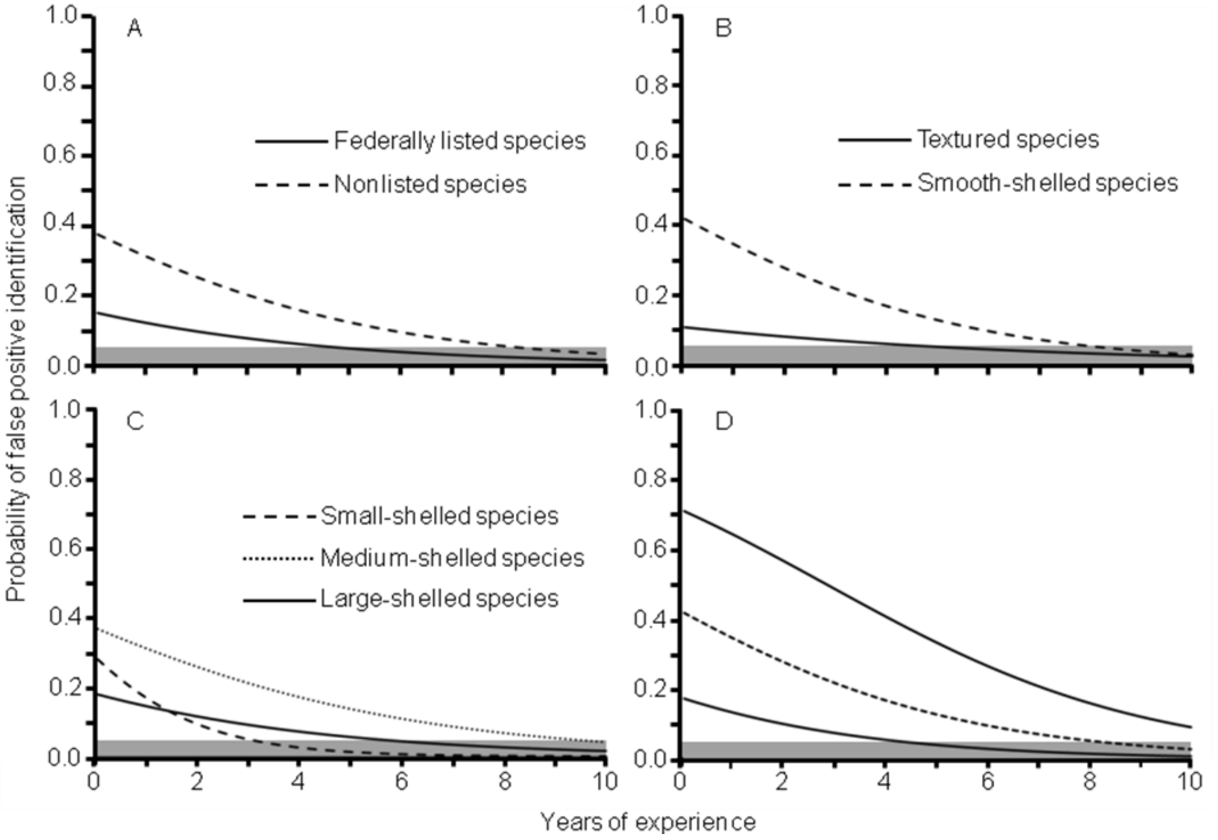

Figure 2.1. Influence of observer experience and federal status (A), shell texture (B), and shell size (C) on the probability of false positive identification of mussel species in the Apalachicola–Chattahoochee–Flint (ACF) basin. Misidentification rates outside of the shaded region (>5%) are known to severely bias species presence models. Panel D denotes interobserver variability in the probability of false positive identification for non-listed, medium-sized, smooth-shelled species after controlling for observer experience. The dashed line in panel D represents the estimated mean error rate, and the solid lines represent the upper and lower bounds (mean ± observer-level random effect, respectively).

CHAPTER 3

ESTIMATING THE CURRENT STATUS AND DISTRIBUTION OF FRESHWATER MUSSEL SPECIES IN THE LOWER FLINT RIVER BASIN, GEORGIA

ABSTRACT

North American freshwater mussels have been subjected to a wide array of stressors in recent decades that may have contributed to observed declines in the status and distribution of extant species. To evaluate the relative influence of natural and anthropogenic factors on freshwater mussels, we developed statistical models relating mussel species occupancy to various site- and landscape-level factors, including land use, drought, stream size, and reach isolation due to impoundment for 21 mussel species native to the Flint River Basin, Georgia. The occupancy models accounted for potential biases associated with both incomplete detection and misidentification of mussel species. Modeling results suggested that mussel species occupancy was strongly and negatively related to drought and reach isolation by impoundments. Mussel species were, on average, 4× less likely to be present following severe drought, but the negative effects of drought declined rapidly with increasing stream size. Similarly, mussel species were, on average, 15× less likely to be present in small streams that were isolated from mainstem tributaries by impoundments. This study provides insight into the effects of natural and anthropogenic factors on freshwater mussel populations and provides a useful tool for identifying locations within the lower Flint River Basin that may harbor populations of rare species or

especially diverse mussel assemblages, thereby allowing managers to develop more informed and effective and management and conservation strategies.

INTRODUCTION

Biologists and managers face recurring decisions regarding the management and conservation of water resources. Such decisions must address diverse and growing human water demands (Fitzhugh and Richter 2004). However, consideration also must be given to the potential effects of water resource development (e.g., expansion of urban and agricultural water infrastructure, construction of impoundments) and conservation activities (e.g. streamflow restoration) on stream-dwelling biota (Richter et al. 2003). In recent decades, freshwater mussels throughout North America have experienced substantial population declines (Williams et al. 1993, Neves et al. 1997, Ricciardi and Rasmussen 1999, Strayer et al. 2004) that have been attributed to a variety of factors, including periodic drought (Golladay et al. 2004, Haag and Warren 2008), the construction of impoundments (Watters 1996, Vaughn and Taylor 1999), excessive sedimentation (Brim Box and Mossa 1999), environmental contaminants (Augspurger et al. 2003), and streamflow alteration (Layzer and Madison 1995, Gangloff and Feminella 2007, Peterson et al. 2011). Despite the wide range of attributed factors, their relative influence on observed mussel population declines remains poorly understood for many species (Strayer et al. 2004, Strayer 2008, Downing et al. 2010). As such, it is currently difficult for biologists and managers to identify the primary factors contributing to mussel population declines, which may in turn inhibit the development of management and conservation strategies that protect at-risk species.

The challenges faced by biologists and managers are typified in the Flint River Basin (FRB), Georgia. From its headwaters south of Atlanta, the Flint River flows southwesterly 560 km through Piedmont and Coastal Plain physiographic provinces until joining the Chattahoochee River to form the Apalachicola River. The lower Flint River Basin (LFRB) is located completely within the Coastal Plain physiographic province and encompasses 13,952 square kilometers in southwestern Georgia. Within the LFRB, row-crop agriculture and farm-gate infrastructures currently generate 34% of the regional economy, making it one of the most productive agricultural regions in the country (McKissick 2004). Agricultural activities in the LFRB rely heavily on irrigation water withdrawn from surface and groundwater sources, particularly since center pivot irrigation systems were installed extensively throughout the LFRB in the mid-1970s to drought-proof crops and increase quality and quantity of yields. From 1970 to 1976, groundwater withdrawals for irrigation increased more than 100% (Pierce et al. 1984), and agricultural water withdrawals (surface and groundwater) currently comprise approximately 90% of the total water used in the LFRB during the April to September growing season (McDowell 1996).

Approximately 80% of the water used for irrigation in the LFRB is extracted from the Upper Floridan aquifer, a prolific carbonate aquifer that underlies most of the Coastal Plain province of the southeastern United States including parts of South Carolina, Georgia, Alabama, Louisiana and all of Florida (Hicks et al. 1987, Hook et al. 2005). Surface waters throughout the Coastal Plain are connected heterogeneously to the Upper Floridan aquifer, particularly in the Dougherty Plain physiographic district, where interchange between groundwater and surface water occurs rapidly and frequently through sinkholes, springs, and other dissolution paths (Mosner 2002, Torak and Painter 2006, Opsahl et al. 2007). Because a large proportion of the LFRB is contained within the Dougherty Plain, the mainstem Flint River and many of its tributaries in this region are in direct contact with the Floridan aquifer (Torak et al. 1996). Agricultural withdrawals often pump directly from the Floridan aquifer; hence, they frequently result in decreased base-flow to springs and streams that are in direct contact with the aquifer (Torak et al. 1996). Peak water withdrawals often coincide with periods of reduced summer flows and high evapotranspiration rates that can exacerbate low-flow periods (Torak et al. 1996). Indeed, the evaluation of long-term datasets from the U.S. Geological Survey (USGS) indicates that 7Q10 (the lowest discharge that occurs over 7 consecutive days with a 10 year recurrence interval; Annear et al. 2004) has been lowered in multiple LFRB tributaries since the implementation of intensive irrigation (Stamey 1996). Since 1999, the LFRB also has experienced two severe and prolonged droughts (NCDC 2010). The combined effects of high agricultural intensity, periodic drought, and the unique geologic and hydrologic characteristics of LFRB streams has had the potential to substantially affect aquatic communities in the Region.

The FRB harbors one of the most diverse and imperiled freshwater mussel assemblages in the southeastern United States (Clench and Turner 1956, Brim Box and Williams 2000, Williams et al. 2008). Thirty mussel species are believed to have occurred historically throughout the Basin, two of which are currently presumed extinct or extirpated: *Lampsilis binominata* (lined pocketbook) and *Lasmigona subviridis* (green floater); four are federally endangered: *Amblema neislerii* (fat threeridge), *Hamiota subangulata* (shinyrayed pocketbook), *Medionidus penicillatus* (Gulf moccasinshell), and *Pleurobema pyriforme* (oval pigtoe); two are federally threatened: *Elliptio chipolaensis* (Chipola slabshell) and *Elliptoideus sloatianus* (purple bankclimber); and several more are state protected or considered species of special concern (Brim Box and Williams 2000, Williams et al. 2008, GADNR 2010). In the LFRB, the availability of a long-term dataset spanning 19 (1991 to 2010) may provide valuable insight into the factors contributing to the poor conservation status of these and other LFRB mussel species

(Brim Box and Williams 2000, Brim Box et al. 2000, Golladay et al. 2004, Gagnon et al. 2006). However, considerable uncertainty exists regarding the extent to which the status and distributions of LFRB mussel species has changed during this time. Thus, there is a need for a comprehensive assessment of the current status and distribution of mussel species, in addition to quantification of how LFRB mussel species have responded to environmental stressors.

Effective conservation and recovery planning for freshwater mussel species in the LFRB can be achieved, in part, through the implementation (or continuation) of monitoring programs. The quality of such monitoring data, however, is influenced by spatial and temporal variation in mussel sample data. Freshwater mussels are often difficult to detect during sampling because of their benthic nature, ability to burrow, and clumped distributions (Strayer and Smith 2003, Thompson 2004). As such, mussel sampling data are highly susceptible to biases associated with incomplete detection of individuals and species. Additionally, identification ability likely differs among investigators and may change through time as new skills are acquired. Hence, species misidentification presents an additional and potentially substantial source of bias in mussel monitoring data. Biases associated with both incomplete detection and misidentification of species can potentially obscure true ecological patterns, or worse, suggest false patterns (Yoccoz et al. 2001, Elphick 2008). These sources of bias can accommodated, provided that details of historical and ongoing mussel collections are known (i.e., sampling location, sampling method, and the identities of investigators), which may help to improve our understanding of spatial and temporal trends in ecological patterns and our ability to develop effective conservation strategies.

The goal for this chapter was to assess the current status and distribution of freshwater mussel species native to the LFRB by developing predictive models of species occurrence in relation to site- and watershed-level characteristics while accounting for potential biases associated with incomplete detection and misidentification of mussel species during sampling. The objectives were to: 1) incorporate methods for correcting historical mussel collection data that were subject to errors associated with incomplete detection and misidentification of species during surveys; 2) develop predictive models of occurrence for LFRB mussel species in relation to site and watershed-level characteristics; 3) estimate the influence of severe drought on mussel species occupancy.

METHODS

Our primary objective was to identify the factors influencing the current status and distribution of freshwater mussel species native to the LFRB using a long-term database comprising mussel collection data spanning almost 20 years (1991-2010). Samples collected from 1991-2010 were conducted by a variety of personnel representing state and federal agencies, university faculty and students, and private environmental consulting firms. Because one of our primary objectives was to update existing knowledge of mussel species distributions throughout the LFRB, we conducted supplementary sampling from August 2007 through April 2010. To adequately represent the range of stream types and sizes present within the LFRB, we randomly selected 32 sampling locations from small, medium, and large tributaries in each of the each of the 5 major subbasins (Ichawaynochaway, Kinchafoonee-Muckalee, Lower Flint, Middle Flint, and Spring). Sites that were sampled prior to but not since 2000 were given highest priority for re-sampling because these surveys could potentially provide information regarding changes in mussel species distributions in response to record low flows from 2000-2002. Eight additional sites that were never previously sampled also were randomly selected for sampling. These sites were selected by assigning random numbers to stream/road crossings in each subbasin. Road crossings with the lowest random number were selected for sampling. For each of the five major subbasins, at least one previously un-sampled site was selected; however, two sites were selected from the Kinchafoonee-Muckalee Creek, Ichawaynochaway Creek, and Spring Creek subbasins.

For the entire time period (1991-2010), we classified mussel collections into three time periods: pre-2000 (samples collected from 1991-1999, prior to the onset of severe drought in the LFRB in 2000); 2000-2006 (samples collected following the onset of severe drought in 2000 but prior to another drought that began in 2007); and post-2007 (samples collected between 2007 and 2010, following the onset of severe drought in 2007). Our rationale for defining these periods was that we could not safely assume that the status of mussel species (i.e., the presence or absence of species) remained unchanged following severe drought, thereby violating assumptions of population closure necessary for subsequent data analyses (see *multi-species occupancy modeling*, below). Additionally, the post-2000 and post-2007 mussel collection data could potentially provide information regarding changes in the status and distribution of mussel species following record low streamflow conditions. For the entire dataset, mussel collection data were included only if: (1) the sampling date was known, (2) the site-locality was geo-referenced or otherwise recorded (e.g., there was a description of a road crossing), (3) freshwater mussel species were the primary sampling target, (4) the sampling method was known; and (5) the identity of the field crew who conducted the sample was known.

The resulting dataset consisted of detection/non-detection data for 25 mussel species collected from 246 stream reaches throughout the LFRB from 1991-2010. However, we combined data for two species, *Elliptio pullata* and *Elliptio fumata,* into *Elliptio sp.* because these species are very difficult to distinguish during field sampling and were usually recorded by field crews as *Elliptio sp.* (i.e., field crews chose not to make a species identification). Similarly, we combined data for *Pyganodon cataracta* and *Pyganodon grandis* into *Pyganodon sp.* because these species are indistinguishable in the LFRB without the use of genetics (J. Williams, Florida Museum of Natural History, personal communication) and were usually recorded as *Pyganodon sp.* Additionally, two species (*Alasmidonta triangulata* and *Anodonta heardi* were extremely rare in the LFRB (each has been collected from only a single location since 1991) and were excluded from the dataset. Hence, the resulting dataset consisted of detection/non-detection records for 21 mussel species collected from 246 stream reaches throughout the LFRB from 1991-2010.

Total sampling effort varied among sites and time periods. Of the 246 stream reaches sampled from 1991-2010, 84 were sampled *only* during the pre-2000 period (1991-1999), 113 were sampled *only* during the post-2000 period (2000-2006), and 8 were sampled *only* during the post-2007 period (2007-2010). Of the remaining 41 sites, 18 were sampled during the pre-2000 and post-2000 periods, 7 were sampled during the pre-2000 and post-2007 periods, 8 were sampled during the post-2000 and post-2007 periods, and 8 were sampled during all three periods. The number of repeat-visit sites (i.e., instances where the same location was re-sampled within the same period) also differed among the three time periods. Of the 119 total sites sampled prior to 2000, 91 were sampled on a single occasion, 24 were sampled on two occasions, 3 were sampled on three occasions, and 1 was sampled on four occasions. Of the 130 total sites sampled between 2000 and 2006, 98 were sampled on a single occasion, 27 were sampled on 2 occasions, 3 were sampled on three occasions, and 2 were sampled on four occasions. Of the 32 sites sampled between 2007 and 2010, 13 were sampled on at least two occasions, 1 was sampled eleven times, 1 was sampled ten times, 2 were sampled nine times, 1 was sampled eight times; 2 were sampled seven times; 2 were sampled three times, 4 were sampled twice, and the remaining 19 sites were sampled once. Across time periods, the amount of time between repeated surveys at the 74 repeat-visit sites ranged from 0 years (i.e., repeat surveys were conducted within the same year) to 7 years, averaging 4.3, 2.4, and 1.2 years during the pre-2000, post 2000, and post 2007 periods, respectively.

Sampling protocols

To account for differences in sampling methodology, we classified each sample occasion in the entire dataset according to one of four general sampling protocols: Qualitative, semi-quantitative, full-coverage, and transect sampling. Qualitative samples were those for which sample effort was expressed in time spent searching and was conducted on at least one occasion for 91 of the 119 sites sampled from 1991-1999 and 28 of 130 sites sampled from 2000-2006. Most (91) of the timed search surveys were conducted during the summers of 1991 and 1992. During these surveys, all mussels were collected by hand using SCUBA, snorkeling, or by direct observation in shallow areas; all possible habitats where mussels could occur were searched, including root mats, rock crevices, and logs; and all mussel species were targeted during sampling (Brim Box and Williams 2000). Total sampling effort for the 1991-1992 surveys varied among sites but averaged 1.9 person hours per site and ranged from 0.3 to 7.6 person hours (Brim Box and Williams 2000). Sampling effort for the remaining 28 qualitative sample sites was unavailable; however, we assumed that sampling effort was identical to that of the other 91 timed search surveys.

Semi-quantitative sampling was most frequently used during the post-2000 drought period. Semi-quantitative surveys were conducted by Georgia Department of Natural Resources personnel, as well as private consulting firms who were required to conduct sampling according to protocols developed by the United States Fish and Wildlife Service (Carlson et al. 2008). All of the semi-quantitative surveys were conducted using the USFWS sampling protocol (or very similar protocol; S. Abbott, U.S. Fish and Wildlife Service, personal communication), which involved sampling the entire wetted stream area 100 m and 300 m downstream and upstream, respectively, of potential impact sites (e.g., bridge crossings). Tactile surveys of the streambed were conducted in all available habitats using a variety of methods, such as snorkeling and SCUBA diving, where appropriate. Semi-quantitative surveys were conducted during at least one occasion for all of the 113 sites surveyed from 2000-2006.

Full-coverage surveys were the most-labor intensive sampling method used and were conducted on at least one sampling occasion at 47 of 119 study reaches surveyed during the pre-drought period and 3 of 32 study reaches surveyed during the post-2007 drought period. The full-coverage sampling protocol differed depending on stream size. In small streams (<12m wide), crews consisting of multiple personnel lined up side-by-side (perpendicular to streamflow) and sampled the entire surface of the streambed in an upstream direction throughout a 100 m-long study reach (Golladay et al. 2004). In larger stream reaches (≥12m-wide), full coverage sampling was conducted by crews searching six parallel transects running longitudinally in an upstream direction throughout a100 m reach (Golladay et al. 2004). All mussels collected during sampling were placed in submerged mesh bags within the study reach until sampling of the entire reach was completed. During full-coverage surveys conducted between 2007 and 2010, all captured mussels were identified to species and shell lengths (parallel to hingeline) were measured to the nearest millimeter. When sampling was complete, all collected mussels were randomly distributed throughout the study reach, with each mussel returned by hand and placed anteriorly into the sediment.

Transect sampling was the least frequently used sampling protocol and was conducted by University of Georgia and Georgia Department of Natural Resources personnel at 32 study sites from 2007-2010. In all stream sizes, the following protocol was used: a random start point was selected as the lower end of a 100-m-long study reach. Because most sites were accessed at road crossings, the starting point was a random distance (on average, approximately 100 m) measured from the upper-most portion of the bridge or scour pool (if present) associated with the bridge. Next, thirty 1-m-wide cross-sectional stream transects (perpendicular to streamflow) were randomly assigned to specific locations along the length of the 100 m sample reach. The location of each cross-sectional transect was measured upstream from meter 0 (the downstream-most end of the 100 m reach) and marked with brightly colored orange flags on both the left and right banks. During sampling, a 1-m wide band of the streambed was tactilely searched by a single person to a depth of approximately 5 cm. All mussels collected from each transect were placed in submerged mesh bags that were placed adjacent to a transect flag until sampling of the remaining transects was completed. During transect surveys, all captured mussels were identified to species and shell lengths (parallel to hingeline) measured to the nearest millimeter. When sampling was complete, all collected mussels were randomly distributed throughout the study reach, with each mussel placed by hand anteriorly into the sediment.

Watershed-level characteristics

To evaluate the relations between land use characteristics and mussel species presence, we used a HUC12 sub-watershed as the largest sample unit (USGS 1999). Using existing Geographic Information Systems (GIS) layers, we summarized the land use characteristics of 122 HUC12 sub-watersheds corresponding to the 246 mussel sample site locations (Table 3.1). For the land cover data, we used the 2001 National Land Cover Dataset (USGS 2001a) and calculated the percent agriculture, forest, urban, and wetland coverage (expressed as a percentage of the total HUC12 sub-watershed area) for each of the 122 HUC12 subwatersheds. Additionally, we defined a stream reach as 'isolated' if it was separated from the mainstem Flint River or any of the 5 major tributaries (Ichawaynochaway, Muckalee, Kinchafoonee, Chickasawhatchee, and Spring Creeks) by an impoundment. To determine reach isolation, we used the National Inventory of Dams (USACE 2010) data layer in ArcGIS 9.2 to visually assess the locations of known impoundments in the LFRB. Lastly, for each study site we calculated stream size (link magnitude; Shreve 1966) by manually counting the number of first order tributaries contributing to each study reach based on 1:24K NHD stream network layers (USGS 2001b).

Multi-species occupancy modeling

We used a multi-species occupancy modeling approach (MacKenzie et al. 2006, Royle and Dorazio 2008) to estimate mussel species occupancy and detection probability for 21 species in relation to sample-, site- and watershed-level characteristics. Occupancy models produce two types of probability-based estimates: occupancy (ψ) and detection (p). Occupancy is defined as the probability that a species is present at a sample location during sampling (MacKenzie et al.

2002). Detection is defined as the probability of detecting a species, given it is present at a study site (MacKenzie et al. 2002). Provided replicate surveys are conducted at study locations and assuming the occupancy status of species is constant across replicate surveys, occupancy and detection can be jointly modeled using a binomial likelihood with a zero-inflated class as:

$$P(Y=1)=\psi_{ij}\binom{K}{y_{ijk}}p^{y_{ijk}}\left(1-p\right)^{K-y_{ijk}} \mid \; (Y=0)=\psi_{ij}\left(1-p_{ijk}\right)^{K}+\left(1-\psi_{ij}\right)$$

, where y_{ijk} represented the recorded detections of species *j* at site *i* during each of *K* surveys, ψ_{ij} was the probability that site *i* was occupied by species *j*, and p_{ijk} was the probability of detecting species *j* at site *i* during occasion *k*, given the species was present. Using the entire dataset, we modeled species detection probability using the detection/non-detection data collected at the 74 repeat-visit sample sites (described above). We used the predicted detection probabilities (i.e., average) estimated from the repeat-visit sites to model occupancy at sites that were visited on only a single occasion. For all sample locations, we assumed that the occupancy status of all species did not change within each time period (pre-2000, post-2000, and post-2007). For example, if a study site was sampled in 1991, 1995, and 1999, we assumed that the species assemblage at that site did not change between the three sampling occasions. We believe that this assumption was valid because there were no widespread, severe disturbances (e.g., drought) that we deemed capable of extirpating entire species from study reaches *within* any of the time periods.

The occupancy modeling approach described above requires that species are identified without error during surveys (i.e., species are not permitted to be detected where they do not exist). Such errors are often referred to as false-positives and are rarely formally accommodated during occupancy modeling procedures. In some cases, ignoring the potential for species misidentification may be reasonable, provided the investigator is certain that all species identifications were correct. However, based on empirical evaluation of misidentification rates for LFRB mussel species (see Chapter 2, Shea et al. 2011), we determined that the assumption of perfect identification during historical mussel surveys in the LFRB was not valid. Hence, we used a modification of occupancy modeling following Royle and Link (2006) that accounts for potential biases associated with false positive mussel species identification and modeled mussel species occupancy (ψ_{ij}), detection (p_{11ijk}), and misidentification (p_{10ijk}) as,

$$P(Y=1) = \psi_{ij}\binom{K}{y_{ijk}}p_{11ijk}{}^{y_{ijk}}\left(1-p_{11ijk}\right)^{K-y_{ijk}} + (1-\psi_{ij})\binom{K}{y_{ijk}}p_{10ijk}{}^{y_{ijk}}\left(1-p_{10ijk}\right)^{K-y_{ijk}} \Big|$$

$$(Y=0) = \psi_{ij}\left(1-p_{11ijk}\right)^{K} + \left(1-\psi_{ij}\right)$$

, where y_{ijk} represented the total number of detections of species j at site i during K surveys, ψ_{ij} represented the probability of occupancy, p_{11ijk} represented the probability of detecting species j during occasion k given it was present at site i, p_{10ijk} represented the probability of falsely-identifying species j given it was detected during occasion k but did not actually occur at site i, and K represented the total number of replicate surveys. In practice, jointly estimating species detection (p_{11}) and misidentification (p_{10}) can be difficult in the absence of strict assumptions of parameters values (e.g., specifying that $p_{11} > p_{10}$; Royle and Link 2006, Royle and Dorazio 2008). Alternatively, supplementary data can be used as *a priori* knowledge and incorporated directly into modeling procedures by using informative prior distributions representing prior knowledge of likely species misidentification rates (Royle and Dorazio 2008). Thus, we used informative priors on the misidentification parameter p_{10} based on empirically-derived estimates of predicted misidentification rates for LFRB mussel species (Table 3.2). Across all time periods, species misidentification rates ranged from <1% to 31%, depending on specific combinations of species traits (small, medium, or large shells) and crew experience (1 to 16 years) (Table 3.2).

Using the above-described approach, we fitted multi-species occupancy models relating mussel species presence to site and watershed-level characteristics to evaluate the influence of these factors on LFRB mussel species occupancy. However, this approach cannot account for dependence (i.e., autocorrelation) among repeated samples, and we suspected that repeated observations on mussel species at locations throughout the LFRB were dependent (i.e., spatial autocorrelation) (Royle and Dorazio 2008). To account for dependence among species and locations, we fitted hierarchical occupancy models to the mussel species data. Hierarchical occupancy models differ from more familiar occupancy modeling techniques in that dependence among observations collected at lower level units (here, detection/non-detection data for multiple species across multiple study locations) within upper level units (here, sites and species), is incorporated by including random effects for the lower level intercept and slopes (Royle and Dorazio 2008). The species-level random effects were assumed to be normally distributed with a grand mean (intercept or slope) and random effect-specific variance (Bryk and Raudenbush 2002). The site-level random effect was assumed to be normally distributed with a mean 0 and random effect-specific variance. The random components represented unique effects associated with sites and species that were unexplained by covariates included in the model. To accommodate this complex model structure, we used Markov Chain Monte Carlo (MCMC) as implemented in WinBUGS software, version 1.4 (Spiegelhalter et al. 2006) to fit candidate hierarchical multi-species occupancy models. The number of iterations was determined by fitting the global model running three parallel chains and testing for convergence using the Gelman-Rubin diagnostic (Gelman and Rubin 1992). All models were fit using 200,000 iterations and 75,000 iteration burn in (i.e., the first 75,000 MCMC iterations were dropped). We used diffuse priors for all parameters, with the exception of the misidentification parameter p_{10}, for which informative priors were incorporated using a beta distribution with parameters alpha and beta. The alpha and beta parameters that defined the prior distributions were calculated via method of moments using the mean and standard deviation of predicted misidentification rates for specific combinations of experience and species characteristics (Table 3.2).

Prior to fitting candidate models, we evaluated the relative fit of ten different variance structures for the hierarchical multi-species occupancy model random effects using the global (all predictors) model. The ten variance structures contained different combinations of fixed effect and random effects associated with species, sites, a single site-level predictor (link magnitude), and covariance between the various random effects (Table 3.3). The variance structure associated with the best-fitting model was then used in all candidate hierarchical multi-species occupancy models.

Our primary hypotheses of interest were to evaluate the relative influence of site and watershed-level characteristics on mussel species occupancy. Secondarily, we sought to identify the factors influencing mussel detection probability. We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate the relative influence of site- and watershed-level factors on mussel species occupancy and detection. We first constructed a set of candidate models corresponding to our hypotheses regarding the influence of site and watershed-level factors on mussel species occupancy in the LFRB (Table 3.4). To facilitate model-fitting, we standardized all continuous predictor variables (link magnitude, percent agricultural land use, percent urban land use, and percent wetland coverage) with a mean zero and standard deviation of 1 (Table 3.1). The drought predictors included 2000-2002 drought and 2007-2008 drought and were binary coded as '1' for any sample that was conducted during or following the onset of severe drought (2000-2006 and 2007-2010). We distinguished between the post-2000 and post-2007 droughts to evaluate the relative influence of the two distinct droughts on LFRB mussel assemblages. The global (saturated) model contained the following predictors: link magnitude, reach isolation, percent agriculture, percent urban, and percent wetland land cover, 2000-2002 drought, and 2007-2008 drought. The global model also contained 2-way interactions between link magnitude and 2000-2002 drought, percent agriculture, percent urban, and percent wetland. The global detection probability model contained link magnitude and covariates corresponding to occasion-specific sampling methods (qualitative, semi-quantitative, full coverage, and transect sampling) and drought. We then developed additional candidate models by systematically excluding variables, for a total of 32 candidate models.

We evaluated the relative plausibility of each candidate model by calculating Akaike's Information Criteria (AIC; Akaike 1973) with the small-sample bias adjustment (AIC_c; Hurvich and Tsai 1989). AIC is an entropy-based measure used to compare candidate models with lower AIC values indicating better predicting models (Burnham and Anderson 2002). To count model parameters, we counted all fixed effects as 1 and random coefficients as 2 parameters. To facilitate comparisons among models, we calculated Akaike weights that range from zero to one with the best approximating candidate model having the highest weight (Burnham and Anderson 2002). The ratio of Akaike weights for two candidate models can be used to assess the degree of evidence for one model over another (Burnham and Anderson 2002). For example, a model with an Akaike weight of 0.5 is 10 times more likely to be the best predicting model compared to a model with an Akaike weight of 0.05. We considered the most plausible models to be those with AIC_c weights that were at least 10% of the best-approximating model, which is similar to Royall's general rule-of-thumb of 1/8 or 12% for evaluating strength of evidence (Royall 1997).

We assessed the precision of parameter estimates for each model by calculating 95% Bayesian credible intervals (Congdon 2001), which are analogous to 95% confidence intervals. To facilitate interpretation, we calculated odds ratios (OR) for each fixed effect parameter estimate (Hosmer and Lemeshow 2000). The OR for all continuous predictors were interpreted as a change in odds associated with a 1 SD change in the value of a predictor variable. We assessed Goodness-of-fit (i.e., MCMC convergence) for each model in the confidence set using the diagnostics detailed by Gelman and Rubin (1992).

RESULTS

From 1991 to 2010, 246 individual stream reaches were sampled on at least one occasion. Across all sampling locations and occasions, 21 species were detected during both the pre-2000 and post-2000 periods. Only 20 species were detected during the post-2007 period. The single species that was undetected during the post-2007 period, *Villosa villosa*, is generally uncommon in the LFRB and tends to inhabit small, spring-fed streams and backwater sloughs and impoundments (Williams et al. 2008). The most commonly collected species during the pre-2000 period were *Elliptio fumata/pullata* (64% of study locations), *Villosa vibex* (50%), *Villosa lienosa* (43%), and *Quadrula infucata* (42%). The most commonly collected species during the post-2000 and post-2007 periods were *Elliptio pullata/fumata* (59%), *Villosa lienosa* (40%), *Villosa vibex* (38%), *Toxolasma paulum* (31%), and *Uniomerus columbensis* (28%). During the pre-2000 period, surveyors did not detect any mussel species at 7% (8/119) of study locations, whereas surveyors failed to detect any mussel species at 27% (43/162) of sample locations during the post-2000 and post-2007 periods.

The best approximating variance structure for the multi-species occupancy models included random effects associated with the species-level occupancy intercept, the occupancy slope associated with stream size, and a site-level random effect, with no covariance between the random effects. The best approximating model of species detection probability included full coverage sampling, link magnitude, qualitative sampling, and drought. Thus, all candidate models included these random effects in the occupancy models and these covariates in the detection probability model. The best-fitting multi-species occupancy model relating mussel species presence to site- and watershed-level characteristics contained link magnitude, percent agricultural land use, post-2000 drought, post-2007 drought, reach isolation, and three 2-way interactions: link magnitude × post-2000 drought, link magnitude × agriculture, and agriculture × post-2000 drought (Table 3.5). Based on AIC weights, the best-fitting model was 33× more plausible than the next best-fitting model that included urban, agriculture, link magnitude, post-2000 drought, post-2007 drought, isolation, and five 2-way interactions: link magnitude × post-2000 drought, urban × link magnitude, agriculture × link magnitude, urban × post-2000 drought, and agriculture × post-2000 drought (Table 3.4). There was very little support for any of the remaining candidate models; hence, we reported parameter estimates for only the best-fitting model (Table 3.6).

Parameter estimates based on the best-fitting model indicated that mussel species presence was strongly and negatively related to the 2000 drought and reach isolation (Table 3.6). Odds ratios (OR) suggested that mussel species were, on average, 4.01× less likely to be present following the 2000 drought and 15.03× less likely to be present in stream reaches that were isolated by an impoundment from major tributaries or the mainstem Flint River (Table 3.6). Parameter estimates for two interaction terms, link magnitude × drought and link magnitude × agriculture, indicated that the negative relations between mussel species occupancy and the 2000 drought and percent agriculture decreased with increasing stream size (Table 3.6). The parameter estimate for the remaining interaction term, drought × agriculture, indicated that the negative relation between occupancy and drought decreased with increasing agricultural land use; however, the parameter estimate was imprecise (Table 3.6). Parameter estimates also suggested that mussel species occupancy was weakly and positively related to percent agricultural land use and negatively related to the 2007-2008 drought, but the parameter estimates were generally imprecise (Table 3.6). Lastly, species-level random effects indicated substantial heterogeneity remained among mussel species regarding overall occupancy (i.e., intercept) and the relationship (i.e., slope) between stream size and occupancy (Table 3.6).

DISCUSSION

Numerous factors have been implicated in recent declines of North American freshwater mussel populations. Previous studies have demonstrated relationships between mussel population declines and reach isolation (Watters 1996, Vaughn and Taylor 1999), land use (Poole and Downing 2004), and drought (Golladay et al. 2004, Haag and Warren 2008). However, few studies have directly estimated the influence of these factors on mussel species, and we are unaware of any published studies that have accounted for potential biases in survey data associated with both incomplete detection and misidentification of species during mussel surveys. We found that freshwater mussels in the LFRB were strongly influenced by drought, reach isolation, and stream size. We also found that the strong negative influence of drought was less severe with increasing stream size, suggesting that management and conservation efforts should focus on recovering mussel species and populations that occur in small to mid-order LFRB streams, as well as protecting populations in higher order tributaries because they may serve as important refugia for many LFRB species.

Mussel assemblages in the LFRB appear to have experienced substantial reductions in species richness since the onset of severe drought in 2000. Various reaches of several streams in the LFRB were reported dry during the 2000 drought (Golladay et al. 2004), particularly in small to mid-order tributaries, and many other stream reaches consisted of isolated pools with little or no flowing water. Strayer (1999) suggested that during extremely low flow periods, mussel mortality can be severe due to prolonged emersion, thermal stress, and predation. Hence, reduced streamflows during the 2000 drought may have resulted in poor water quality and inhospitable conditions that reduced mussel survival. Haag and Warren (2008) reported that several species that were rare prior to the onset of severe drought were not detected at study reaches following severe drought, and post-drought mussel abundance was largely a function of pre-drought abundance. Several species in the LFRB appear to be both rare and restricted to small to mid-order tributaries, including federally and state listed species such as *Anodontoides radiatus*, *Elliptio purpurella*, *Hamiota subangulata*, *Medionidus penicillatus*, and *Pleurobema pyriforme*.

Rare species that occur primarily in small to mid-order LFRB tributaries may be exceptionally prone to reduced survival and possibly local extirpation (i.e., extirpation from a study reach) in response to severe drought.

Despite being equally and perhaps more severe and prolonged, the 2007-2008 LFRB drought appears to have affected mussel assemblages to a lesser extent than the drought that occurred during 2000-2002. Although this was counter to our expectations, some possible explanations exist. Prior to 2000, the most recent severe drought in the LFRB occurred during 1954-1955 (Cook et al. 1999), whereas since 2000 the LFRB has experienced two severe and prolonged droughts. Hence, LFRB mussel populations appear to have experienced a long period (~50 years) over which they could potentially recover from the presumably negative effects of the 1954-1955 drought. Mussel populations in the LFRB have had comparatively little time to recover from the 2000 drought, as another severe drought began in 2007. We hypothesize that LFRB mussel species in drought-affected stream reaches have been slow to fully recover from the effects of the 2000-2002 drought because of drought-induced reductions in survival and recruitment. For mussel populations to persist, they likely rely heavily on both local recruitment (i.e., recruitment of individuals from the local stream-reach population) and immigration of individuals from neighboring populations. However, freshwater mussels are long-lived organisms that, although highly fecund, generally exhibit very low recruitment and may only have successful recruitment every few years (Payne and Miller 2000). In natural freshwater mussel populations, considerably less than 1% of glochidia produced by females will survive to become a free-living juvenile (McMahon and Bogan 2001). Successful recruitment from local populations in drought-affected reaches may be further impeded by reduced survival and reproduction (e.g., aborted glochidia) from drying of habitat and temperature and dissolved oxygen extremes (Aldridge and McIvor 2003, Strayer 2008). Further, juvenile mussel survival also appears to be more affected by low dissolved oxygen concentrations (Sparks and Strayer 1998) and temperature extremes (Dimock and Wright 1993) than adults, and dissolved oxygen concentrations within stream sediments (where juvenile mussels live) tend to be much lower than that of the overlying water (Strayer et al. 1997). Successful recruitment from local and neighboring populations may also be impeded by the temporary loss of host fish species from drought-affected reaches (McCargo and Peterson 2010).

The adverse effect of drought on LFRB mussels was much less severe in larger streams. Haag and Warren (2008) reported similar findings in that mussel abundance and assemblage composition changed little in larger streams following extreme drought. Additionally, Golladay et al. (2004) reported that larger stream reaches generally maintained adequate stream flows during the 2000 drought. Previous work in the LFRB also has determined that although stream-reach-level mesohabitat availability (e.g., total volume of run, pool, riffle, and edgewater habitats) was reduced during drought conditions, reductions in habitat availability became less pronounced with increasing stream size (Peterson et al. 2009). Consequently, fish assemblages in higher order stream reaches were less affected by drought conditions (i.e., fewer species were lost) compared to those inhabiting small- to mid-order streams (McCargo and Peterson 2010). Mussel assemblages in higher order stream reaches may be similarly resilient to the direct effects of drought (i.e., habitat loss and subsequent emersion and desiccation), as well as secondary effects such as increased water temperature and decreased water quality. Hence, despite reduced stream discharges during the drought, stream flow conditions in larger streams were likely sufficient to maintain the physical habitat conditions necessary for sustaining many LFRB mussel populations. The greater resiliency of large-river mussel assemblages also suggests that demographic support from mainstem-tributary populations (if present) may be critical to the persistence of some mussel species in smaller tributaries. A metapopulation structure has been postulated for freshwater mussels (Vaughn 1997, Strayer 2008); however, metapopulation dynamics within the context of freshwater mussels are currently poorly understood (Newton et al. 2008).

Mussel species occupancy was negatively influenced by the presence of impoundments. These results are consistent with previous studies (Watters 1996, Vaughn and Taylor 1999), which have demonstrated the adverse effects of impoundments on freshwater mussel assemblages. For example, low-head dams in small tributaries are known to prevent the movement of potential host fish species into upstream reaches (Watters 1996). Many fish species in the LFRB have been shown to respond to reach isolation in this manner (McCargo and Peterson 2010). Moreover, widespread disturbances such as severe drought may permanently eliminate some mussel and fish species from affected reaches, and natural re-colonization through host fish dispersal may be inhibited by the presence of impoundments. This suggests that the combined effects of drought and reach isolation may cause many LFRB mussel populations to become increasingly fragmented and potentially more vulnerable to local extinction. The removal of existing impoundments in the basin may benefit stream-dwelling organisms, including freshwater mussels (Poff and Hart 2002). However, such activities should be carefully evaluated, as dam removal may cause increased sediment loads in downstream reaches (Sethi et al. 2004). Additionally, some small impoundments have been shown to positively influence the persistence of mussel populations, and removal of these structures may increase the risk local extinction for some populations (Singer and Gangloff 2011).

The composition of mussel species assemblages in the LFRB appears to vary substantially among streams of different sizes. Although many mussel species are known to have an affinity for streams of particular sizes (Strayer 1993), the mechanisms responsible for these affinities are not well understood. Presumably, some mussel species require particular host fish species that inhabit specific types of streams (e.g., large rivers, small headwater wetlands). In contrast, other mussel species may have broader host fish requirements, or they may utilize a host fish that inhabits a wide variety of streams. Mussel species also may differ in their ability to persist in particular environmental conditions. For example, some species may be better adapted to slow-flowing headwater tributaries that exhibit substantial variability in dissolved oxygen, temperature, and streamflow conditions, whereas other may be better adapted to more stable habitat conditions found in higher order stream reaches. Several LFRB mussel species appear to be largely restricted to higher order tributaries and the mainstem Flint River, including *Elliptio crassidens, Elliptoideus sloatianus*, *Lampsilis floridensis*, *Megalonais nervosa*, and *Quadrula infucata*. However, the majority of LFRB mussel species, including several state and federally protected species (e.g., *Anodontoides radiatus*, *Elliptio purpurella*, *Hamiota subangulata*, *Pleurobema pyriforme*, and *Medionidus penicillatus*), appear to occur more commonly in small to mid-order tributaries. Populations of most LFRB mussel species in small- to mid-order tributaries may therefore be highly susceptible to local population declines and possibly local extinction (i.e., extirpation of species from affected reaches) in the event of severe, recurrent drought.

When compared to the long-term climate history in Georgia (~1600s to present), the middle 1950s through the 1990s was an unusually wet period that was characterized by relatively infrequent and short-duration droughts (Cook et al. 1999). In contrast, the climatic conditions since 2000-drought (i.e., two prolonged droughts between 2000 and 2010) appear to be more indicative of long-term climatic conditions in Georgia (Cook et al. 1999), although contemporary droughts are compounded by the effects of agricultural water withdrawals (Rugel et al. 2011). Hence, future management and conservation efforts should not discount the risk of severe drought conditions returning in the near future and should therefore focus on the development of conservation and management strategies that (1) contribute to the recovery of mussel populations in small- and mid-order tributaries, and (2) protect existing populations in higher order tributaries that may serve as important refugia for many LFRB mussel species. This study provides insight into the effects of natural and anthropogenic factors on freshwater mussel populations and provides a useful tool for identifying locations within the LFRB that may harbor populations of rare species, thereby allowing managers to develop more effective management and conservation strategies.

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Table 3.1. Mean, standard deviation (SD), and range of habitat characteristics of the 246 sample sites used to model unionid species occupancy and detection.

Characteristic	Mean	SD	Range
Link magnitude	913.5	1552.3	1 – 4000
Number of isolated sites	17		
Number of post drought sites	166		
12-digit HUC land use (% composition)			
Row crop agriculture	36.8	15.9	4-69
Urban	5.6	3.0	2-23
Wetland	15.5	8.9	3-51

Table 3.2. Means and standard deviations (SD) of predicted false-positive error rates for freshwater mussel species collected from 246 sample locations throughout the lower Flint River Basin from 1991 to 2010. For each combination, the mean and SD were used to calculate alpha and beta parameters (via method of moments) for beta prior distributions on mussel species misidentification rates. Predicted error rates are based on the best-fitting hierarchical logistic regression model relating false-positive error rates to species characteristics and observer experience as detailed in Shea et al. 2011.

Combination	Shell Size Category	Crew Experience (months)	Mean	SD
1	Small	12	0.1876	0.0983
2	Small	24	0.1107	0.0719
3	Small	36	0.0651	0.0527
4	Small	48	0.0388	0.0386
5	Small	60	0.0237	0.0284
6	Small	72	0.0148	0.0212
7	Small	84	0.0095	0.0160
8	Small	96	0.0062	0.0123
9	Small	144	0.0014	0.0051
10	Small	156	0.0010	0.0043
11	Small	168	0.0007	0.0036
12	Small	180	0.0005	0.0031
13	Small	192	0.0004	0.0027
14	Medium	12	0.3169	0.0880
15	Medium	24	0.2647	0.0785
16	Medium	36	0.2185	0.0701
17	Medium	48	0.1788	0.0629
18	Medium	60	0.1453	0.0568
19	Medium	72	0.1176	0.0513

20	Medium	84	0.0949	0.0465
21	Medium	96	0.0766	0.0421
22	Medium	144	0.0327	0.0286
23	Medium	156	0.0266	0.0262
24	Medium	168	0.0218	0.0241
25	Medium	180	0.0178	0.0223
26	Medium	192	0.0147	0.0208
27	Large	12	0.1748	0.1015
28	Large	24	0.1421	0.0873
29	Large	36	0.1148	0.0746
30	Large	48	0.0923	0.0635
31	Large	60	0.0740	0.0540
32	Large	72	0.0592	0.0460
33	Large	84	0.0473	0.0393
34	Large	96	0.0379	0.0337
35	Large	144	0.0159	0.0195
36	Large	156	0.0130	0.0174
37	Large	168	0.0106	0.0158
38	Large	180	0.0086	0.0145
39	Large	192	0.0071	0.0135

Table 3.3. Alternative variance structures evaluated for fitting candidate multi-species hierarchical occupancy models. Parameters included in each scenario are denoted by X. The best-fitting error structure (D, indicated in bold) was used to fit subsequent candidate hierarchical multi-species occupancy models.

	Error Structure									
Parameter	A	B	C	**D**	E	F	G	H	I	J
Random Intercept (species)	X	X	.	**X**	X	.	X	X	.	.
Random Intercept (site)	X	.	X	**X**	.	X	X	.	X	.
Random Slope (Link Magnitude by Species)	X	X	X	**X**	X	X	.	.	.	.
Covariance (Site intercept & Link magnitude)	X	.	X	**.**	.	.	.	.	.	.
Covariance (Species intercept & Link Magnitude)	X	X	.	**.**	.	.	.	.	.	.
Covariance (Both intercepts & Link Magnitude)	X	.	.	**.**	.	.	.	.	.	.

Table 3.4. List of variables included in candidate multispecies occupancy models for freshwater mussels in the Lower Flint River Basin, Georgia, with corresponding ecological interpretation.

Parameter	Interpretation/ hypothesis
Percent agriculture	Agricultural land use influences mussel species by decreasing water quality, increasing sedimentation, and increased water use (reduced streamflows).
Percent urban	Urban land use influences mussel species by altering stream flows and decreasing water quality.
Percent wetland	Wetland coverage influences mussel species by reducing host-fish availability and water quality (extreme DO and temperature).
Link magnitude	Stream size influences mussel species but the relationship varies substantially among species.
2000-2002 drought	Mussel assemblages were negatively affected by severe prolonged drought during 2000-2002.
2007-2008 drought	Mussel assemblages were negatively affected by severe prolonged drought during 2007-2008.
Agriculture × Link magnitude	The effect of agricultural land use decreases with increasing stream size.
Urban × Link magnitude	The effect of urban land use decreases with increasing stream size.
Wetland × Link magnitude	The effect of wetland coverage decreases with increasing stream size.
2000-2002 drought × Agriculture	The effect of severe drought increases with increasing amount of agricultural land use.
2000-20002 drought × Urban	The effect of severe drought increases with increasing amounts of urban land use.
2000-2002 drought × Wetland	The effect of severe drought increases with increasing amounts of wetland coverage.
2000-2002 drought × Link magnitude	The effect of severe drought decreases with

	increasing stream size.
Reach isolation	Mussels are negatively influenced by isolation of stream reaches (impoundments) due to the elimination of potential colonists.

Table 3.5. Akaike Information Criterion (AIC_c), number of parameters (K), ΔAIC_c, and AIC_c weights (w_i) for the confidence set of models (i) estimating multi-species occupancy (ψ) and detection probability (p) for unionid species in the Lower Flint River Basin, Georgia. Only models with at Akaike weights >0.001 are included.

Candidate model	AIC_c	K	ΔAIC_c	w_i
ψ (link magnitude, post drought, agriculture, post drought × link magnitude, post drought × agriculture, post 2007 drought, isolation), p(full coverage, qualitative sampling, link magnitude, post drought)	4297.116	20	0.000	0.971
ψ (link magnitude, post drought, agriculture, urban, post drought × link magnitude, post drought × agriculture, post drought × urban, link × agriculture, link × urban, post 2007 drought, isolation), p(full coverage, qualitative sampling, link magnitude, post drought)	4304.157	23	8.040	0.029

Table 3.6. Parameter estimates, standard deviation (SD), upper and lower 95% credibility intervals (CI), scaled odds ratio (OR), and upper and lower 95% OR credibility intervals for the best-approximating multi-species occupancy *(ψ)* and conditional detection probability (p) models. Models were fit using standardized data for the continuous predictor variables; hence, parameter estimates and odds ratios should be interpreted for a one standard deviation change in the predictor variable.

		95% CI			95% OR CI	
Parameter	Estimate	Lower	Upper	OR	Lower	Upper
Occupancy (ψ)						
Fixed Effects						
Intercept	-2.729 (0.277)	-3.778	-1.602			
Link magnitude	-0.570 (0.596)	-1.753	0.604	0.566	0.173	1.829
Agriculture	0.039 (0.201)	-0.350	0.436	1.039	0.705	1.546
Link by Agriculture	0.392 (0.164)	0.075	0.721	1.480	1.078	2.057
2000-2002 Drought	-1.390 (0.277)	-1.940	-0.850	0.249	0.144	0.427
2000-2002 Drought × Agriculture	0.203 (0.234)	-0.261	0.659	1.226	0.770	1.932
Link × 2000-2002 Drought	0.877 (0.291)	0.300	1.447	2.403	1.350	4.250
2007-2008 Drought	-0.497 (0.300)	-1.093	0.085	0.608	0.335	1.089
Isolation	-2.710 (0.705)	-4.144	-1.384	0.067	0.016	0.250
Random effects						
Intercept (species)	6.199 (2.412)	3.051	12.160			
Intercept (site)	3.833 (0.682)	2.671	5.329			
Stream size (species)	7.029 (2.950)	3.157	14.400			
Detection (p)						
Fixed Effects						
Intercept	1.099 (0.214)	0.689	1.530			
Link magnitude	0.237 (0.154)	-0.044	0.559			
Full coverage	1.103 (0.297)	0.569	1.733			
Qualitative	-0.741 (0.239)	-1.204	-0.272			
Drought	0.533 (0.219)	0.099	0.959			

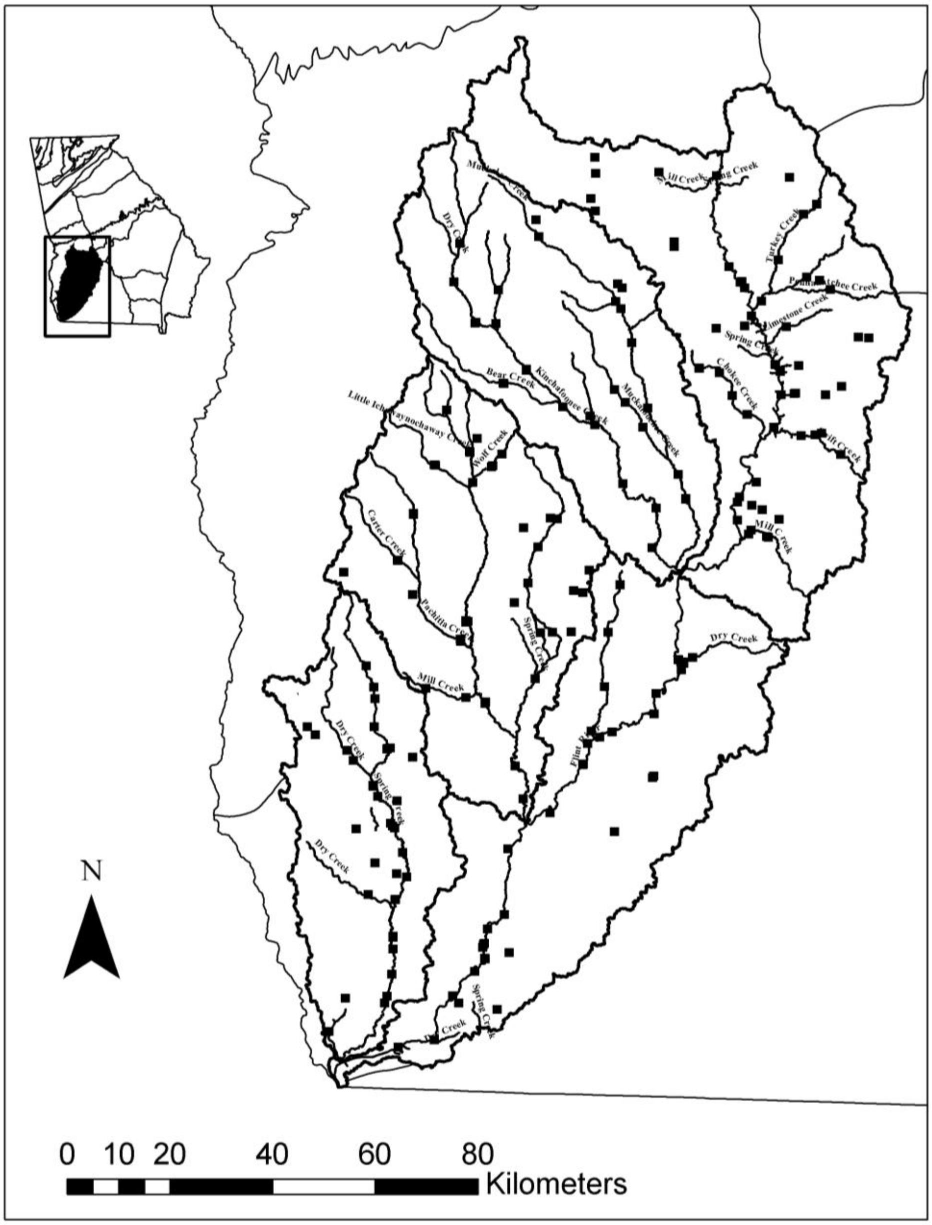

Figure 3.1. Locations within the lower Flint River Basin where freshwater mussel sampling was conducted from 1991-2010. The mussel collection data were used to develop predictive models of species occupancy for 21 freshwater mussel species native to the LFRB.

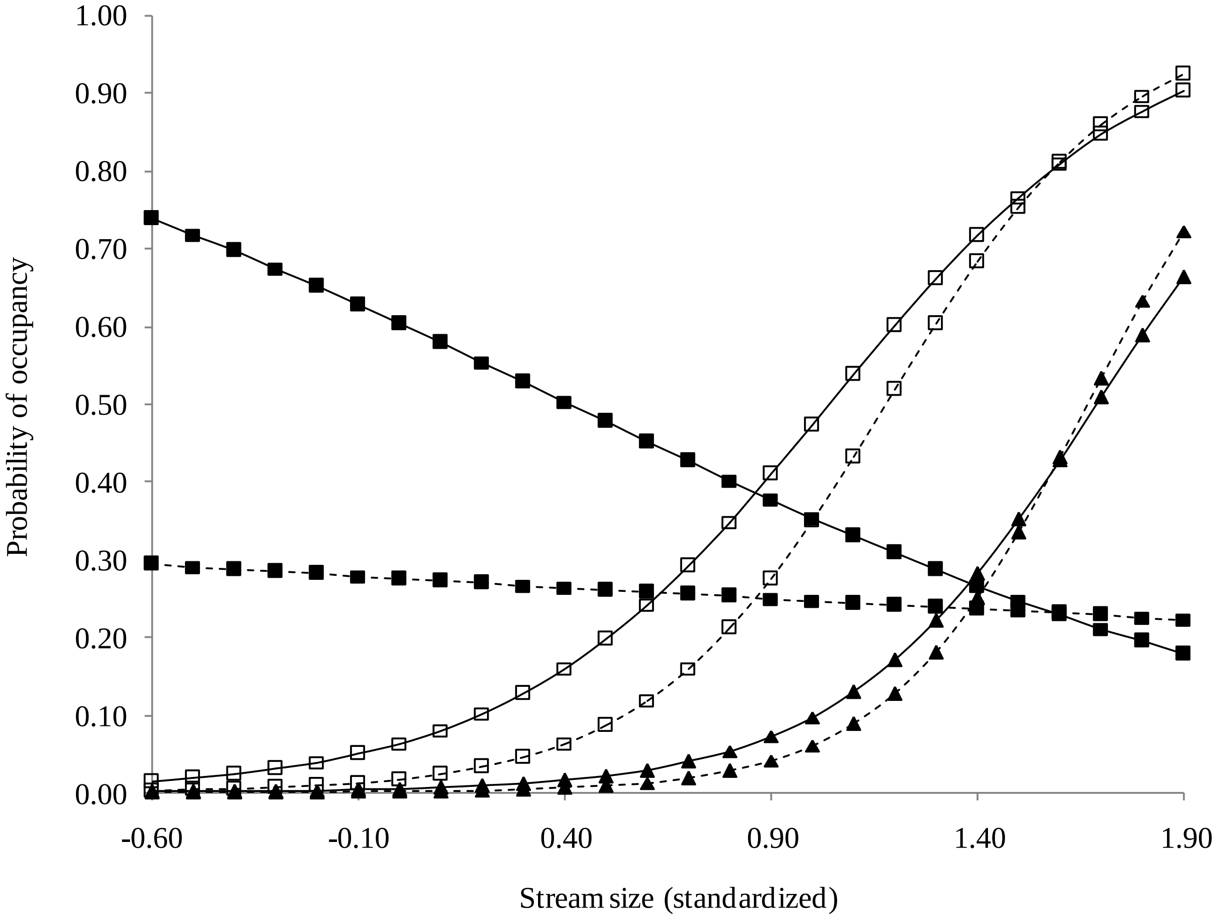

Figure 3.2. Predicted occupancy during pre-drought (solid lines) and post-drought (broken lines) conditions for three representative LFRB mussel species: *Villosa vibex* (filled squares), *Elliptio crassidens* (open squares), and *Elliptoideus sloatianus* (filled triangles). *Villosa vibex* represents the predicted drought response of LFRB mussel species that primarily inhabit small- to medium-sized tributaries. *Elliptio crassidens* represents the predicted drought response of LFRB mussel species that primarily inhabit medium- and large-sized tributaries but occasionally inhabits small tributaries. *Elliptoideus sloatianus* represents the predicted drought response of LFRB species that are generally restricted to large tributaries and almost never inhabit small tributaries.

CHAPTER 4

MODELING AND ESTIMATION OF FRESHWATER MUSSEL METAPOPULATION DYNAMICS IN THE LOWER FLINT RIVER BASIN, GEORGIA

ABSTRACT

At relatively large spatial extents (e.g., river basins) and long time frames (e.g., years), the dynamics of animal populations can be viewed from the perspective of local populations undergoing metapopulation dynamics. Metapopulation dynamic rates may vary among locations (i.e., patches) and species depending upon a variety of biotic and abiotic factors. Efforts to model metapopulation dynamic as a function of these attributes can provide insight into the predominant factors contributing to (or inhibiting) the persistence of animal populations. We used dynamic multi-state occupancy models to estimate metapopulation dynamic rates for 13 freshwater mussel species in the lower Flint River Basin, Georgia, in relation to seasonal streamflow conditions, stream reach characteristics, and species traits. Modeling results indicated an elevated risk of local population extinction in the presence of short-term summer flooding events. Modeling results also suggested that mussel species colonization rates were generally low and decreased in the presence of short-term high flow event during the spring, whereas local recruitment to existing populations decreased in the presence of short-term low winter flow conditions. Mussel populations in stream reaches that were isolated from major tributaries and the mainstem Flint River by an impoundment exhibited an elevated risk of local extinction and

reductions in local colonization and recruitment. Our results provide evidence that natural and anthropogenic factors influence freshwater mussel metapopulation dynamics, but considerable uncertainty remains regarding the precise mechanisms involved. Thus, there is a need for further research into the specific mechanisms responsible for the relations between meta-demographic rates and streamflow conditions.

INTRODUCTION

At relatively large spatial extents (e.g., river basins) and long time frames (e.g., years), the dynamics of animal populations can be viewed from the perspective of local populations undergoing metapopulation dynamics (Levins 1969, Hanski 1997, Hanski and Gaggiotti 2004). Metapopulations are characterized by groups of populations that occur within patches of suitable habitat, in which the state of a population at any given time is generally expressed in one of two states: present or absent. These populations are isolated from one another to varying degrees and are subject to processes of local extinction and colonization (hereafter, meta-demographic rates). Interactions among populations (i.e., immigration and emigration) are mediated by the dispersal of individuals to and from neighboring patches (Hanski 1998). Meta-demographic rates may vary among locations, depending upon the size and configuration of patches, proximity to neighboring patches, and environmental factors such as climate and local resource availability (Hanski 1997, Fagan 2002). Meta-demographic rates also may vary among species, depending on factors such as sensitivity to disturbance, range size, population density, and dispersal ability (Fagan et al. 2002). Efforts to model meta-demographic rates as a function of these and other attributes may therefore provide insight into the predominant factors contributing to (or inhibiting) the persistence of animal populations and species. In the context of stream systems, such an approach may be useful for evaluating the influence of changes in the availability of critical resources (e.g., water) on stream-dwelling organisms.

Metapopulations have been proposed as a potentially useful conceptual framework for assessing spatial and temporal changes in the distribution and abundance of freshwater mussel species (Vaughn 1993, Vaughn 1997, Strayer 2008). Many freshwater mussel species exhibit naturally patchy distributions throughout stream systems (Strayer et al. 2004), presumably because they are dependent on specific (though often unknown) environmental conditions, such as streamflow (Strayer 1999), geomorphology (Gangloff and Feminella 2007), and substrate characteristics (Zigler et al. 2008). Adult freshwater mussels have extremely limited dispersal capabilities, generally on the order of 10's of m (Balfour and Smock 1995, Schwalb and Pusch 2007); hence the dispersal of mussel species throughout stream systems is largely driven by (1) the movement of encysted glochidia that are attached to host-fish species (Schwalb et al. 2011) and (2) the direct transport of juveniles and glochidia in the water column (Morales et al. 2006, Schwalb et al. 2010). In recent decades, habitat alteration associated with water resource development activities (e.g., excessive sedimentation, channelization, stream impoundment, and streamflow modification) has presumably contributed to reductions in survival, recruitment, and dispersal rates for many mussel species (Strayer et al. 2004, Strayer 2008). As such, water resource development activities have likely contributed to the formation of mussel populations that are increasingly fragmented (Strayer et al. 2004, Bogan and Roe 2008). Combined, these factors suggest that metapopulations are a highly applicable conceptual framework for approaching the management and conservation of freshwater mussel species.

Temporal changes in the occurrence of a mussel population at a location presumably reflect the outcome of meta-demographic processes (MacKenzie et al. 2003, 2006). Modeling the complex effects of streamflow conditions on mussel populations can therefore be simplified into modeling the relationship between streamflow conditions and meta-demographic rates over successive time periods. However, most freshwater mussel species are long-lived organisms (>10 y) that generally respond slowly to changes in the environment (Bauer 1992, Bauer and

Wächtler 2001, Strayer 2008). Colonization and extinction processes may therefore occur, on average, at very low rates, and the consequences of large-scale metapopulation dynamics (i.e., changes in species distributions) may not become apparent for years or even decades (Strayer 2008). Thus, potentially low rates of mussel colonization and extinction may inhibit our ability to estimate mussel meta-demographic rates, particularly with respect to how they are influenced by local environmental conditions.

Expressing the status of mussel populations in terms of species presence or absence may indeed be too coarse to adequately represent slow system dynamics, which may inhibit the ability of managers and biologists to identify the factors influencing mussel species persistence. However, the population status of mussels can be expressed at a slightly finer, multi-state resolution, such as abundance classes (e.g., absent, rare, or abundant) or the presence or absence of different life history stages (e.g., juveniles and adults, breeding and non-breeding individuals) (MacKenzie et al. 2009). A multi-state perspective still allows for estimation of local colonization and extinction rates (i.e., relatively coarse processes that may occur at very low rates), but also enables consideration of subtler system dynamics, such as a population transitioning from one abundance class to another (e.g., abundant to rare and vice versa). Estimation of additional state transitions may allow for better representation of metapopulation dynamics that occur slowly over long time periods. From an ecological perspective, a finer resolution representation of system dynamics does not change the outcome of ongoing dynamics (i.e., a species will either persist or not). From a management perspective, however, a finer resolution may provide insight into the factors that are driving metapopulation dynamics that are difficult to observe because they occur over long time periods.

The purposes of this study were to: 1) develop dynamic multi-state occupancy models to estimate meta-demographic rates for 13 mussel species in the lower Flint River Basin (LFRB), Georgia, 2) estimate the influence of seasonal streamflow conditions on mussel species meta-demographic rates, and 3) estimate the influence of species traits and stream-reach characteristics on meta-demographic rates.

METHODS

We evaluated the relative influence of seasonal streamflows and stream characteristics on meta-demographic rates for 13 freshwater mussel species at 16 study sites in the Ichawaynochaway Creek subbasin (Figure 4.1). Ichawaynochaway Creek is one of the 5 major (HUC 8) subbasins in the lower Flint River Basin (LFRB) in southwestern Georgia and generally exhibits the typical range of streams types and sizes found throughout the LFRB. We restricted our analysis to Ichawaynochaway Creek primarily because detailed streamflow models were available for this subbasin (see Streamflow estimation, below), which were required for calculation of seasonal streamflow components (see Dynamic multi-state occupancy modeling, below). For each of the 16 study sites, we calculated stream size (link magnitude; Shreve 1966) by manually counting the number of first order tributaries contributing to each study reach based on 1:24K NHD stream network layers (USGS 2001). Additionally, we defined a stream reach as ‘isolated’ if it was separated from the mainstem Flint River or any of the 2 major tributaries (Ichawaynochaway and Chickasawhatchee Creeks) by an impoundment. To determine reach isolation, we used the National Inventory of Dams (USACE 2011) data layer in ArcGIS 9.2 to visually assess the locations of known impoundments in the subbasin.

Mussel sampling

Mussel sampling was conducted at the 16 study sites on at least 2 occasions from summer 1997 through summer 2006. Twelve sites were sampled on two occasions during this time period, and three sites were sampled on 3 occasions, for a total of 35 sampling events. To account for differences in sampling methodology, we classified each sample occasion in the entire dataset according to one of three sampling methods: semi-quantitative, full-coverage, and qualitative sampling. Of the 35 total sampling occasions, 23 were conducted using semi-quantitative methods, 9 were conducted using full coverage methods, and 3 were conducted using qualitative methods.

The 23 semi-quantitative surveys were conducted by Georgia Department of Natural Resources personnel, as well as private consulting firms that were required to conduct sampling according to protocols developed by the United States Fish and Wildlife Service (Carlson et al. 2008). The USFWS protocol involved tactile searches of all available habitats using a variety of methods (e.g., snorkeling and SCUBA diving) over a distance of approximately 100 m and 300 m downstream and upstream, respectively, of potential impact sites (e.g., bridge crossings). All semi-quantitative surveys were conducted using the USFWS sampling protocol (or very similar protocol (S. Abbott, U.S. Fish and Wildlife Service, personal communication).

Full-coverage surveys were the most-labor intensive sampling method. The full-coverage sampling protocol differed depending on stream size. In small streams (<12m wide), crews consisting of multiple personnel lined up side-by-side (perpendicular to streamflow) and sampled the entire surface of the streambed in an upstream direction throughout a 100 m-long study reach (Golladay et al. 2004). In larger stream reaches (>12m-wide), full coverage sampling was conducted by crews searching six parallel transects running longitudinally in an upstream direction throughout a100 m reach (Golladay et al. 2004). Full coverage surveys were conducted on 9 of the 35 sampling occasions.

Qualitative samples were those for which sample effort was expressed in time spent searching. During these surveys, all mussels were collected by hand using SCUBA, snorkeling, or by direct observation in shallow areas; all possible habitats where mussels could occur were searched, including root mats, rock crevices, and logs; and all mussel species were targeted during sampling (Brim Box and Williams 2000). Total effort for the 3 qualitative surveys was unknown, but effort for similar surveys conducted during the summers of 1991 and 1992 averaged 1.9 person hours per site and ranged from 0.3 to 7.6 person hours (Brim Box and Williams 2000). Hence, we assumed that effort for the 3 qualitative surveys in this study was similar and that sample collections adequately represented the existing mussel assemblages.

Definitions and statistical analyses

<u>Streamflow estimation.</u> – One of our objectives was to identify the seasonal stream flows that had the greatest influence on local mussel species meta-demographic rates. We used existing streamflow models developed by the U.S. Geological Survey to calculate seasonal flow statistics. The streamflow models were developed using the Precipitation Runoff Modeling System (PRMS; Leavesley et al. 1983). PRMS is a distributed-parameter, physically based watershed model under which watersheds are partitioned into hydrologic response units (HRUs) using a geographic information system (GIS) interface (Hay et al. 2002). PRMS combines daily inputs

of the climate variables precipitation, maximum temperature, minimum temperature, and solar radiation with calibrated stream gauge data to produce a streamflow time series for all stream segments comprising each HRU (Hay et al. 2002). Precipitation, temperature, and calibrated stream gauge data are obtained from long-term climate and gauging stations, whereas solar radiation is computed using algorithms in PRMS (Hay et al. 2002).

To evaluate the influence of stream flows on mussel meta-demographic rates, we calculated seasonal flow statistics for each site using the average daily streamflows generated by PRMS. We defined seasons as: spring, March-June; summer, July-October; and winter, November-February. Our primary hypotheses of interest focused on evaluating the relative influence of three seasonal flow regime components on mussel meta-demographic rates: short-term low flows, short-term high flows, and long-term average flows. We characterized short-term low flows as the 10-day low discharge, which was calculated as the lowest average discharge for 10 consecutive days during each seasonal period prior to mussel sampling. The short-term high flows were similarly calculated as the highest average discharge for 10 consecutive days during each seasonal period prior to mussel sampling. Long-term flow conditions were calculated as the median discharge during each seasonal period prior to mussel sampling. Stream sizes varied substantially among study locations (Table 4.1), potentially complicating the evaluation of the effects of flow components on local mussel meta-demographic rates. To facilitate the evaluation, we standardized the seasonal discharge statistics (described above) for each site by dividing each statistic by the contributing watershed area.

Dynamic multi-state occupancy modeling.– We estimated mussel meta-demographic rates using multi-state, multi-season, multi-species occupancy models (hereafter, dynamic multi-state occupancy models; MacKenzie et al. 2009). For each survey, we considered three population states (z) for each species: unoccupied ($z = 0$), occupied and rare ($z = 1$), and occupied and abundant ($z = 2$). To assign population states, we used existing knowledge of the relative abundance of each species to determine thresholds for assigning whether or not a species was rare or abundant during a given survey. For example, we used a threshold of 50 individuals for *Elliptio sp. (Elliptio pullata* and *Elliptio fumata)*, which are two widely distributed and locally abundant ACF species (i.e., populations were considered rare if <50 individuals were detected and abundant if 50 or more individuals were detected). In contrast, we used a threshold of 3 individuals for *Medionidus penicillatus*, which is a critically endangered species that is extremely rare in the ACF. Thresholds for the remaining 11 species were similarly assigned based on our knowledge and that of an experienced LFRB mussel biologist (J. Wisniewski, Georgia Department of Natural Resources, personal communication) of the relative abundance of LFRB mussel species (Table 4.2).

To model meta-demographic rates, each of the 13 mussel species could undergo one of the following 6 annual state transitions: (1) rare to absent; (2) abundant to absent, (3) absent to rare; (4) absent to abundant, (5) rare to abundant, and (6) abundant to rare (Figure 4.2). The probability of a site being unoccupied by a species at year t was estimated as:

$$\Psi_t^0 = \left((1-\gamma_t) \cdot \Psi_{t-1}^0 + \varepsilon 1_t \cdot \Psi_{t-1}^1 + \varepsilon 2_t \cdot \Psi_{t-1}^2 \right);$$

occupied and rare as,

$$\Psi_t^1 = \left(\gamma_t \cdot \Psi_{t-1}^0 + (1-\varepsilon 1_t) \cdot \Psi_{t-1}^1 + \varphi 1_t \cdot \Psi_{t-1}^2 \right);$$

and occupied and abundant as,

$$\Psi_t^2 = \left(\gamma_t \cdot \Psi_{t-1}^0 + \varphi 2_t \cdot \Psi_{t-1}^1 + (1-\varepsilon 2_t)\cdot \Psi_{t-1}^2\right),$$

where Ψ_t^z was the probability of being in state *z*, γ_t was the probability of colonization (transitioning from absent to rare or abundant), $\varepsilon 1_t$ was the probability of extinction for rare populations, $\varepsilon 2_t$ was the probability of extinction for abundant populations, $\varphi 1_t$ was the probability of transitioning from abundant to rare, and $\varphi 2_t$ was the probability of transitioning from rare to abundant.

In general, not all individuals and species are detected during animal surveys (Williams et al. 2002, MacKenzie et al. 2002, Tyre et al. 2003), and freshwater mussels can be difficult to identify correctly (Shea et al. 2011). Hence, the multi-state models also accounted for incomplete detection (i.e., false absences) and species misidentification (i.e., false presences) during surveys. To account for incomplete detection of species during surveys, we used auxiliary mussel collection data from 12 study sites that were sampled from 2007-2010 to estimate state-specific detection probabilities for each species using multi-state occupancy models in Program MARK (White and Burnham 1999; Table 4.2). To accommodate false presences, we used an existing model (developed in Chapter 2; see also Shea et al. 2011) to predict species-specific misidentification rates for each of the 35 surveys based on our knowledge of the experience level of the survey crew and the shell size of each species. Additionally, we assumed that there was a risk of false-positive species identification only when species were rare (i.e., abundant populations were observed without error). The probability of observing that a site was unoccupied by a species at year *t* was estimated as:

$$\pi_t^0 = \left((1 - p3_t) \cdot \Psi_{t-1}^0 + (1 - p1_t) \cdot \Psi_{t-1}^1 + (1 - p2_t) \cdot \Psi_{t-1}^2 \right);$$

occupied and rare as,

$$\pi_t^1 = \left(p3_t \cdot \Psi_{t-1}^0 + p1_t \cdot \Psi_{t-1}^1 + p12_t \cdot \Psi_{t-1}^2 \right);$$

and occupied and abundant as,

$$\pi_t^2 = \left(p2_t \cdot \Psi_{t-1}^2 \right),$$

where π_t^z was the probability of observing state *z* at year *t*, $p1_t$ was the probability of detecting state 1 given the species was in state 1, $p12_t$ was the probability of incorrectly detecting state 1 when the species was actually in state 2, $p2_t$ was the probability of detecting state 2 given the species was in state 2, and $p3_t$ was the probability of incorrectly classifying a species as present and in state 1 when it was actually absent.

For some study locations, mussel sampling began following severe drought that occurred in the LFRB from 2000-2002. We were concerned that the initial occupancy ($t = 0$) at each site would reflect a mussel assemblage that was already affected by drought conditions. Therefore, we used existing occupancy models developed in Chapter 3 to predict the initial occupancy state for each species at each of the 16 study sites. These models, which were developed using data collected from 246 stream reaches throughout the LFRB, were used to predict species-specific initial occupancy probabilities at each site as a function of link magnitude, land use, and reach isolation. The initial occupancy probabilities were then included as informative priors (statistical distributions that represent prior knowledge of possible parameter values; Gelman et al. 2004) for the initial occupancy state for each species at each study location.

Model selection.– We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate the relative influence of seasonal streamflow components, stream characteristics, and species traits on mussel species meta-demographic rates. Our primary hypotheses of interest were to evaluate the relative influence of short- and long-term seasonal flows on mussel meta-demographic rates (Table 4.3). Secondarily, we sought to determine the influence of species traits and stream characteristics on the relations between flow components and mussel meta-demographic rates (Table 4.3). Because of the large number of flow regime components (9) and meta-demographic rates (5), the total number of possible candidate models was extremely large. Thus, to reduce the total number of candidate models, we made following two simplifying assumptions. First, because each of the 5 meta-demographic rates represented either a population decline ($\varepsilon 1_t$, $\varepsilon 2_t$, and $\varphi 1_t$) or a population increase (γ_t and $\varphi 2_t$), we assumed that the population-level processes contributing to population declines (i.e., mortality) and increases (i.e., local recruitment and colonization) were similar. Hence, we modeled all meta-demographic rates representing population declines as a function of the same streamflow component, and all meta-demographic rates representing population increases as a function of the same streamflow component. It is important to clarify that this was done to simply to reduce the total number of models and that the response to a given streamflow component could differ among all 5 meta-demographic rates. Second, we assumed that the meta-demographic parameters representing local population declines ($\varepsilon 1_t$, $\varepsilon 2_t$, and $\varphi 1_t$) were primarily influenced by the seasonal streamflow conditions that occurred during the year immediately preceding sampling. In contrast, we assumed that meta-demographic parameters representing local population increases (γ_t and $\varphi 2_t$) were influenced by the seasonal streamflow conditions that occurred 2 years prior to sampling. Our rationale for incorporating a 2-year time lag was that (1) juvenile unionids are essentially unobservable because they are very small and remain burrowed until they are at least 2-3 years old (Balfour and Smock 1995, Schwalb and Pusch 2007), and (2) recent evidence from a small ACF tributary suggests that seasonal streamflows that occurred 2 years prior to sampling most heavily influenced recruitment rates for populations of 3 federally endangered ACF mussel species (Peterson et al. 2011).

In addition to seasonal streamflow components, we also modeled meta-demographic rates as a function of site- and species-specific characteristics. Previous research has suggested that small-shelled species are particularly susceptible to local extirpation and extinction (Strayer 2008). Hence, we evaluated the influence of adult mussel shell size on $\varepsilon 1_t$, $\varepsilon 2_t$, and $\varphi 1_t$. Using published species accounts (Brim Box and Williams 2000, Williams et al. 2008), we classified the 13 mussel species as small (maximum adult shell length $\leq$ 60 mm) or medium (maximum shell length >60 mm). We included only small and medium as shell-size predictors because none of the 13 species included in this analysis were large-shelled species (Table 4.2). Additionally, because the local recruitment and dispersal ability of mussel species may be influenced by the seasonal timing and duration of reproductive activities, we evaluated the influence of brooding strategy (short-term vs. long-term brooding species) on γ_t and $\varphi 2_t$ (Tables 4.2 and 4.3). To account for differences among study locations, we included two site-level characteristics, stream size and reach isolation, as site-specific predictor variables influencing meta-demographic rates (Table 4.3). Prior to evaluating the fit of the candidate models, the streamflow statistics and link magnitude were standardized (mean=0, SD=1) to facilitate MCMC model fitting. Additionally, reach isolation was binary coded, with isolated reaches coded as 1 and 0 otherwise. Similarly, categorical species traits predictors (long-term vs. short-term brooder, small vs. medium-sized shell) were binary coded, with long-term brooders and small-shelled species coded as 1 and 0 otherwise.

The resulting candidate model set contrasted 25 models that included stream size, reach isolation, mussel shell size, brooding strategy, and a single flow regime component each for meta-demographic parameter representing population declines and population increases. The candidate model set also included the global model that included all flow regime components, stream characteristics, and species traits.

To accommodate the complex model structure, we used Markov Chain Monte Carlo (MCMC) as implemented in WinBUGS software, version 1.4 (Spiegelhalter et al. 2006) to fit the dynamic multi-state occupancy models. All models were fit based on 50,000 iterations with 20,000 burn in (i.e., the first 20,000 MCMC iterations were dropped). The number of iterations was determined by fitting the global model running three parallel chains and testing for convergence using the Gelman-Rubin diagnostic (Gelman and Rubin 1992). We used diffuse priors for all model parameters, with the exception of initial occupancy state, for which we used informative priors. We evaluated the relative support for each candidate model by calculating Akaike's Information Criteria (AIC; Akaike 1973) with the small-sample bias adjustment (AIC_c;

Hurvich and Tsai 1989). We also calculated AIC weights that range from zero to one, with the most plausible candidate model having the highest weight (Burnham and Anderson 2002). We then constructed a confidence set of models as those candidate models that had AIC_c weights that were at least 10% of the highest AIC_c weight, which is similar to the cut-off established by Royall (1997) for evaluating strength of evidence. All inferences were based on the confidence model set. The precision of each fixed effect in the best supported models was estimated by computing 90% credible intervals (Congdon 2001), which are analogous to 90% confidence intervals.

RESULTS

From 1997 to 2006, surveys crews conducted 35 samples at 16 study reaches throughout the Ichawaynochaway Creek subbasin (Table 4.1). The most commonly collected species were *Elliptio sp.* (57% of samples), *E. crassidens* (57%), *Villosa lienosa* (49%), *Villosa vibex* (46%), *Uniomerus columbensis* (43%), and *Toxolasma paulum* (34%). The remaining 8 species were collected from as few as 3% of surveys (*Anodontoides radiatus* and *Medionidus penicillatus*) to as many as 20% of surveys (*Quadrula infucata*) (Table 4.2). Streamflows varied considerably throughout this time period, and based on comparisons with long-term U.S. Geological Survey GS streamflow records represented among the lowest and highest streamflows that typically occur in the Basin (Figure 4.3). Across study sites, the lowest streamflows generally occurred during winter 2001 and the highest streamflows occurred during spring 2003 and 2004.

The best-approximating multi-state occupancy model relating mussel meta-demographic rates to seasonal streamflow components, species traits, and site characteristics included link magnitude, reach isolation, small shell size, maximum10-day summer discharge (strong, positive influence on local extinction), and minimum 10-day winter discharge (strong, positive influence on local recruitment and colonization; Table 4.4). Based on AIC_c weights, the best-approximating model was 1.65, 1.65, 2.72, 4.49, and 4.49 times more plausible than the next 5 best-fitting models, respectively (Table 4.4). Across the confidence set of models, Akaike weights indicated that support was highest for maximum 10-day summer discharge (sum of AIC_c weights = 0.58) and median summer discharge (0.31) influencing local extinction, whereas support was highest for maximum 10-day spring (0.36), minimum 10-day winter (0.36), and maximum 10-day winter discharge (0.17) influencing local colonization and recruitment. There was very little support for any of the remaining candidate models; hence, all inferences were based on the confidence set of models.

Local extinction

Rare populations - Parameter estimates based on the confidence set of models indicated that local extinction of rare populations was negatively related to stream size (Table 4.5). Odds ratios (OR) suggested that for every 1 SD increase in link magnitude, rare mussel populations were 3.96 times less likely to become locally extinct. The parameter estimate for a single interaction term, link magnitude × maximum 10-day summer discharge, indicated that the negative influence of maximum 10-day summer discharge decreased with increasing stream size (Table 4.5, Figure 4.4). Parameter estimates also suggested local extinction of rare populations was greater for small-shelled species, weakly and positively related to maximum 10-day summer discharge, and strongly and positively related to reach isolation; however, the estimates were generally imprecise (Table 4.5).

Abundant populations - Parameter estimates based on the confidence set of models indicated that local extinction of abundant populations was strongly and positively related to median and maximum 10-day summer discharge (Table 4.5, Figure 4.5). Parameter estimates also indicated that the risk of local extinction was higher for small-shelled mussel species compared to species with medium-sized shells. Odds ratios suggested that abundant populations of small-shelled species were, on average, 8.3 times more likely to become locally extinct than abundant populations of medium-sized species (Table 4.5). The risk of local extinction of abundant populations also was strongly and positively related to reach isolation and weakly and negatively related to stream size; however, the parameter estimates were generally imprecise (Table 4.5).

Local colonization

Parameter estimates based on the confidence set of models indicated that the probability of colonization was very low, particularly for long-term brooding species. Odds ratios indicated that long-term brooding species were 6.77 times less likely to colonize unoccupied stream reaches compared to short-term brooding species (Table 4.5). The interaction term, link magnitude × maximum 10-day spring discharge indicated that as the magnitude of maximum 10-day spring discharge increased, colonization rates declined, particularly in large streams (Table 4.5, Figure 4.6). Parameter estimates also suggested that colonization was negatively related to reach isolation and maximum 10-day spring discharge, and positively related to link magnitude; however, the estimates were generally imprecise (Table 4.5).

Local recruitment

Parameter estimates based on the confidence model set indicated that recruitment to existing populations was strongly and positively related to minimum and maximum 10-day winter discharge. Odds ratios suggested that for every 1 SD increase in minimum and maximum 10-day winter discharge, mussels were 9.97 and 4.56 times more likely, respectively, to successfully recruit to existing populations (Table 4.5, Figure 4.7). Additionally, the interaction term, link magnitude × maximum 10-day winter discharge, suggested that the positive effect of maximum 10-day winter discharge on local recruitment was greater in larger streams (Table 4.5). Parameter estimates also indicated that local recruitment was strongly and negatively related to reach isolation, but the estimate was imprecise (Table 4.5).

DISCUSSION

Metapopulation dynamics have repeatedly been proposed as a potentially useful approach for assessing changes in the status and distribution of freshwater mussel species (Vaughn 1993, Vaughn 1997, Newton et al. 2008, Strayer 2008). We are unaware of any studies that have estimated freshwater mussel meta-demographic rates, and to the best of our knowledge there are no published studies that have modeled meta-demographic rates for stream-dwelling organisms as a function of streamflow conditions. We found that mussel species meta-demographic rates were influenced by local streamflow conditions, stream-reach characteristics, and species traits. We also found that the influence of streamflow conditions on meta-demographic rates varied seasonally and among locations, which suggests that mussel species meta-demographic rates are highly context dependent. Our study demonstrates that, provided efforts are made to account for potential biases associated with incomplete detection and misidentification of mussel species, long-term mussel collection data can be useful for quantitatively assessing the predominant factors influencing changes in the status and distribution of mussel species over large spatial and temporal extents. Given the slow dynamics of freshwater mussel species, our modeling approach could be combined with monitoring programs to provide insight into the factors influencing mussel species metapopulation dynamics that are otherwise difficult to observe. Understanding the relationships between meta-demographic rates and site- and species characteristics, however, also requires understanding of the population-level mechanisms that influence metapopulation dynamics.

Rare, episodic events such as droughts and floods are important factors influencing the distribution and abundance of aquatic organisms in general (Resh et al. 1988, Allan 1995, Lake 2000), and benthic aquatic organisms in particular (Biggs et al. 1999, Hastie et al. 2001, Haag and Warren 2008). We found that short-term high flow conditions during the summer elevated the risk of local extinction for mussel populations, particularly in small tributaries. The displacement of adults and juveniles caused by high shear stress is thought to play a role in determining mussel distributions and local abundance (Tucker 1996, Hardison and Layzer 2001), and freshwater mussels are known to inhabit areas of low shear stress, in part, because these habitats are thought to be effective refugia during floods (Strayer 1999, Howard and Cuffey 2006). The importance of summer floods in our study also suggests that the risk of local extinction is related to seasonal aspects of freshwater mussel ecology and behavior. Freshwater mussels generally ascend to the streambed surface during spring and summer (Amyot and Downing 1997), presumably for activities related to feeding (filtering food from the water column) and reproduction (e.g., gamete release, fertilization, host-fish attraction, and glochidial release). Most mussel species exhibit peak reproductive activity beginning in spring and continuing through summer (Amyot and Downing 1997, Culp et al. 2011), and the bulk of mussel feeding and growth also typically occurs during spring and summer (Negus 1966, Strayer 2008). We hypothesize that these seasonal behaviors may cause a large proportion of mussel populations to be located at the streambed surface during summer; consequently, a relatively large proportion of mussel populations may be especially vulnerable to the scouring effects of floods during summer compared to other seasons. Mussel populations in small- and mid-order tributaries may be particularly prone to local extinction because they are exposed to relatively frequent, localized flooding events, and rapidly changing streamflow conditions compared to populations in higher order stream reaches (Gomi et al. 2002). Further, although we found little evidence that low flow conditions elevated the risk of local extinction, Golladay et al. (2004) reported that many mussel species tend to congregate in isolated pools during prolonged drought. Although these habitats may be suitable refugia during drought, they generally become zones of streambed scour and relatively high shear stress during floods (Lake 2000, Lepori and Hjert 2006). Thus, it is possible that some mussel populations may be particularly susceptible to the scouring effects of high flow events that occur during periods of prolonged drought.

A cursory review of the status of North American freshwater mussel species reveals that a disproportionate number of species that are classified as imperiled or extinct are small-shelled species (<75mm) (Strayer 2008). We found that the risk of local extinction was substantially higher for small-shelled species compared to medium-sized species. Contrary to our expectations, however, we found little evidence that small-shelled species were more susceptible than larger-shelled species to local extinction in response to summer flooding events. As such, factors unrelated to local streamflow conditions may be responsible for this general pattern. Of the five species we classified as small-shelled, two are federally endangered (*Medionidus penicillatus* and *Pleurobema pyriforme*), two are classified as a state-listed species of special concern (*Elliptio purpurella* and *Quadrula infucata*), and only one (*Toxolasma paulum*) is considered currently stable throughout its range (Williams et al. 1993, Williams et al. 2008). The elevated risk of local extinction for small species in our study may therefore reflect ongoing and long-term declines for these species, perhaps resulting from historical disturbances (i.e., unobserved during the course of our study) such as land use (e.g., excessive sedimentation; Trimble 1974) or reduced water quality (Augspurger et al. 2003). Additionally, previous research has shown that the reproductive capacity of freshwater mussels generally increases with maximum shell length (Downing et al. 1993, Haag and Staton 2003). Although we did not evaluate the influence of shell size on local colonization and recruitment, we believe it is possible that the reduced reproductive capacity of small-shelled species may render some populations incapable of compensating for local mortality, thereby elevating the risk of local extinction for these populations due to long-term reductions in population growth rates (Hughes and Parmalee 1999, Ricciardi and Rasmussen 1999).

Colonization of unoccupied stream reaches was generally very low and was most heavily influenced by the magnitude of short-term flooding events during the spring. We assumed that for mussel species to successfully colonize unoccupied stream reaches, individuals immigrated to unoccupied reaches via (1) glochidial attachment to host fish species that locally inhabited a stream reach or that migrated to a reach from neighboring (upstream and downstream) populations, or (2) direct transport of juveniles and glochidia within the water column from upstream populations. Although we were unable to quantify the relative contribution of host-fish transport versus the transport of free-living juveniles in the water column, both processes are thought to play important roles in the colonization of new habitats (Morales et al. 2006, Schwalb et al. 2010). We found that exceptionally high spring flow events substantially reduced local colonization rates, particularly in large rivers. We hypothesize that spring flood pulses may inhibit the ability of mussels to colonize unoccupied stream reaches by altering seasonal movements of potential host fish species (and attached glochidia), as well as by displacing or killing newly settled juveniles or drifting glochidia. In the Ohio River, Payne and Miller (2000) found attributed successful recruitment for *Fusconaia ebena* to short-term spring floods that aggregated their host over mussel beds, which presumably enhanced glochidial infestation. Payne and Miller (2000) also speculated that a rapid return to normal flow conditions was important for the successful settlement and subsequent survival of juvenile mussels. Hence, exceptionally large spring floods may reduce local mussel colonization rates by (1) impairing the ability of host fishes to move throughout streams systems, and (2) by causing free-living juvenile mussels and glochidia to be crushed, buried, or otherwise displaced to unsuitable habitats (Layzer and Madison, 1995, Morales et al. 2006). Regardless of the precise mechanisms, spring flood pulses appear to be important factors influencing the ability of mussel species to colonize unoccupied stream reaches.

Flow-mediated restrictions on juvenile settlement are thought to play an important role in determining the distribution and local abundance of mussel species (Hardison and Layzer 2001). Previous studies have suggested that low streamflow conditions can enhance local recruitment for some freshwater mussel species (Payne and Miller 2000, Gore et al. 2001). We found that the ability of juvenile mussels to successfully recruit to existing populations was strongly and positively influenced by short-term low streamflow conditions during winter. On average, winter streamflows in our study system were lowest during November and December (i.e., early winter). We assumed that recruitment to existing populations (i.e., populations transitioning from rare to abundant) represented instances where juvenile mussels recruited (1) to an existing local population via local reproduction, (2) from neighboring upstream and downstream populations via transport on host fish species, or (3) from a neighboring upstream population via transport within the water column. The ability of juvenile mussels to settle within suitable habitats is thought to be critically important for their survival (Morales et al. 2006, Vaughn and Taylor 2000), and although the specific factors that define suitable juvenile mussel habitat are poorly understood, they are known to inhabit depositional areas (Neves and Widlack 1987) where they burrow and siphon interstitial water (Yeager et al. 1994). We found that low baseflow conditions were an important factor influencing the ability of mussels to recruit to local populations; however, we also found that local mussel recruitment declined substantially in the presence of extreme low winter flow conditions. In general, juvenile mussels are thought to be considerably more sensitive than adults to extreme environmental conditions, such as those that can arise during prolonged drought (e.g., temperature and dissolved oxygen extremes; Dimock and Wright 1993, Sparks and Strayer 1998). Hence, we hypothesize that short-term low winter flow conditions reduce survival of newly recruited juvenile mussels (i.e., mussels that are < 1 year old) by promoting habitat conditions that inhibit the ability of juvenile mussels to successfully settle, burrow, and feed within the substrate. Thus, exceptionally low flow conditions (i.e., prolonged drought that continues into early winter) may substantially reduce local recruitment rates, possibly by causing reductions in juvenile survival.

Interestingly, successful recruitment to existing mussel populations also was positively related to maximum winter flows, and the positive effect was most pronounced in larger streams. This was counter to our expectations, as we expected that streambed scour associated with large floods would negatively influence mussel recruitment, regardless of seasonality. However, the winter ecology and biology of freshwater mussels (and many other aquatic taxa) has received little attention in the scientific literature and is generally poorly understood. In our study system, peak winter flow events were, on average, more common and higher in magnitude during late winter (January and February). Floods during this time may have triggered late-winter/early-spring stream fish migrations, particularly in larger streams where many fish species may have migrated (e.g., from nearby stream reaches and tributaries) in search of winter refugia (Butler and Fairchild 2005, Peterson and Rabeni 2001). Many fish species, even those generally considered to have low vagility (e.g., cyprinids and centrarchids), can move considerable distances (e.g., up to several hundred meters) in response to peak streamflow events during winter and spring (Freeman 1995). Alternatively, Hastie et al. (2003) proposed that periodic floods may benefit mussel populations by flushing harmful materials from the stream bottom (e.g., accumulated sediment and contaminants), which may cause flood-induced mortality to be compensated by increased post-flood survival of juveniles in the improved habitat conditions. Additionally, although displacement and mortality likely occur during winter floods, adult and juvenile mussels are generally endobenthic (burrowed) during this time, which may protect them from displacement during floods (Balfour and Smock 1995). Despite uncertainty regarding specific mechanisms, our results suggest that winter streamflow conditions may be an important driver of mussel species population and metapopulation dynamics.

The role of impoundments in the decline of North American freshwater mussels is well-documented (Bogan 1993, Vaughn and Tayor 1999, Strayer et al. 2004, Watters and Flaute 2010). We found that mussel species meta-demographic rates were influenced by the presence of impoundments. Specifically, mussel populations in isolated stream reaches exhibited an elevated risk of local extinction, reduced local recruitment, and reduced colonization. Thus, freshwater mussel populations in isolated stream reaches appear to be more susceptible to local extinction and may experience reductions in demographic support (i.e., immigration of new individuals) from neighboring populations. This observation is consistent with the findings of other studies (Strayer et al. 2004, Strayer 2008, Sethi et al. 2004) and further demonstrates the importance of downstream-upstream linkages in the maintenance of aquatic ecosystems (Pringle 1997). Of the meta-demographic rates considered in this study, we were surprised that local colonization was least affected by the presence of impoundments. However, colonization of unoccupied stream reaches was very uncommon in our study, which could have inhibited our ability to detect the influence of impoundments on local colonization rates. Our finding that recruitment to existing populations was substantially lower in isolated stream reaches, however, does support the notion that dams are effective barriers to the dispersal of host fishes and mussels (Watters 1996, McLaughlin et al. 2006). The removal of existing impoundments, particularly low-head dams, may be therefore be an appealing course of action for management plans aimed at restoring at-risk mussel populations. However, recent studies have shown that downstream reaches of some impoundments can support unique and diverse mussel assemblages (Singer and Gangloff 2011), and habitat changes following dam removal (e.g., the release of sediments and contaminants, altered stream flow patterns) can substantially reduce or even eliminate mussel populations from stream reaches up- and downstream of former impoundments (Doyle et al. 2003, Sethi et al. 2004, Singer and Gangloff 2011). Thus, although the removal of impoundments may improve connectivity of stream systems, the potential effects of dam removal on mussel populations is likely best evaluated on a case-by-case basis.

The long life span, complex life history, and cryptic behavior of freshwater mussels pose significant challenges to their management and conservation. In spite of these challenges, we believe that our study highlights the potential usefulness of a metapopulation framework for quantifying long-term changes in the status and distribution of freshwater mussel species. We estimated mussel species meta-demographic rates over a 10-year time-span, which we believe is likely the minimum time-span required to adequately represent the slow system dynamics exhibited by freshwater mussels in the Flint and likely many other river systems. However, our modeling approach could be incorporated into long-term monitoring programs that, when used in conjunction with Adaptive Resource Management, would only serve to improve our ability to account for the slow and incompletely observed dynamics of metapopulations into research and management supporting mussel species conservation.

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Table 4.1. Site numbers, site names, number of samples (*N*), and general site information for the 16 study locations included in multi-season, multi-state occupancy models.

Site Number	*N*	Stream	County	X (m)	Y (m)	Coordinate System	Isolated	Link Magnitude
1	2	Brantley Ck.	Terrell	177338	3512791	NAD83, UTM17	No	17
2	2	Carter Ck.	Randolph	147074	3505984	NAD83, UTM17	No	62
3	2	Carter Ck., Tributary	Randolph	139561	3516463	NAD83, UTM17	No	5
4	2	Carter Ck.	Randolph	140294	3517810	NAD83, UTM17	No	5
5	3	Little Ichawaynochaway Ck.	Randolph	155316	3524256	NAD83, UTM17	No	33
6	2	Pinehead Ck.	Terrell	164000	3529097	NAD83, UTM17	Yes	7
7	2	Tabor Br.	Randolph	138032	3514273	NAD83, UTM17	Yes	1
8	2	Tallahassee Ck.	Dougherty	181071	3498270	NAD83, UTM17	No	14
9	2	Wolf Ck.	Terrell	166562	3523504	NAD83, UTM17	No	14
10	2	Chickasawhatchee Ck.	Baker	168455	3470739	NAD83, UTM17	No	236
11	3	Chickasawhatchee Ck.	Baker	172695	3481623	NAD83, UTM17	No	230

12	2	Chickasawhatchee Ck.	Dougherty	172306	3500367	NAD83, UTM17	No	145
13	2	Chickasawhatchee Ck.	Dougherty	174180	3490529	NAD83, UTM17	No	168
14	2	Ichawaynochaway Ck.	Terrell	162324	3526685	NAD83, UTM17	No	52
15	2	Kiokee Ck.	Dougherty	184358	3502247	NAD83, UTM17	No	31
16	3	Mill Ck.	Baker	158935	3478674	NAD83, UTM17	No	7

Table 4.2. Subfamilies, tribes, and species, population state thresholds, and state-specific detection (p1= rare populations; p2 = abundant populations; p12= incorrect classification as rare when actually abundant) used in dynamic multi-state occupancy models. Abundance thresholds indicate the number of individuals required to consider a population state as rare ($\leq$ threshold) versus abundant (> threshold).

		Brooding Strategy		Shell Size		Detection Probability			
Subfamily, tribe, species	Threshold	Long-term	Short-term	Small	Medium	p1	p2	p12	Proportion of Samples
Ambleminae, Pleurobemini									
Elliptio arctata	5	0	1	0	1	0.53	0.74	0.62	0.20
Elliptio crassidens	50	0	1	0	1	0.76	0.94	0.56	0.57
Elliptio purpurella	5	0	1	1	0	0.53	0.74	0.62	0.06
Elliptio sp.	50	0	1	0	1	0.76	0.94	0.56	0.57
Pleurobema pyriforme	5	0	1	1	0	0.53	0.74	0.62	0.11
Ambleminae, Lampsilini									
Hamiota subangulata	5	1	0	0	1	0.53	0.74	0.62	0.17

Medionidus penicillatus	3	1	0	1	0	0.49	0.49	0.65	0.03
Toxolasma paulum	10	1	0	1	0	0.71	0.94	0.59	0.34
Villosa lienosa	25	1	0	0	1	0.71	0.94	0.56	0.49
Villosa vibex	25	1	0	0	1	0.71	0.94	0.56	0.46
Ambleminae, Quadrulini									
Quadrula infucata	10	0	1	1	0	0.71	0.94	0.59	0.14
Uniomerus columbensis	10	1	0	0	1	0.71	0.94	0.59	0.43
Unioninae, Anodontini									
Anodontoides radiatus	2	1	0	0	1	0.49	0.49	0.68	0.03

Table 4.3. List of variables included in candidate dynamic multi-state occupancy models relating streamflows, site characteristics, and species traits to meta-demographic rates for 13 freshwater mussels in the Lower Flint River Basin, Georgia, with corresponding ecological interpretation.

Parameter	Interpretation/ Hypothesis
Min10dQ (spring, summer, winter)	Minimum 10-day discharge influences mussel species meta-demographic rates and represents acute or short-term low flow conditions. In general, mussel species are negatively influenced by acute low flow conditions through direct effects such as desiccation and stranding and indirect effects such as reduced habitat availability and temperature and dissolved oxygen extremes. The negative influence of acute low-flow conditions varies seasonally and will be greatest during summer when base-flow conditions are at their lowest.
Max10dQ (spring, summer, winter)	Maximum 10-day discharge influences mussel species meta-demographic rates and represents acute or short-term high flow conditions. In general, mussel species are negatively influenced by flushing flows through direct effects such as displacement and mortality resulting from streambed scour. The negative influence of acute high flow conditions varies seasonally and will be greatest during summer when mussels are acclimated to low base-flow conditions.

Median (spring, summer, winter)	Minimum 10-day discharge influences mussel species meta-demographic rates and represents average streamflow conditions experienced by mussels. In general, higher median flow conditions will decrease the risk of local extinction. However, the influence of average flow conditions will vary seasonally.
Link magnitude	Stream size influences mussel species meta-demographic rates.
Link magnitude × Min10dQ	The effect of seasonal minimum 10-day streamflows on mussel species meta-demographic rates varies with stream size.
Link magnitude × Max10dQ	The effect of seasonal maximum 10-day streamflows on mussel species meta-demographic rates varies with stream size.
Link magnitude × Median	The effect of seasonal median streamflows on mussel species meta-demographic rates varies with stream size.
Shell size	Local extinction and population decline meta-demographic rates vary among species depending on adult shell size.
Shell size × Min10dQ	The effect of seasonal minimum 10-day streamflows on local extinction and population declines varies depending on whether a species is a small- or medium-sized shell.

Shell size × Max10dQ	The effect of seasonal maximum 10-day streamflows on local extinction and population decline varies depending on whether a species is a small- or medium-sized shell.
Shell size × Median	The effect of seasonal median streamflows on local extinction and population decline varies depending on whether a species is a small- or medium-sized shell.
Brooding strategy	Local colonization and population growth meta-demographic rates vary among species depending on brooding strategy. Short-term brooding species are generally gravid for 2-3 months (spring to early summer), whereas long-term brooding species are generally gravid from late-summer to the following spring or summer.
Brooding strategy × Min10dQ	The effect of seasonal minimum 10-day streamflows on colonization and population growth varies depending on whether a species is a short-term or long-term brooding mussel.
Brooding strategy × Max10dQ	The effect of seasonal maximum 10-day streamflows on colonization and population growth varies depending on whether a species is a short-term or long-term brooding mussel.
Brooding strategy × Median	The effect of seasonal median streamflows on colonization and population growth varies depending on whether a species is a short-term or long-term brooding mussel.

Reach isolation	Mussel populations in isolated stream reaches are more prone to local extinction due to the elimination of demographic support from neighboring populations and because impoundments serve as an effective barrier to potential host fishes for existing populations.

Table 4.4. Akaike Information Criterion (AIC_c), number of parameters (K), ΔAIC_c, and AIC_c weights (w_i) for the confidence set of dynamic multi-state occupancy models (*i*) relating meta-demographic rates associated with local population extinction or declines (*ε1, ε2, and φ1*) and colonization or growth (*γ and φ2*) to seasonal stream discharge, site characteristics, and species traits for 13 unionid species at 16 study sites in the Lower Flint River Basin, Georgia.

Candidate Model	K	AIC_c	ΔAIC_c	w_i
ε1, ε2, and φ1 (Link magnitude, small shell size, reach isolation, Summer Max10dQ, link magnitude × Summer Max10dQ, small shell size × Summer Max10dQ); *γ and φ2* (link magnitude, long-term brooder, reach isolation, Spring Max10dQ, link magnitude × Spring Max10dQ , long-term brooder × Spring Max10dQ)	35	1086.014	0.000	0.295
ε1, ε2, and φ1 (Link magnitude, small shell size, reach isolation, Summer Max10dQ , link magnitude × Summer Max10dQ, small shell size × Summer Max10dQ); *γ and φ2* (link magnitude, long-term brooder, reach isolation, Winter Min10dQ, link magnitude × Winter Min10dQ, long-term brooder × Winter Min10dQ)	35	1087.014	1.000	0.179

ε1, ε2, and φ1 (Link magnitude, small shell size, reach isolation, Summer Median, link magnitude × Summer Median, small shell size × Summer Median); *γ and φ2* (link magnitude, long-term brooder, reach isolation, Winter Min10dQ, link magnitude × Winter Min10dQ, long-term brooder × Winter Min10dQ)	35	1087.014	1.000	0.178
ε1, ε2, and φ1 (Link magnitude, small shell size, reach isolation, Summer Max10dQ, link magnitude × Summer Max10dQ, small shell size × Summer Max10dQ); *γ and φ2* (link magnitude, long-term brooder, reach isolation, Winter Max10dQ, link magnitude × Winter Max10dQ, long-term brooder × Winter Max10dQ)	35	1088.014	2.000	0.108
ε1, ε2, and φ1 (Link magnitude, small shell size, reach isolation, Summer Median, link magnitude × Summer Median, small shell size × Summer Median); *γ and φ2* (link magnitude, long-term brooder, reach isolation, Spring Max10dQ, link magnitude × Spring Max10dQ, long-term brooder × Spring Max10dQ)	35	1089.014	3.000	0.066

ε1, ε2, and φ1 (Link magnitude, small shell size, reach isolation, Summer Median, link magnitude × Summer Median, small shell size × Summer Median) ; *γ and φ2* (link magnitude, long-term brooder, reach isolation, Winter Max10dQ, link magnitude × Winter Max10dQ, long-term brooder × Winter Max10dQ)	35	1089.014	3.000	0.066

Table 4.5. Parameter estimates, standard deviations, and 90% credible intervals (90% CI) based on the confidence set of multi-state, multi-season occupancy models relating streamflow conditions, site characteristics, and species traits to mussel species meta-demographic rates in LFRB streams.

Best-Approximating Model			90% CI		
Parameter	Estimate	SD	Lower	Upper	OR
ε1(extinction probability if rare)					
Intercept	-1.975	1.545	-4.331	0.755	
Link Magnitude	-1.376	1.024	-3.062	0.264	0.253
Summer Max10dQ	0.022	1.262	-1.917	2.182	1.023
Link Magnitude × Summer Max10dQ	-1.620	1.356	-3.603	0.807	0.198
Small Shell Size	1.009	1.541	-1.679	3.405	2.743
Small Shell × Summer Max10dQ	-0.709	1.374	-2.920	1.681	0.492
Isolated	1.128	1.524	-1.438	3.600	3.089
ε2 (extinction probability if abundant)					
Intercept	-1.782	1.303	-3.846	0.482	
Link Magnitude	-0.085	0.998	-1.773	1.448	0.919
Summer Max10dQ	1.493	1.268	-0.526	3.588	4.450
Link Magnitude × Summer Max10dQ	-0.488	1.724	-3.170	2.295	0.614
Small Shell Size	1.559	1.150	-0.251	3.437	4.754
Small Shell Size × Summer Max10dQ	-0.358	1.314	-2.446	1.918	0.699

Isolated	1.818	1.553	-0.872	4.235	6.160
γ (probability of local colonization)					
Intercept	-6.255	0.771	-7.613	-5.051	
Link Magnitude	0.552	0.671	-0.593	1.584	1.737
Spring Max10-dQ	-0.744	0.714	-1.951	0.354	0.475
Link Magnitude × Spring Max10dQ	-1.411	0.827	-2.785	-0.155	0.244
Long-term Brooder	-1.913	1.168	-3.938	-0.079	0.148
Long-term Brooder × Spring Max10dQ	0.350	1.079	-1.488	2.032	1.419
Isolated	-0.723	1.342	-3.083	1.370	0.485
φ1 (probability of population decline)					
Intercept	0.935	1.623	-1.922	3.441	
Link Magnitude	1.101	1.196	-0.748	3.126	3.007
Summer Max10dQ	0.191	1.728	-2.587	3.186	1.210
Link Magnitude × Summer Max10dQ	0.256	1.633	-2.553	2.760	1.292
Small Shell Size	-0.158	1.592	-2.849	2.345	0.854
Small Shell Size × Summer Max10dQ	0.279	1.583	-2.357	2.872	1.321
Isolated	-0.666	1.620	-3.404	2.050	0.514
φ2 (probability of population growth)					
Intercept	-1.211	1.502	-3.731	1.232	
Link Magnitude	-0.801	1.301	-2.711	1.621	0.449
Spring Max10dQ	-0.931	1.248	-3.018	1.071	0.394

Link Magnitude × Spring Max10dQ	1.014	1.409	-1.250	3.358	2.757
Long-term Brooder	-0.617	1.251	-2.752	1.334	0.539
Long-term Brooder × Spring Max10dQ	-0.140	1.359	-2.409	2.071	0.869
Isolated	-1.740	1.456	-4.131	0.603	0.176

Second Best-Approximating Model

			90% CI		
Parameter	Estimate	SD	Lower	Upper	OR
ε1(extinction probability if rare)					
Intercept	-3.124	1.254	-5.033	-0.931	
Link Magnitude	-0.744	0.953	-2.321	0.772	0.475
Summer Max10dQ	0.739	1.167	-1.176	2.624	2.093
Link Magnitude × Summer Max10dQ	-1.319	1.307	-3.410	0.911	0.267
Small Shell Size	0.373	1.596	-2.390	2.845	1.453
Small Shell Size × Summer Max10dQ	-0.562	1.444	-2.948	1.852	0.570
Isolated	1.034	1.598	-1.588	3.664	2.812
ε2 (extinction probability if abundant)					
Intercept	-0.783	1.241	-2.974	1.114	
Link Magnitude	-0.750	1.032	-2.494	0.892	0.472
Summer Max10dQ	1.677	1.105	-0.104	3.519	5.349
Link Magnitude × Summer Max10dQ	-0.416	1.529	-2.952	1.993	0.660
Small Shell Size	1.873	1.207	-0.093	3.911	6.508
Small Shell Size × Summer Max10dQ	-0.365	1.368	-2.527	1.937	0.694

Isolated	1.742	1.488	-0.767	4.144	5.709
γ (probability of local colonization)					
Intercept	-5.924	1.007	-7.525	-4.075	
Link Magnitude	1.073	1.667	-0.912	4.888	2.924
Winter Min10dQ	0.506	0.799	-0.913	1.670	1.659
Link Magnitude × Winter Min10dQ	1.122	1.304	-0.575	3.871	3.071
Long-term Brooder	-1.266	1.247	-3.430	0.581	0.282
Long-term Brooder × Winter Min10dQ	0.485	1.163	-1.559	2.289	1.624
Isolated	-0.828	1.343	-3.194	1.289	0.437
φ1 (probability of population decline)					
Intercept	0.702	1.441	-1.812	3.038	
Link Magnitude	0.911	1.151	-0.883	2.763	2.487
Summer Max10dQ	0.051	1.795	-2.711	3.198	1.052
Link Magnitude × Summer Max10dQ	0.130	1.617	-2.681	2.658	1.138
Small Shell Size	-0.777	1.658	-3.407	1.979	0.460
Small Shell Size × Summer Max10dQ	0.455	1.560	-2.099	3.067	1.577
Isolated	-0.610	1.579	-3.151	2.009	0.543
φ2 (probability of population growth)					
Intercept	-0.436	1.147	-2.329	1.327	
Link Magnitude	-0.123	1.281	-2.016	2.205	0.885
Winter Min10dQ	2.377	1.306	0.228	4.484	10.773

Link Magnitude × Winter Min10dQ	-0.337	1.505	-2.873	2.111	0.714
Long-term Brooder	-0.651	1.146	-2.534	1.207	0.521
Long-term Brooder × Winter Min10dQ	0.803	1.504	-1.615	3.271	2.232
Isolated	-1.873	1.387	-4.106	0.465	0.154

Third Best-Approximating Model			90% CI		
Parameter	Estimate	SD	Lower	Upper	OR
ε1(extinction probability if rare)					
Intercept	-2.885	1.621	-5.543	-0.227	
Link Magnitude	-0.443	1.146	-2.323	1.436	0.642
Summer Median	1.381	1.211	-0.605	3.367	3.979
Link Magnitude × Summer Median	-0.284	1.319	-2.447	1.880	0.753
Small Shell Size	0.358	1.691	-2.415	3.131	1.430
Small Shell Size × Summer Median	0.048	1.340	-2.149	2.246	1.049
Isolated	0.859	1.607	-1.777	3.494	2.361
ε2 (extinction probability if abundant)					
Intercept	-1.868	1.309	-4.015	0.279	
Link Magnitude	-0.027	1.111	-1.849	1.795	0.974
Summer Median	1.519	0.948	-0.036	3.074	4.568
Link Magnitude × Summer Median	0.176	1.171	-1.744	2.097	1.193
Small Shell Size	1.941	1.254	-0.116	3.998	6.966
Small Shell Size × Summer Median	0.366	1.246	-1.678	2.409	1.442

Isolated	1.808	1.506	-0.662	4.278	6.098
γ (probability of local colonization)					
Intercept	-6.201	0.878	-7.640	-4.762	
Link Magnitude	0.570	1.069	-1.183	2.323	1.768
Winter Min10dQ	0.508	0.814	-0.827	1.842	1.662
Link Magnitude × Winter Min10dQ	0.890	0.982	-0.720	2.500	2.435
Long-term Brooder	-1.361	1.207	-3.340	0.618	0.256
Long-term Brooder × Winter Min10dQ	0.422	1.187	-1.525	2.368	1.525
Isolated	-0.924	1.351	-3.140	1.291	0.397
φ1 (probability of population decline)					
Intercept	0.476	1.617	-2.176	3.127	
Link Magnitude	0.988	1.132	-0.868	2.845	2.686
Summer Median	0.039	1.721	-2.784	2.861	1.039
Link Magnitude × Summer Median	-0.652	1.565	-3.219	1.915	0.521
Small Shell Size	-0.749	1.729	-3.585	2.087	0.473
Small Shell Size × Summer Median	0.310	1.591	-2.300	2.919	1.363
Isolated	-0.522	1.613	-3.167	2.124	0.594
φ2 (probability of population growth)					
Intercept	-0.427	1.104	-2.237	1.384	
Link Magnitude	0.140	1.341	-2.059	2.339	1.150
Winter Min10dQ	2.300	1.264	0.227	4.373	9.974

Link Magnitude × Winter Min10dQ	-0.423	1.501	-2.885	2.038	0.655
Long-term Brooder	-0.792	1.165	-2.702	1.119	0.453
Long-term Brooder × Winter Min10dQ	0.795	1.457	-1.595	3.184	2.214
Isolated	-1.793	1.381	-4.058	0.472	0.166

Fourth Best-Approximating Model

Parameter	Estimate	SD	90% CI		OR
			Lower	Upper	
ε1(extinction probability if rare)					
Intercept	-2.211	1.599	-4.833	0.411	
Link Magnitude	-1.147	1.060	-2.885	0.591	0.318
Summer Max10dQ	0.296	1.321	-1.870	2.463	1.345
Link Magnitude × Summer Max10dQ	-0.877	1.401	-3.175	1.421	0.416
Small Shell Size	0.459	1.594	-2.156	3.073	1.582
Small Shell Size × Summer Max10dQ	-0.530	1.466	-2.934	1.874	0.589
Isolated	1.132	1.585	-1.467	3.731	3.102
ε2 (extinction probability if abundant)					
Intercept	-1.813	1.158	-3.712	0.086	
Link Magnitude	-0.460	0.962	-2.037	1.117	0.631
Summer Max10dQ	1.207	1.071	-0.549	2.963	3.343
Link Magnitude × Summer Max10dQ	-0.986	1.375	-3.241	1.269	0.373
Small Shell Size	2.125	1.201	0.155	4.095	8.373
Small Shell Size × Summer Max10dQ	-0.833	1.323	-3.003	1.337	0.435

Isolated	1.771	1.516	-0.715	4.257	5.877
γ (probability of local colonization)					
Intercept	-6.186	0.853	-7.585	-4.787	
Link Magnitude	0.496	0.913	-1.001	1.992	1.641
Winter Max10dQ	-0.024	0.772	-1.290	1.242	0.976
Link Magnitude × Winter Max10dQ	0.729	1.065	-1.017	2.476	2.073
Long-term Brooder	-1.345	1.270	-3.428	0.738	0.261
Long-term Brooder × Winter Max10dQ	0.306	1.180	-1.629	2.241	1.358
Isolated	-0.756	1.382	-3.022	1.511	0.470
φ1 (probability of population decline)					
Intercept	1.076	1.533	-1.438	3.590	
Link Magnitude	1.032	1.160	-0.870	2.934	2.807
Summer Max10dQ	-0.028	1.822	-3.016	2.960	0.972
Link Magnitude × Summer Max10dQ	0.060	1.597	-2.559	2.679	1.062
Small Shell Size	-0.136	1.645	-2.834	2.562	0.873
Small Shell Size × Summer Max10dQ	0.250	1.618	-2.404	2.903	1.284
Isolated	-0.583	1.621	-3.241	2.076	0.558
φ2 (probability of population growth)					
Intercept	-0.769	1.142	-2.642	1.104	
Link Magnitude	0.293	1.415	-2.028	2.613	1.340
Winter Max10dQ	1.517	0.961	-0.060	3.094	4.559

Link Magnitude × Winter Max10dQ	2.431	1.330	0.250	4.612	11.370
Long-term Brooder	-0.926	1.204	-2.900	1.049	0.396
Long-term Brooder × Winter Max10dQ	-0.348	1.221	-2.350	1.655	0.706
Isolated	-1.461	1.395	-3.749	0.827	0.232

Fifth Best-Approximating Model			90% CI		
Parameter	Estimate	SD	Lower	Upper	OR
$\varepsilon 1$(extinction probability if rare)					
Intercept	-1.377	1.813	-4.426	1.557	
Link Magnitude	-1.383	1.224	-3.440	0.538	0.251
Summer Median	0.666	1.430	-1.989	2.793	1.946
Link Magnitude × Summer Median	-0.228	1.451	-2.526	2.251	0.797
Small Shell Size	0.890	1.729	-2.105	3.636	2.435
Small Shell Size × Summer Median	-0.117	1.492	-2.648	2.301	0.890
Isolated	0.914	1.556	-1.643	3.373	2.494
$\varepsilon 2$ (extinction probability if abundant)					
Intercept	-2.865	1.222	-4.772	-0.765	
Link Magnitude	0.611	1.039	-1.212	2.226	1.842
Summer Median	1.244	0.863	-0.142	2.635	3.469
Link Magnitude × Summer Median	-0.577	1.102	-2.376	1.250	0.562
Small Shell Size	1.665	1.157	-0.260	3.565	5.286
Small Shell Size × Summer Median	0.281	1.136	-1.436	2.289	1.325

Isolated	1.700	1.627	-1.082	4.333	5.474
γ (probability of local colonization)					
Intercept	-6.306	0.784	-7.680	-5.087	
Link Magnitude	0.405	0.674	-0.736	1.431	1.499
Spring Max10dQ	-0.743	0.753	-2.012	0.415	0.476
Link Magnitude × Spring Max10dQ	-1.189	0.862	-2.558	0.250	0.305
Long-term Brooder	-1.895	1.209	-3.892	0.036	0.150
Long-term Brooder × Spring Max10dQ	0.342	1.139	-1.534	2.137	1.407
Isolated	-0.769	1.346	-3.099	1.378	0.463
φ1 (probability of population decline)					
Intercept	0.853	1.769	-2.201	3.594	
Link Magnitude	0.947	1.211	-0.882	3.003	2.577
Summer Median	-0.286	1.531	-2.571	2.505	0.751
Link Magnitude × Summer Median	0.003	1.557	-2.587	2.459	1.003
Small Shell Size	-0.403	1.708	-3.198	2.368	0.668
Small Shell Size × Summer Median	0.252	1.557	-2.335	2.814	1.286
Isolated	-0.598	1.625	-3.277	2.092	0.550
φ2 (probability of population growth)					
Intercept	-1.241	1.435	-3.688	1.034	
Link Magnitude	-0.484	1.320	-2.344	2.112	0.616
Spring Max10dQ	-1.006	1.263	-3.175	0.952	0.366

Link Magnitude × Spring Max10dQ	1.158	1.446	-1.198	3.543	3.184
Long-term Brooder	-0.802	1.228	-2.894	1.132	0.448
Long-term Brooder × Spring Max10dQ	-0.261	1.343	-2.498	1.943	0.770
Isolated	-1.708	1.416	-3.989	0.599	0.181

Sixth Best-Approximating Model			90% CI		
Parameter	Estimate	SD	Lower	Upper	OR
ε1(extinction probability if rare)					
Intercept	-1.668	1.826	-4.663	1.327	
Link Magnitude	-1.046	1.219	-3.045	0.953	0.351
Summer Median	0.538	1.734	-2.305	3.382	1.713
Link Magnitude × Summer Median	0.296	1.571	-2.281	2.872	1.344
Small Shell Size	0.539	1.712	-2.269	3.347	1.714
Small Shell Size × Summer Median	-0.173	1.526	-2.675	2.330	0.841
Isolated	0.896	1.589	-1.710	3.502	2.450
ε2 (extinction probability if abundant)					
Intercept	-2.638	1.179	-4.572	-0.704	
Link Magnitude	0.260	1.028	-1.426	1.946	1.296
Summer Median	1.168	0.961	-0.408	2.744	3.216
Link Magnitude × Summer Median	-0.464	1.153	-2.355	1.427	0.629
Small Shell Size	2.220	1.225	0.211	4.229	9.207
Small Shell Size × Summer Median	0.130	1.219	-1.869	2.129	1.139

Isolated	1.704	1.569	-0.869	4.277	5.496
γ (probability of local colonization)					
Intercept	-6.287	0.830	-7.648	-4.926	
Link Magnitude	0.294	0.816	-1.043	1.631	1.342
Winter Max10dQ	0.017	0.772	-1.248	1.283	1.017
Link Magnitude × Winter Max10dQ	0.757	1.025	-0.924	2.438	2.132
Long-term Brooder	-1.330	1.262	-3.400	0.740	0.264
Long-term Brooder × Winter Max10dQ	0.220	1.185	-1.724	2.163	1.246
Isolated	-0.797	1.352	-3.014	1.421	0.451
φ1 (probability of population decline)					
Intercept	1.083	1.766	-1.813	3.979	
Link Magnitude	0.907	1.164	-1.002	2.816	2.476
Summer Median	-0.310	1.665	-3.041	2.421	0.733
Link Magnitude × Summer Median	-0.268	1.540	-2.793	2.258	0.765
Small Shell Size	-0.191	1.735	-3.036	2.655	0.826
Small Shell Size × Summer Median	0.236	1.596	-2.381	2.854	1.267
Isolated	-0.552	1.629	-3.223	2.120	0.576
φ2 (probability of population growth)					
Intercept	-0.727	1.108	-2.544	1.090	
Link Magnitude	0.510	1.420	-1.819	2.838	1.665
Winter Max10dQ	1.405	0.948	-0.149	2.959	4.076

Link Magnitude × Winter Max10dQ	2.478	1.329	0.298	4.658	11.917
Long-term Brooder	-1.025	1.200	-2.993	0.943	0.359
Long-term Brooder × Winter Max10dQ	-0.345	1.217	-2.341	1.651	0.708
Isolated	-1.440	1.368	-3.684	0.804	0.237

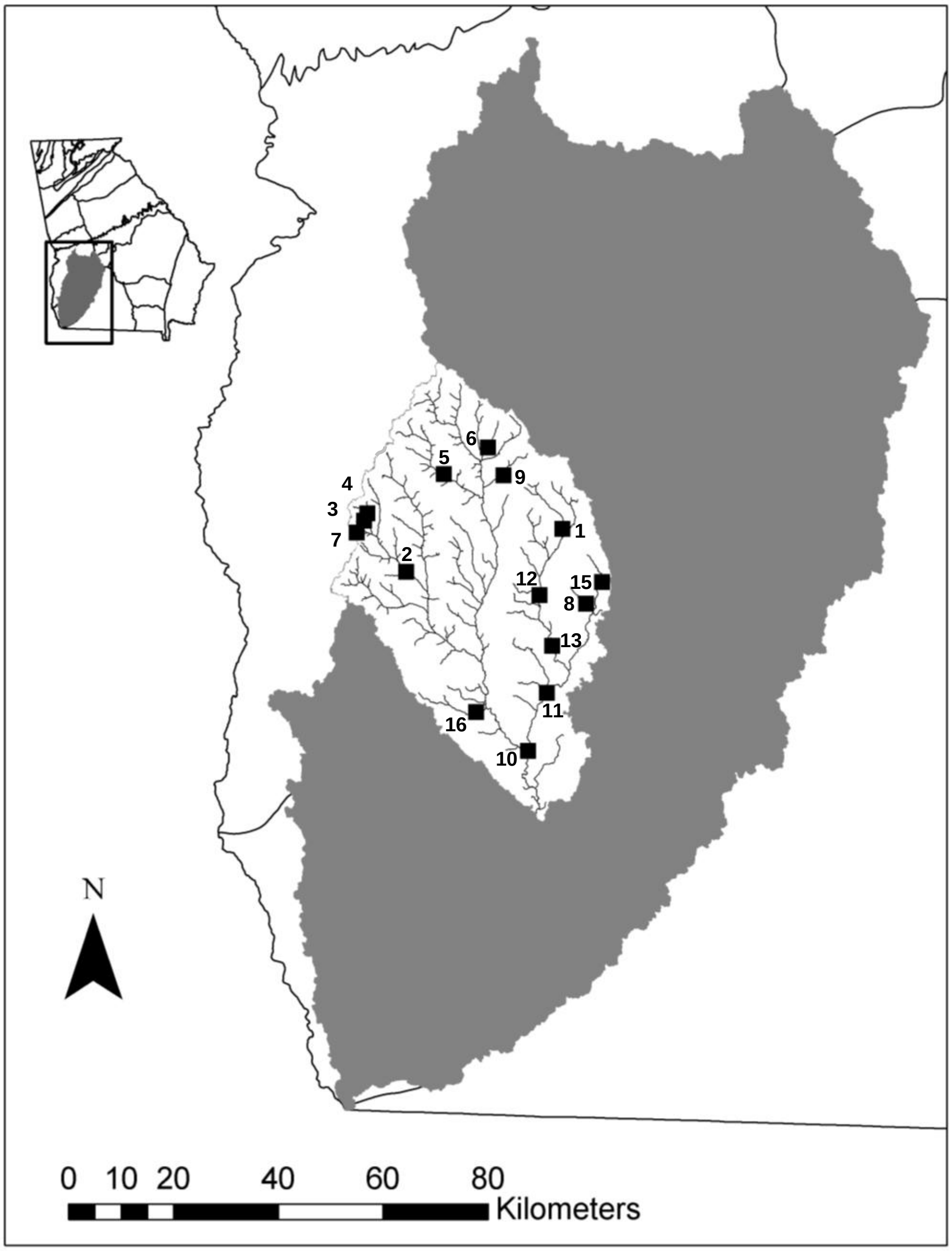

Figure 4.1. Map of the lower Flint River Basin (shaded region) and Ichawaynochaway Creek subbasin showing major tributaries and locations of the 16 study sites (filled squares) at which mussel sampling was conducted on at least 2 occasions from 1997-2006. Numbers adjacent to sites correspond to the site numbers listed in Table 4.1.

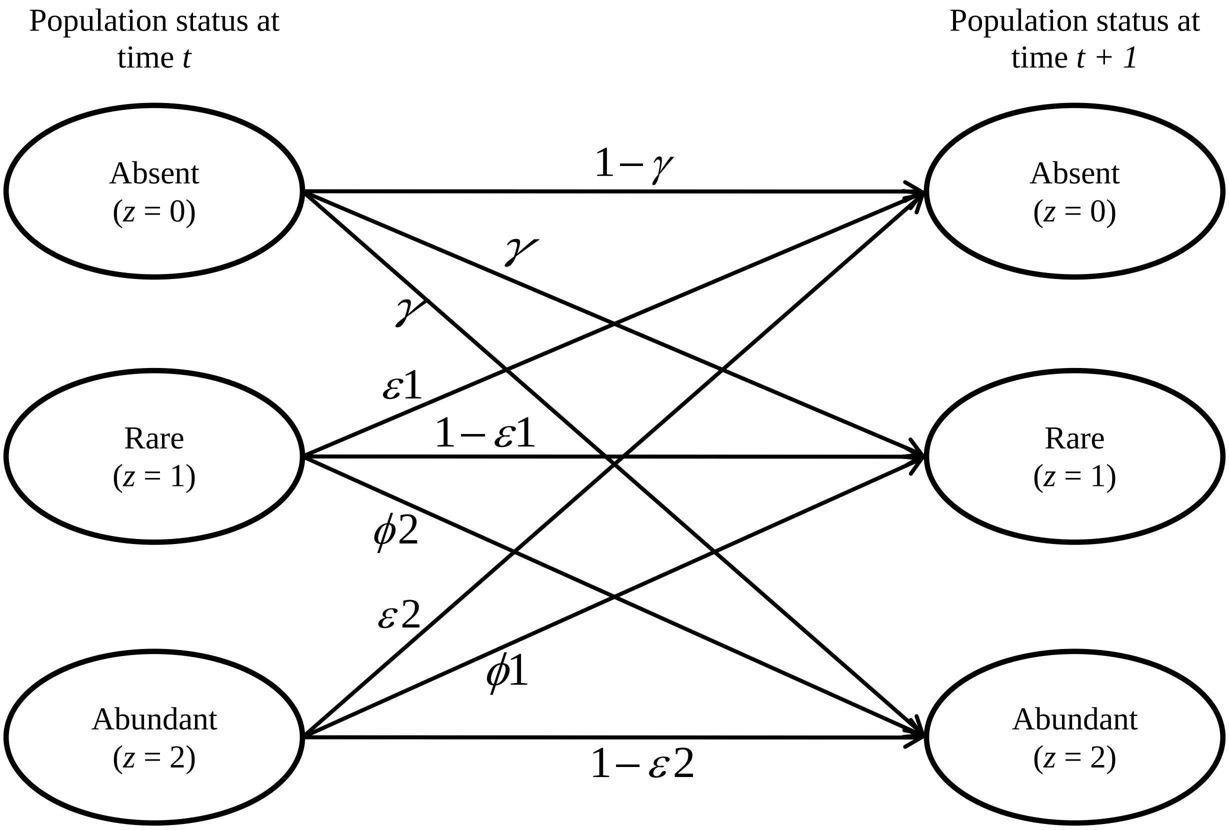

Figure 4.2. Conceptual diagram showing possible population state transitions and corresponding meta-demographic parameters over single time step for freshwater mussel species in the lower Flint River Basin, Georgia.

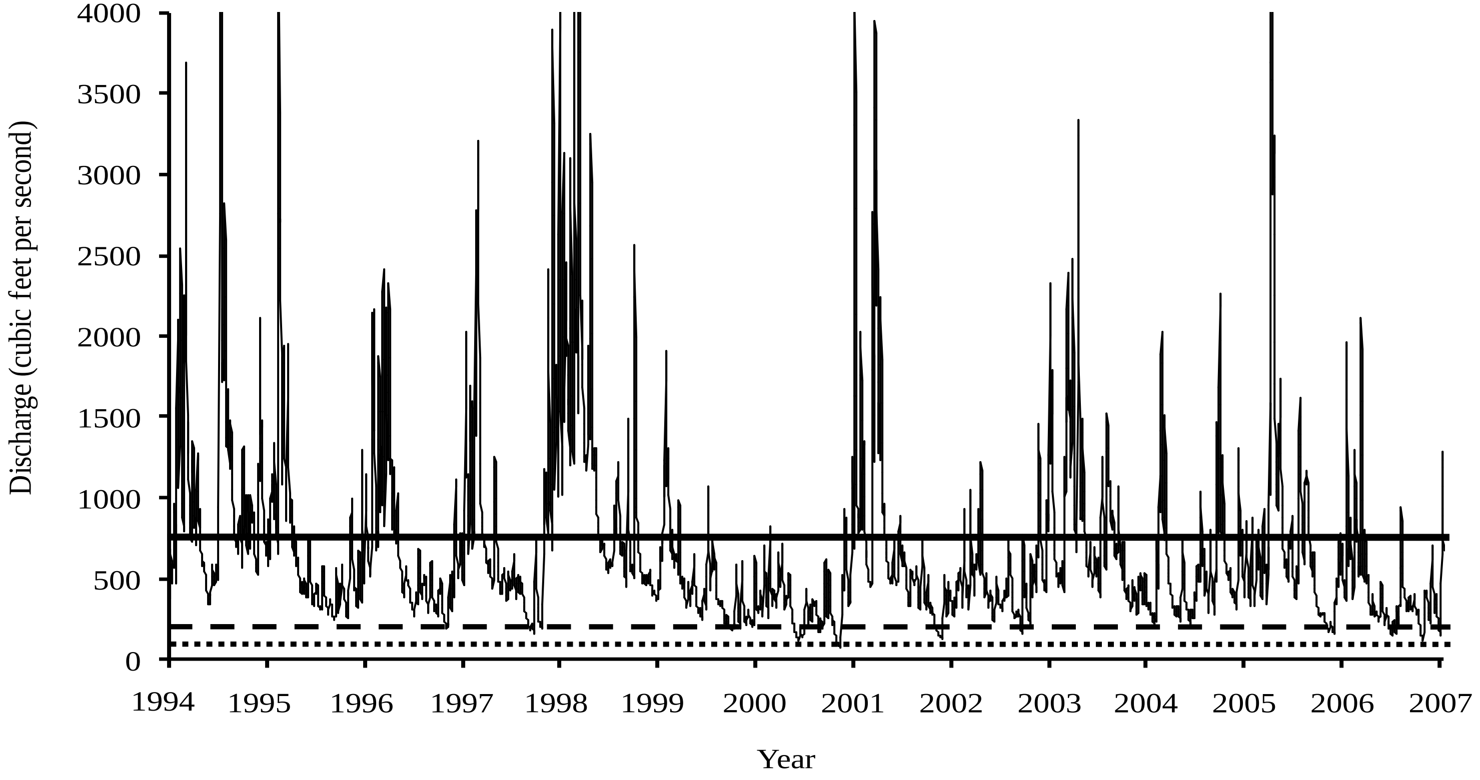

Figure 4.3. Estimated stream discharge (cubic feet per second; cfs) at Ichawaynochaway Creek at SR216 during the study period (1994-2007). The horizontal lines represent the estimated mean annual (solid line; 780 cfs), 30Q2 (dashed line; 290 cfs), and 7Q10 (dotted line; 140 cfs) streamflow statistics for this location based on long-term (1905-present) streamflow records (U.S. Geological Survey Gage 02353500, Ichawaynochaway Creek at Milford, Georgia).

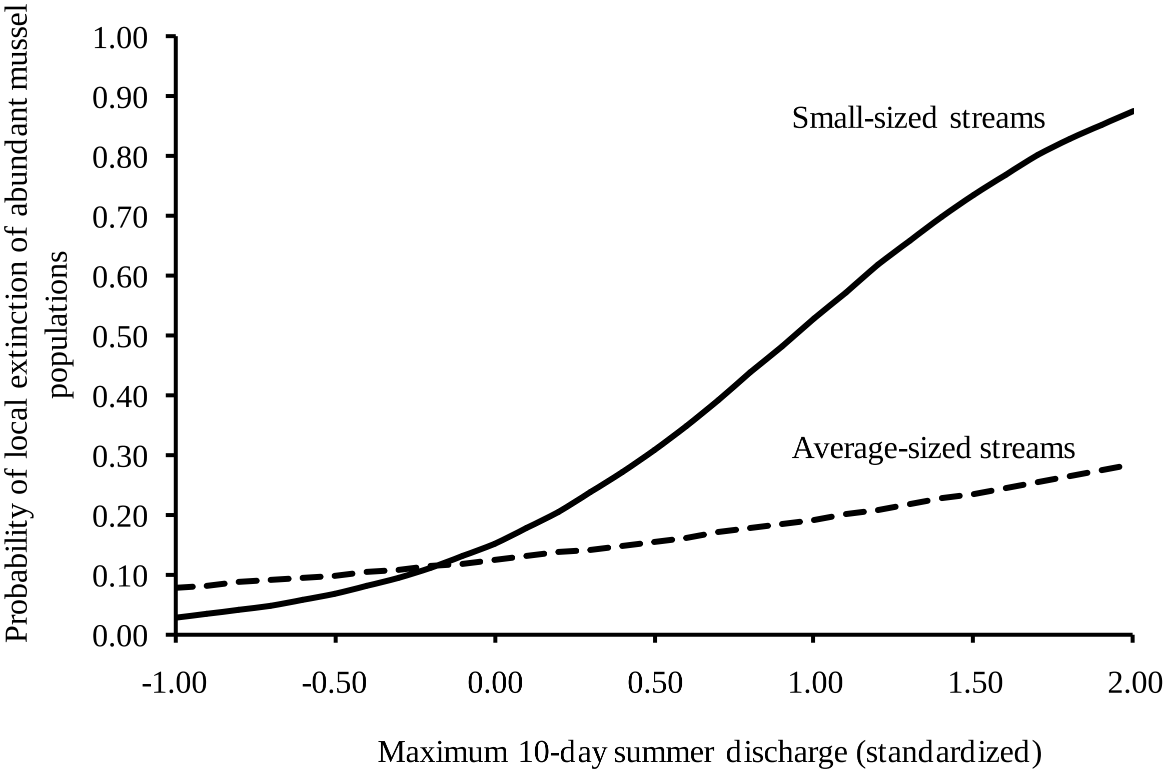

Figure 4.4. Influence of maximum 10-day summer discharge on local extinction of rare mussel populations in small (solid line) and average-sized (broken line) tributaries in the lower Flint River Basin, Georgia.

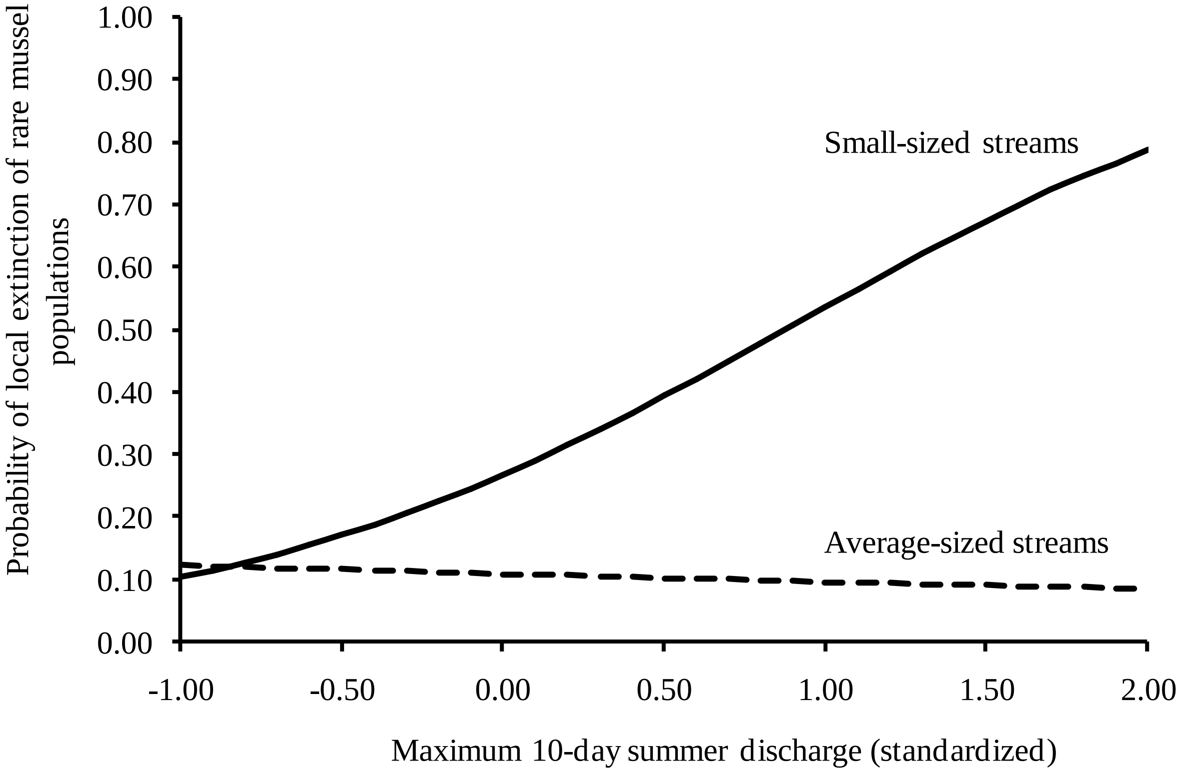

Figure 4.5. Influence of maximum 10-day summer discharge on local extinction of abundant mussel populations in small (solid line) and average-sized (broken line) tributaries in the lower Flint River Basin, Georgia.

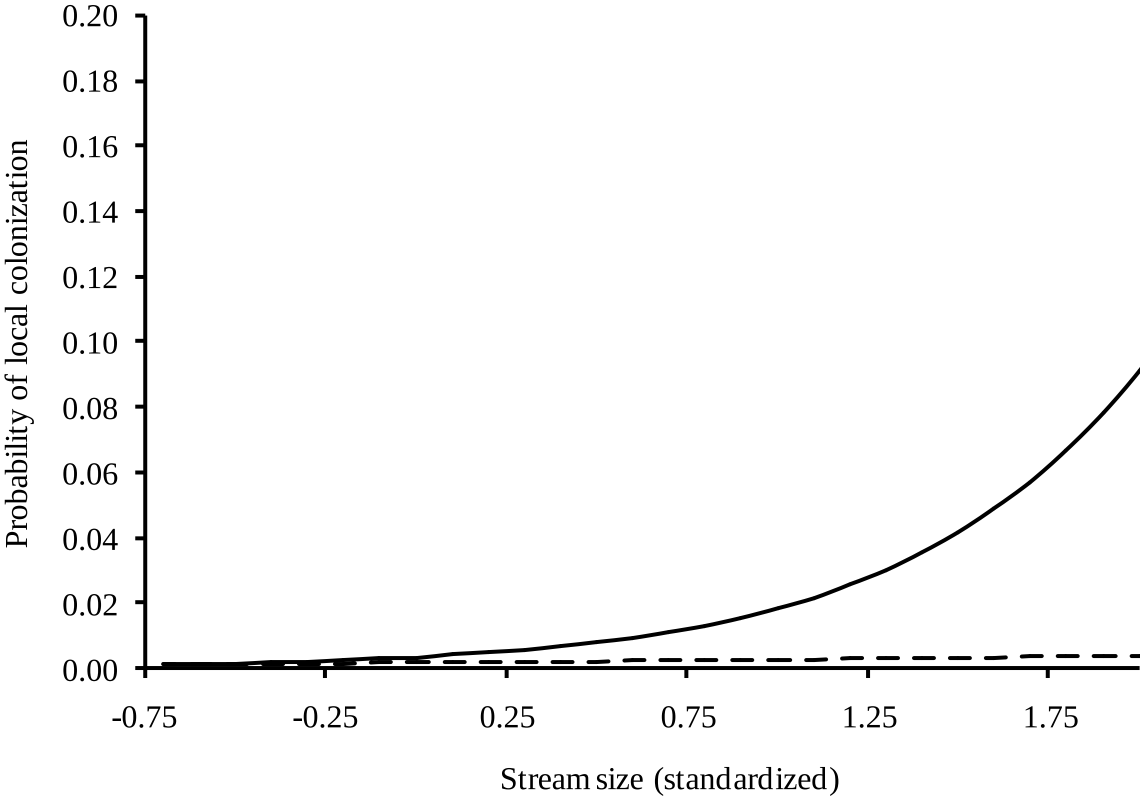

Figure 4.6. Influence of stream size and maximum 10-day spring discharge on the probability of Flint River basin mussel species colonizing unoccupied stream reaches. The solid and dashed lines represent the influence of low and high magnitude spring floods, respectively, on local mussel species colonization. Note truncated y-axis.

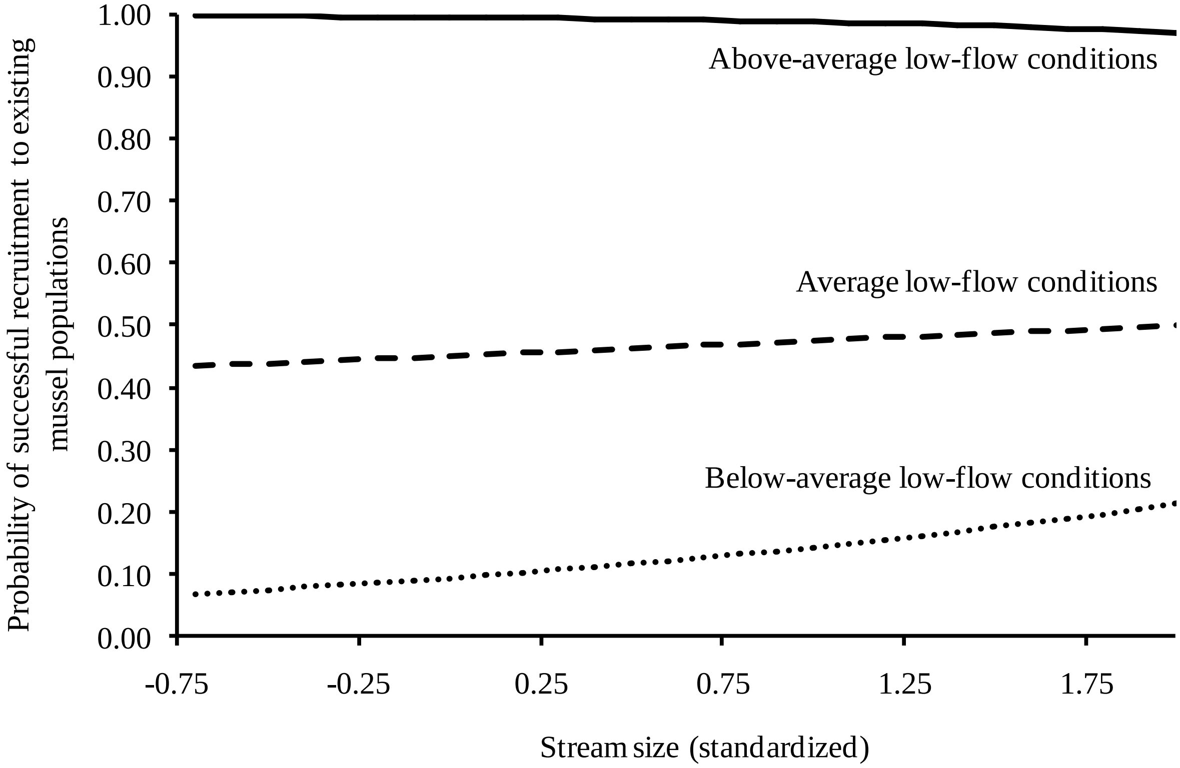

Figure 4.7. Influence of stream size and minimum 10-day winter discharge on the probability of juvenile mussels successfully recruiting to existing mussel populations. The solid, dashed, and dotted lines represent the influence of above-average, average, and below-average low flow conditions, respectively, on local recruitment.

CHAPTER 5

CHAPTER SYNTHESIS AND CONCLUSIONS

INTRODUCTION

Little debate exists regarding the imperiled status of many North American freshwater mussel species. However, it has proven challenging to determine the predominant factors and specific mechanisms contributing to observed mussel population declines (Downing et al. 2010). Strayer (2008) emphasized the critical need in freshwater mussel ecology for predictive models of mussel occurrence, abundance, and population response in relation to environmental and biological variables. In this dissertation, I have developed predictive models of lower Flint River Basin (LFRB) mussel species occurrence and metapopulation dynamics in relation to streamflow conditions, species traits, and site- and watershed-level characteristics. I also have addressed several key challenges associated with (but not unique to) the management and conservation of freshwater mussels, namely incomplete detection, species misidentification, and slow system dynamics. In Chapters 2 and 3, I focused on the development of predictive models of mussel species occurrence that accounted for potential biases associated with incomplete detection and misidentification of species. In Chapter 4, I developed predictive models of mussel species metapopulation dynamics that also accounted for potential detection and misidentification biases. Combined, my hope is that these approaches will provide a useful conceptual and modeling framework for managers and biologists to assess the factors contributing to spatial and temporal changes in the status and distribution of LFRB mussel species. The LFRB undoubtedly presents its own unique set of management and conservation challenges, most notably the conservation of existing mussel populations in the presence of high levels of agricultural water use and recurrent drought. However, the LFRB is in many ways representative of the general challenges faced by most natural resource agencies charged with managing and conserving stream-dwelling biota. Thus, I believe that the concepts and methods discussed in this dissertation are applicable to the management and conservation of aquatic biota in virtually any stream system.

CHAPTER SYNTHESIS

Animal surveys in almost all ecological systems are subject to potential biases associated with incomplete detection and species misidentification, and failing to account for these sources of bias can influence perceptions of how natural and anthropogenic factors influence the status and dynamics of animal populations. The magnitude of detection and misidentification bias often varies depending on factors that also influence the abundance and distribution of stream-dwelling biota. Accordingly, the underlying ecological patterns of management interest may be confounded with those induced by incomplete detection and species misidentification. My study results from Chapters 2 and 3 corroborate and supplement previous findings that species detection and misidentification rates are influenced by natural (e.g., species traits, stream size, local streamflow conditions) and anthropogenic (e.g., sample method, crew experience) factors. In general, I found that mussel species detection rates were low and varied among streams and sample methods. I also found that the risk of species misidentification varied among species depending on shell characteristics, and among observers depending on their experience identifying local mussel species.

To account for these sources of bias, I developed methods for assessing the magnitude of species misidentification in mussel collection data and formally incorporated this knowledge into species presence models that also accounted for incomplete detection. After accounting for potential detection and misidentification biases, my results indicate that mussel species occurrence in the LFRB has decreased from earlier to more recent surveys, coincident with the occurrence of two severe droughts. The population declines appear to be more pronounced in smaller streams, suggesting that many LFRB mussel species are experiencing basin-wide range contractions. Previous studies have suggested that many North American freshwater mussel species are experiencing ongoing range thinning and contraction (Strayer 2008), but few studies have quantified the influence of purported contributing factors (Downing et al. 2010). In the LFRB, mussel population declines appear to be related to both natural and anthropogenic factors, most notably climatic drought and reach isolation due to impoundment. This and other studies of mussel population response to drought have found that population declines were most pronounced in small- and mid-order tributaries (Golladay et al. 2004, Haag and Warren 2008). During prolonged drought, mussel populations likely experience elevated mortality resulting from both direct (i.e., emersion, desiccation, and predation) and indirect (e.g., temperature and dissolved oxygen extremes, reduced habitat availability) factors. I believe that these factors influence mussel populations, but their effects are most pronounced in small- and mid-order streams that cease flowing, are reduced to isolated pools, or become entirely dewatered during drought (Golladay et al. 2004, Haag and Warren 2008). As stream size increases, I believe that these effects of drought become buffered, primarily because of greater habitat availability and more persistent streamflows. This is reflected by the apparent greater resiliency of mussel assemblages in larger tributaries observed in this study. Further research, however, would help to resolve remaining uncertainties regarding the specific mechanisms involved.

Compared to drought, identifying the population-level mechanisms contributing to mussel species occupancy declines in isolated stream reaches appears to be relatively straightforward. The detrimental effects of impoundments on mussel population are generally well-understood, and results from this study provide additional evidence that mussel species occurrence is substantially reduced in isolated streams. Most impoundments in the LFRB are small, low-head dams (e.g., mill ponds) that are known to be effective barriers to upstream mussel and fish dispersal. As a result, isolated populations in upstream reaches likely experience substantial reductions in demographic support from neighboring downstream populations (e.g., glochidia attached to host fishes). Although the influence of impoundments on mussel species meta-demographic rates was somewhat inconclusive, results from this study indicated that mussel populations in isolated stream reaches exhibited decreased local recruitment and local colonization, and an elevated risk of local extinction. Hence, impoundments appear to have contributed to the formation of highly vulnerable mussel populations that receive little demographic support from neighboring populations. This source of population fragmentation, which is largely restricted to small and mid-order tributaries, may be another important factor contributing to range contractions and possibly range thinning for many LFRB mussel species. Water resource management plans that include the construction or expansion of impoundments in the LFRB should therefore carefully consider the potential consequences to local mussel populations.

Results from this dissertation provide evidence that natural and anthropogenic factors influence freshwater mussel population dynamics, but considerable uncertainty remains regarding the precise mechanisms involved. For example, my results from Chapter 3 indicated that prolonged drought contributed to declines in mussel species occupancy in small- and mid-order tributaries, which is similar to the findings of others (Golladay et al. 2004, Haag and Warren 2008). I found little evidence that low-flow conditions elevated the risk of local population extinction. Rather, my results suggested that high flow events during summer elevated the risk of local population extinction. The negative influence of high flow events on mussel survival and persistence has been observed by others (Hastie et al. 2001, Peterson et al. 2011), and I believe that high flow events play an important role in shaping the structure and composition of local mussel assemblages. Although the lack of support for low flow conditions influencing mussel population dynamics, particularly local extinction, appears to contradict my results from Chapter 3, some possible explanations exist. For instance, I found evidence that low winter flow conditions strongly and positively influenced recruitment to existing populations, but exceptionally low winter flow conditions (e.g., prolonged drought that continues into winter) substantially reduced local recruitment. It is therefore possible that population losses (i.e., mortality) resulting from drought could be offset by enhanced survival and recruitment of juvenile mussels during years where winter base-flows return to average or above-average conditions following prolonged summer drought. Freshwater mussels also can experience physiological stress during drought, which can deplete energy stores and reduce their ability to avoid scouring forces (and subsequent displacement) during periodic flooding events by borrowing deeper into the substrate (Tucker 1996, Allen and Vaughn 2009). As such, in the event of a localized flooding event *during* a period of severe drought, freshwater mussels may be more prone to being killed or displaced to unsuitable habitats as streamflows return to (low) baseflow conditions. I hypothesize that such processes (e.g., periods of prolonged drought that are punctuated by short-term flooding events; prolonged drought followed by normal flow conditions during fall and winter) may be important determinants of the extent to which high and low streamflow conditions ultimately influence mussel populations. I also believe that such processes may have impaired my ability to detect the population-level effects of drought conditions on LFRB mussels. Clearly there is a need for further research into the specific mechanisms responsible for the relations between meta-demographic rates and streamflow conditions.

Given the evidence for ongoing population declines and range contractions for many LFRB mussel species, it is important to note that many streams in the basin currently support relatively diverse mussel assemblages. In terms of specific localities, model predictions and observations during sampling indicated that diverse mussel assemblages persist in mid-order reaches of all major LFRB tributaries (i.e., Chickasawhatchee, Ichawaynochaway, Kinchafoonee, Muckalee, and Spring Creeks). Additionally, several relatively small and mid-order tributaries that flow directly into the mainstem Flint River also were observed to support relatively diverse mussel assemblages, specifically Chokee, Cooleewahee, Mercer Mill, and Swift Creeks. Chokee and Swift Creeks represent 2 of 3 known locations that support strong populations of federally endangered *Hamiota subangulata*, *Pleurobema pyriforme*, and

Medionidus penicillatus. Muckaloochee Creek, a tributary of Muckalee Creek, also was observed to support populations of federally (*Hamiota subangulata* and *Pleurobema pyriforme*) and state-listed (*Elliptio purpurella* and *Quadrula infucata*) species. Continued monitoring efforts will be critical for validating predicted species distributions (i.e., predictions based on models developed in Chapter 3), monitoring the status of existing populations (i.e., many populations may be experiencing ongoing declines), and identifying currently undocumented populations of imperiled LFRB mussel species. Additionally, I believe that a comprehensive assessment of the abundance and distribution of LFRB mussel species in the mainstem Flint River is greatly needed. Compared to most FRB tributaries, the mainstem Flint River remains relatively under-studied, despite our model predictions and observations during sampling that some portions of the mainstem Flint River currently support exceptionally diverse and unique mussel assemblages. Knowledge of specific localities will be important for managers and biologists to prioritize and implement alternative management actions (e.g., irrigation water buybacks, construction of impoundments). Such knowledge also may be useful in the event that future management and conservation strategies include the use of brood stock for the culture and propagation of freshwater mussels, or donor populations for augmenting or reestablishing mussel populations.

From a long-term management perspective, I believe that to reduce uncertainty (i.e., improve understanding of how the system functions and responds to management actions; Nichols et al. 2011) the approaches and concepts outlined in this dissertation are best implemented within an Adaptive Resource Management (ARM) framework. As stated previously, freshwater mussels present several important challenges associated with research and management, namely slow system dynamics and biases associated with incomplete detection and misidentification of species and individuals. Slow system dynamics (and presumably slow population responses to management actions) likely represents the most challenging aspect of managing LFRB mussel populations into the future. Every management action involves decisions that are made to achieve a goal, and these decisions are made based on how managers believe the system will respond to a given action. ARM exploits the opportunity provided by recurrent management decisions to improve understanding of system responses, which in turn, may help to reduce uncertainty associated with the effects of future management decisions (Nichols et al. 2011). In the context of freshwater mussels, the main challenge then becomes maximizing the ability of managers and biologists to rapidly and efficiently improve their understanding of system responses to management actions. Several recent studies have emphasized the value of 'active' adaptive resource management versus more traditional 'passive' adaptive resource management. In both cases, management decisions are made sequentially and system responses are evaluated during each time step, resulting in the ability to improve understanding of system responses to management actions through time. However, active adaptive resource management places emphasis on the implementation of management actions that explicitly promote learning (McDonald-Madden et al. 2010), whereas in passive adaptive management no attempt is made to impose management actions specifically with the intention of learning (McDonald-Madden et al. 2010). Alternatively, managers may choose to implement different management actions simultaneously at different points on the landscape, thereby allowing for evaluation of system responses to a variety of management activities over shorter time period compared to strategies in which only a single management action is implemented (i.e., space for time substitution). In such cases, care should be taken to ensure that the areas where management actions are implemented are representative of the system as a whole. The predictive models of mussel species occurrence and dynamics developed in this dissertation could provide an extremely useful framework for managers and biologists to improve understanding of how freshwater mussel populations may respond to changing environmental conditions or alternative management actions. Combined with an ARM framework (active or passive) and effective and ongoing monitoring programs, I believe that the approaches outlined in this dissertation provide a useful tool for approaching the long-term management of LFRB freshwater mussels.

CONCLUSIONS

In this dissertation, I have discussed interrelated topics with respect to the management and conservation of freshwater mussel species in the lower Flint River Basin, Georgia. Most importantly, this dissertation represents a concerted effort to improve our ability to predict the spatial and temporal distributions of freshwater mussel species in relation to natural and anthropogenic factors. Currently, many freshwater mussel species are critically imperiled, and many more species are expected to follow suit without continued efforts to identify and mitigate the predominant factors contributing to population declines. During the past 30 years, significant advances have been made regarding the collective understanding of freshwater mussel ecology and biology. One of the most important advances during this time has been the growing interest in improving the understanding of flow-ecology relationships – understanding how mussel populations respond to changes in the availability of water in stream systems. In the LFRB and elsewhere, the ever-growing demand for water resources will undoubtedly continue to place stressors on populations of freshwater mussels and other stream-dwelling biota (Petts 2009, Richter 2009). My hope is that this dissertation will provide a useful resource and conceptual framework for improving our understanding of the critical resource requirements of freshwater mussels, which will be critical for the development of management and conservation strategies that protect these imperiled organisms.

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