

## ABSTRACT

Title of Document: IDENTIFYING THE ELUSIVE DWARF  
WEDGEMUSSEL HABITAT THROUGH MODELING  
AND FIELD APPROACHES

Cara Ann Campbell, Doctor of Philosophy, 2014

Directed By: Dr. Karen L. Prestegard  
Program of Marine, Estuarine and Environmental Science

Habitat identification is an important step in the conservation of at-risk species, but difficult due to the small, fragmented populations of rare species. In particular, fine-scale habitat features that constrain species occurrence may not be captured by landscape models. Thus, I used both modeling and field-based approaches to identify habitat characteristics for the endangered dwarf wedgemussel, *Alasmidonta heterodon*. Community analyses and modeling were combined to identify characteristics of suitable habitat for *A. heterodon* in the Maryland Coastal Plain. Community analyses suggested that landscape, rather than biological, surrogates would be preferable for predictive habitat modeling. Subsequent MaxEnt modeling associated *A. heterodon* habitat in the Maryland Coastal Plain with the following variables: depth to the water table, pasture/hay land cover, woody wetlands, low intensity development, Tertiary-aged sediments, and minimum elevation. The results from this model directed field work to evaluate thermal, geochemical, and physical

characteristics of *A. heterodon* reaches throughout the species' range. Paired air-water temperature sensors placed in *A. heterodon* reaches suggested a potential thermal threshold of 29°C. Southern sites had higher maximum water temperatures but exhibited less diurnal variation and lower rates of temperature change than northern sites; characteristics that suggest intermediate to deep groundwater sources. Physical and chemical characteristics were measured along the length of Flat Brook, a stream with *A. heterodon* in the Delaware River basin. Data indicated that the mussel occurred in reaches that were stable during bankfull and lower discharges and water chemistry data indicated saturation with respect to aragonite during summer base flow. Field studies suggest several potential essential habitats for *A. heterodon*: (1) habitats with stable streambeds at bankfull and lower discharges; (2) stream waters in equilibrium with aragonite precipitation during baseflow conditions; and (3) habitats with maximum temperatures < 29°C and stable thermal regimes. The different thermal regimes and contributing groundwater sources between northern and southern populations suggest that geographic region be a consideration in species' reintroductions. Until essential habitats are identified and management plans instituted, all populations should be similarly protected and the loss of individual populations prevented.

IDENTIFYING THE ELUSIVE DWARF WEDGEMUSSEL HABITAT THROUGH  
MODELING AND FIELD APPROACHES

By

Cara Ann Campbell

Dissertation submitted to the Faculty of the Graduate School of the  
University of Maryland, College Park, in partial fulfillment  
of the requirements for the degree of  
Doctor of Philosophy  
2014

Advisory Committee:

Dr. Karen L. Prestegaard, Chair  
Dr. Andrew J. Elmore  
Dr. William O. Lamp  
Dr. William A. Lellis  
Dr. Todd R. Lookingbill

© Copyright by  
Cara Ann Campbell  
2014

## Dedication

To my parents;  
the best people I know

## Acknowledgements

I would first like to thank my advisor, Karen Prestegaard, whose amazing insights, ability to see the big picture, and talent for never seeing a negative result proved inspirational during the difficult times. I also thank my committee members (Andrew Elmore, Bill Lellis, and Todd Lookingbill) for their words of encouragement and for seeing me through my graduate program. Thanks to my newest committee member, Bill Lamp, for his help in completing my degree. I also appreciate the support and guidance Bob Hilderbrand provided.

The support of the National Park Service, the U.S. Geological Survey, and the University of Maryland Center for Environmental Science (Appalachian Laboratory) made this project possible.

I am indebted to all those who helped me with field work. Matt Ashton, Christine Baker, Sally Campbell, Terry Campbell, Mike Gangloff, Melissa Grader, Brett Hillman, Rachael Hoch, Susi vonOettingen, and Brian Watson deployed and/or retrieved temperature sensors and loggers. Will Condon was my right-hand man for all the geomorphology work in Flat Brook.

I also thank Matt Ashton for providing me with endless MBSS datasets and for his eagerness to discuss ideas and provide feedback. I appreciate Jim McCann's willingness to share the Maryland bivalve data. John Young kindly provided lidar data for the lower Flat Brook.

I am grateful to the folks at the USGS Northern Appalachian Research Lab for all their patience and support during this crazy ride. Dale Honeyfield and Dan Spooner provided words of wisdom that helped get me through some of the rough patches.

Finally, I thank my family.

# Table of Contents

Dedication .....	ii
Acknowledgements .....	iii
Table of Contents .....	iv
List of Tables .....	vii
List of Figures .....	viii
Chapter 1: Introduction .....	1
1.1 Species Distribution Modeling .....	1
1.2 Freshwater Mussels .....	4
1.3 <i>Alasmidonta heterodon</i> .....	7
1.4 Dissertation Overview: Objectives and Questions .....	11
Chapter 2: Mussel community structure, biological surrogates, and landscape associations in the Maryland Coastal Plain .....	16
2.1 Abstract .....	16
2.2 Introduction .....	17
2.3 Methods .....	19
2.3.1 Study Area .....	19
2.3.2 Biological Databases .....	20
2.3.3 Environmental Databases .....	23
2.3.4 Data Analyses .....	27
2.4 Results .....	29
2.4.1 Mussel Community Structure .....	29
2.4.2 Fish Indicators of Mussel Species or Assemblages .....	32
2.4.3 Mussel Assemblage Associations with Landscape Features .....	32
2.5 Discussion .....	36
2.5.1 Mussel Community Structure and Landscape Associations .....	37
2.5.2 Biological Surrogates .....	39
2.5.3 Conclusion .....	41

Chapter 3: Using maximum entropy to predict suitable habitat for the endangered dwarf wedgemussel in the Maryland Coastal Plain .....	42
3.1 Abstract .....	42
3.2 Introduction .....	42
3.3 Methods .....	45
3.3.1 Study Area .....	45
3.3.2 Biological Database .....	47
3.3.3 Stream Segment Database .....	47
3.3.4 Data Analysis .....	51
3.4 Results .....	52
3.4.1 Model Selection .....	52
3.4.2 Variable Response .....	57
3.4.3 Predicted Suitable Habitat .....	59
3.5 Discussion .....	60
3.5.1 Model Performance .....	60
3.5.2 Species-Environment Relationships .....	60
3.5.3 Model Predictions and Utility .....	63
Chapter 4: A field-based potential thermal limit for <i>Alasmidonta heterodon</i> , an endangered freshwater mussel, and regional differences in underlying thermal regimes .....	66
4.1 Abstract .....	66
4.2 Introduction .....	67
4.3 Methods .....	70
4.3.1 Study Area .....	70
4.3.2 Selection of Sampling Interval for Air and Water Temperatures .....	73
4.3.3 Field Temperature Monitoring Procedures .....	74
4.3.4 Data Analysis .....	75
4.4 Results .....	80
4.4.1 Average Daily Temperature and Daily Temperature Variations .....	80
4.4.2 Water Temperature Maxima .....	80
4.4.3 Air-Water Regression Equations and Characterization of Baseflow Sources .....	83
4.4.4 Predicted Water Temperatures Based on 30-Year Mean August Air Temperatures .....	85



4.5 Discussion .....	86
Chapter 5: Physical and chemical constraints limit the habitat window for an endangered mussel .....	94
5.1 Abstract .....	94
5.2 Introduction .....	95
5.3 Methods .....	97
5.3.1. Study Area .....	97
5.3.2. Geochemical Measurements and Calculations .....	99
5.3.3. Geomorphic Characteristics and Determination of Bed Substrate Stability .....	103
5.4 Results .....	108
5.4.1. Spatial Variations in Water Chemistry .....	108
5.4.2. Spatial Variations in Bed Substrate Mobility .....	108
5.5 Discussion .....	110
5.5.1. Stream Bed Stability .....	110
5.5.2. Aragonite Saturation .....	112
5.5.3. Habitat Window .....	114
Chapter 6: Conclusions and implications .....	117
6.1 Results from the Community Analyses .....	118
6.2 MaxEnt Modeling .....	119
6.3 Suitable Landscape Habitats and Potential <i>A. heterodon</i> Constraints .....	120
6.4 Field Identification of Reach-Scale Habitat Characteristics for <i>A. heterodon</i> .....	122
6.5 Integrating Field and Modeling Results .....	124
6.6 Implications for <i>A. heterodon</i> Management and Recovery .....	127
Bibliography .....	133

## List of Tables

2.1.....	21
2.2.....	25
2.3.....	30
3.1.....	49
3.2.....	54
4.1.....	77
4.2.....	79
5.1.....	102
5.2.....	104

## List of Figures

2.1.....	20
2.2.....	22
2.3.....	31
2.4.....	33
2.5.....	35
3.1.....	45
3.2.....	56
3.3.....	58
3.4.....	59
4.1.....	71
4.2.....	72
4.3.....	73
4.4.....	82
4.5.....	84
5.1.....	98
5.2.....	107
5.3.....	109
5.4.....	115

# Chapter 1: Introduction

Understanding species-environment relationships is critically needed for natural resource conservation and management. Models based on measures of these relationships can make predictions about species attributes and inferences about their adaptations to change (Heglund 2002). Predicting species distributions continues to be problematic, due to factors such as the complexity of ecosystems, disparities between the scale of data collection and processes examined, and difficulties in quantifying ecological patterns and processes (Huston 2002). These difficulties can be exacerbated for rare species that are often of the most interest to natural resource managers and policy makers (Lomba et al. 2010). For example, the sparse and fragmented nature of many freshwater mussel species makes locating populations especially difficult and results in models with little predictive power or that are non-transferable across river systems (Strayer 2008). Yet this knowledge is desperately needed to: (1) identify suitable habitat to guide surveys for undiscovered populations and (2) forecast potential impacts of human activities and global change on species habitat. This project will address the problem of identifying species-environmental relationships for the federally endangered dwarf wedgemussel, *Alasmodonta heterodon*.

## 1.1 Species Distribution Modeling

Species distribution modeling is an important technique used in the conservation and management of rare or endangered species. The technique is rooted

in niche theory (Guisan and Zimmermann 2000), as it is based on the premise that there is a predictable relationship between the occurrence of a species and features of the environment, or its niche (Heglund 2002). This generally refers to the place-based niche focused on the particular physical habitat in which a species lives (Grinnell 1917). Models of this type develop quantitative relationships between a species and features of the environment to determine the species' realized niche. If all the environmental factors required for the indefinite survival and reproduction of a species defines its fundamental niche, the realized niche is that portion constrained by biotic processes (Hutchinson 1957) and is what we observe. Environmental conditions, human disturbance, and climate are spatially and temporally dynamic, thus there is only a portion of the total environment where a species could potentially exist at any given point in time (Heglund 2002). If these constraints are applied to the fundamental niche, a potential niche can be defined that describes the environment potentially capable of supporting a species at a given time (Jackson and Overpeck 2000). It is this potential niche that is being predicted in species distribution modeling using species-habitat relationships determined from the realized niche.

Static species distribution models rely on the assumption that a species is in at least pseudo-equilibrium with its environment (Guisan and Thuiller 2005). Temporal and spatial ecosystem dynamics, biotic interactions, and human modifications can cause individuals of a species to be absent from suitable habitat and present in unsuitable areas. Thus, our perception of the realized niche is a snapshot of species-environment relationships at a given time, and is a product of processes and mechanisms operating across multiple scales (Huston 2002). Systems can often be

organized into discrete units according to functional scale (O'Neill et al. 1986).

Where these systems are hierarchically organized (such as in aquatic systems; Frissell et al. 1986), each layer of the hierarchy contains and constrains those below it. As a result, there is no single scale appropriate to study (Levin 1992), and different analyses may require examining different levels in the hierarchy (Urban et al. 1987).

This suggests that species distribution modeling alone may not be enough to identify critical species-habitat relationships. For example, niche-based species distribution models predict potential habitat based on the similarity between unknown habitat and known habitat (O'Conner 2002). While such patterns may suggest causal mechanisms, the mechanisms themselves are not identified (Strayer 2008). For example, identifying an association between a species distribution and latitude and longitude does not mean anything *per se*, but can be suggestive of thermal constraints (Dunham et al. 1999). To better understand the causal mechanism would require detailed, controlled laboratory experiments to determine thermal tolerances for survival (Elliott 1991; Pandolfo et al. 2010; Ganser et al. 2013) and reproduction (Holste and Peck 2006; Galbraith and Vaughn 2009). As realized- rather than fundamental-niches are used for modeling, the restricted ranges and cryptic nature of many rare species may be more prone to sampling biases that might incorrectly identify ecological constraints (Thompson 2004). Thus, identifying patterns and inferring important underlying processes can be accomplished through predictive species modeling, but identifying causal mechanisms and constraints to species distributions requires finer-scaled field or laboratory approaches.

My project will develop a framework for identifying suitable habitat for rare-species using modeling and field approaches. The focus will be on freshwater mussels whose declining numbers and increasingly fragmented spatial distributions provide ample opportunities to tackle the challenges presented above.

## 1.2 Freshwater Mussels

Native freshwater mussels (families Margaritiferidae and Unionidae) are vital to the functioning of freshwater ecosystems, but are among the most imperiled of freshwater groups (Lydeard et al. 2004; Strayer et al. 2004; Vaughn et al. 2004; Spooner and Vaughn 2006). As benthic filter feeders, they can influence water chemistry and clarity (Vaughn et al. 2004) and are often early indicators of degrading water quality (Bogan 1993a). Species tend to be highly endemic (Haag 2010) and very susceptible to human activities (McRae et al. 2004; Gangloff and Feminella 2007; Randhir and Hawes 2009). Unionids have a unique life history in which mussel larvae (glochidia) attach to a fish host, metamorphose into juveniles, and eventually drop off and settle to the bottom where they grow into adults. This dependency on host fish makes species susceptible to any actions affecting the host fish (Bogan 1993a). As a result, native mussels are among the most imperiled freshwater fauna (Williams et al. 1993; Lydeard et al. 2004), with the widespread declines attributed to habitat and water quality degradation and the introduction of non-native mollusks (Bogan 1993a; Strayer et al. 2004).

Declines of freshwater mussels have thinned species ranges producing spatially fragmented distributions across large areas. Spatial fragmentation in combination with a heterogeneous environment makes identifying ecological and

physiological constraints, and predictive modeling, difficult (Strayer 2008). Attempts to predict freshwater mussel occurrence often produce statistically significant models with low predictive power (Strayer 1993; Strayer and Ralley 1993; Arbuckle and Downing 2002; Mynsberge et al. 2009). Many of these models (e.g., regression models and discriminant analyses) rely on underlying assumptions of a linear response and multivariate normal distributions that are often not met in species-environment relationships (Strayer and Ralley 1993; De'ath and Fabricius 2000; McCune and Grace 2002; Gotelli and Ellison 2004). Modeling techniques that incorporate nonlinear relationships have been used to quantify bivalve-habitat relationships (Gray et al. 2005) and often have greater predictive power than linear models (Steuer et al. 2008; Zigler et al. 2008; Hopkins 2009; Wilson et al. 2011). Difficulties in predicting species distributions has created a new focus on identifying functional attributes (what a mussel needs from its habitat; Strayer 2008), particularly on those most likely to influence occupancy at a given reach (Newton et al. 2008).

Freshwater mussels have a complex life history, thus their functional habitat must accommodate needs across these life stages. To accommodate this life cycle, Strayer (2008) and Newton et al. (2008) outlined several functional characteristics of suitable mussel habitat, several of which are relevant to this project: (1) habitat without excessive shear stress and is stable during floods; (2) habitat with temperatures favorable for survival, growth, and reproduction; (3) habitat that provides calcium for shell growth; and (4) habitat that has host fish. Mussels require a suitable range of stream velocities; fast enough to maintain oxygen levels, provide food, transport nutrients, and flush wastes, yet slow enough to enable settlement of



juveniles (Layzer and Madison 1995; Hardison and Layzer 2001; Morales et al. 2006; Steuer et al. 2008; Strayer 2008; Allen and Vaughn 2010; Maloney et al. 2012).

Mussels generally use habitats with stable streambeds (Steuer et al. 2008; Zigler et al. 2008; Allen and Vaughn 2010; Maloney et al. 2012). These habitats can serve as refuges from high flows (Vannote and Minshall 1982; Strayer 1999; Maloney et al. 2012). Habitats with low hydraulic stress are positively associated with mussel abundance (Hardison and Layzer 2001; Gangloff and Feminella 2007).

Mussel habitat must also provide suitable thermal regimes and essential non-food materials (Strayer 2008). Susceptibility to high water temperatures varies by species and life stage (Pandolfo et al. 2010; Galbraith et al. 2012; Ganser et al. 2013). Heart rate generally increases with increasing temperature until a critical thermal threshold is reached (Pandolfo et al. 2009) beyond which heart rate either remains stable or declines (Braby and Somero 2006). Temperature thresholds can also control the onset and cessation of growth (Goewert et al. 2007; Negishi and Kayaba 2010). Thermal regimes are cues for timing of gamete development (Galbraith and Vaughn 2009) and altered thermal regimes can disrupt the freshwater mussel reproductive cycle, inhibiting successful reproduction (Heinricher and Layzer 1999; Galbraith and Vaughn 2009). The habitat should also provide calcium for shell growth (Strayer 2008). Freshwater mussel shells are composed of calcium carbonate minerals, primarily aragonite (Wilbur 1964). Aragonite may be vital when growth rates are highest and also in reproducing individuals whose calcium carbonate stores are directed toward shell growth in the developing larvae (Pynnönen 1991). Species differ in their ability to store calcium carbonate (Pynnönen 1991), but for long-term

sustainability, mussels must live where the local water chemistry is in equilibrium with the precipitation of aragonite during at least part of the year (Goewert et al. 2007; Lopes-Lima et al. 2009).

Finally, habitats must provide access to host fish (Haag and Warren 1998; Vaughn and Taylor 2000). Most freshwater mussel species have a parasitic life-stage on host fish, with the number and species of fish hosts unique to each mussel species (Zale and Neves 1982; Michaelson and Neves 1995; Gray et al. 2002; Douda et al. 2012; Lellis et al. 2013). Long-distance dispersal may occur during this parasitic life stage and can be dependent on fish movement (Strayer 2008). Therefore, mussel distributions may be patterned according to specific fish host distribution, abundance, and/or environmental requirements (Watters 1992; Vaughn 1997; Haag and Warren 1998; Vaughn and Taylor 2000; Rashleigh and DeAngelis 2007; Schwalb et al. 2013).

### 1.3 *Alasmidonta heterodon*

The focus of my project is the dwarf wedgemussel, *Alasmidonta heterodon*, a federally endangered freshwater mussel of importance to resource agencies along the mid-Atlantic (U.S. Fish and Wildlife Service 1993). The mussel is a member of the subfamily Anodontinae, whose members are typically fast growing with relatively short life spans of ~15 years (Crowley 1957; Negus 1966; Haukioja and Hakala 1978; Michaelson and Neves 1995). *A. heterodon* is small with a shell usually < 57 mm in length however growth rates vary geographically (Master 1986; Michaelson and Neves 1995). *A. heterodon* are unique in having shells with 2 lateral teeth in the right valve and 1 in the left, the reverse of all other North American species with lateral

teeth (Clarke 1981a). In the field, the species can be confused with young *Elliptio*, however the mottled, colorful mantle margin can be a distinguishing factor (Fuller 1977). The gravid period typically spans from late August to the following June; fertilization occurs in mid-summer and fall with glochidia released the following spring and summer (Clarke 1981b). Proportion of gravid females, glochidial density, infection rates, and juvenile recruitment can be directly proportional to mussel abundance (McLain and Ross 2005). Rather than relying on suspension in the current, the hooked glochidia of *A. heterodon* likely rely on the host fish to agitate the bottom to bring the glochidia into close proximity to a host's fin or gill (Howard and Anson 1922; Michaelson and Neves 1995). Thus, host fish for *A. heterodon* include many benthic dwellers and include: *Etheostoma olmstedii* (tessellated darter), *E. nigrum* (Johnny darter), *Cottus bairdi* (mottled sculpin), *C. cognatus* (slimy sculpin), and the diadromous *Salmo salar* (Atlantic salmon) (Michaelson and Neves 1995; B. Wicklow, Saint Anselm College, unpublished data). It has been suggested that the decline of *A. heterodon* is not host-related (Michaelson and Neves 1995). However, an impoundment constructed in 1968 blocked diadromous fish migrations in the Petitcodiac River (New Brunswick, Canada) and presumably caused the extirpation of *A. heterodon* from the river by the 1980's (Locke et al. 2003). The species' range currently extends from the Connecticut River, NH, to the Neuse River, NC (U.S. Fish and Wildlife Service 1993).

Considered a rare and inconspicuous species (Clarke and Berg 1959), *A. heterodon* populations are sparse with generally low densities (Clarke 1981a; Strayer et al. 1996), thus potentially at risk of lower infection rates and juvenile recruitment

(McLain and Ross 2005). The lack of historical population density information makes it impossible to determine if low densities are a natural feature of the species or are the result of human influences (Strayer et al. 1996). Despite these low densities, *A. heterodon* populations can greatly differ in size, with some populations getting quite large ( $10^3 - 10^5$  animals; Strayer et al. 1996). These large populations could provide source animals for reintroductions (Strayer et al. 1996). In most streams, animals occur in widely separated patches, with the extent of populations extending throughout linear, unbranched reaches of the stream (Strayer et al. 1996). This patchy distribution could be an artifact of the limited dispersal capabilities of the mussel's host fish (McLain and Ross 2005). These population characteristics can make it difficult to determine the viability of individual populations and make *A. heterodon* susceptible to threats occurring in upstream or upslope areas (Strayer et al. 1996).

Several studies have examined *A. heterodon* habitat usage. The species occurs in fine substrates with slow to moderate flows and depths (Strayer and Ralley 1993; Michaelson and Neves 1995). Animals have also been found completely buried in detrital mats (W. Lellis, U.S. Geological Survey, unpublished data). *A. heterodon* often occurs in low gradient reaches (Ashton 2010; W. Lellis, U.S. Geological Survey, unpublished data) with stable flows and substrates (Strayer and Ralley 1993; Strayer 1999; Maloney et al. 2012). These areas can provide flow refuges during high flow events (Strayer 1999). However, the use of host fish with limited dispersal abilities (e.g., *E. olmstedii*) suggests that storm-assisted dispersal may be an important dispersal mechanism for *A. heterodon* (McLain and Ross 2005). The species has also been associated with sites having high pH and specific conductivities (Ashton 2010)

and low calcium concentrations (Strayer 1993). It has been suggested that *A. heterodon* distribution may be associated with some factor correlated with calcium concentration (Strayer 1993). Temperature may also influence the distribution of *A. heterodon* as animals have been associated with cool groundwater seeps during the summer (Briggs et al. 2013).

Species extinction has not been considered likely due to population stability in northern systems such as the Connecticut and Delaware River basins. However, a record flood in 2005 decimated the *A. heterodon* population in the Neversink River, NY (J. Cole and B. White, unpublished data), a population critical to the species' survival (U.S. Fish and Wildlife Service 1993). The loss of the Neversink population has added urgency to preserving other existing populations and to finding and protecting new populations, particularly in the southern and mid-Atlantic regions. Surveys have recently discovered unknown populations in the upper Delaware River basin (W. Lellis, U.S. Geological Survey, unpublished data) and the Maryland Coastal Plain (Maryland Natural Heritage Program, unpublished data). However surveys can be labor intensive (i.e., several thousand person-hours of focused stream searching; W. Lellis, U.S. Geological Survey, unpublished data) and can easily miss the species. For example, the site of recent discovery of the mussel in the mainstem Delaware River had been the subject of at least two previous mussel surveys, and the animal was not discovered (Strayer and Ralley 1991; Bogan 1993b). There are thousands of miles of streams within Atlantic drainages that potentially contain *A. heterodon*, and conducting detailed searches of all those streams would be a monumental task, both in time and cost.

An alternative approach to physical search of all waterways is to select streams for survey based upon known habitat usage by the mussel. Predictive models are suitable for this purpose because they develop statistical relationships between a species and a set of predictor variables to map the potential distribution of a species (Guisan et al. 2002). Modeling the suitability of streams for *A. heterodon* could provide a foundation for a prioritized sampling scheme for the species that could guide surveys toward the streams with the best chance of containing the species or, alternatively, away from those streams with little chance of containing *A. heterodon*. Additionally, the model predictions could be used for species' transplants and reintroductions. Strayer et al. (1996) suggested that *A. heterodon* population sizes can vary greatly. Animals from the larger populations could be transplanted or reintroduced into segments according to their suitability. By performing follow up surveys to monitor the animal's survival, it could be possible to identify individual stream segments that show potential for *A. heterodon* reintroductions. These surveys could also uncover unknown *A. heterodon* populations. Thus quantifying species-habitat relationships and predictive modeling can supply information needed for conservation and recovery efforts that could potentially lead toward downlisting the species.

#### 1.4 Dissertation Overview: Objectives and Questions

This project will develop a framework for identifying species-environment relationships for the dwarf wedgemussel, *A. heterodon*. The project is composed of two approaches. First, a modeling approach will be used to identify suitable habitat for *A. heterodon* in the Maryland Coastal Plain. Second, field-based approaches will

be used at known locations of *A. heterodon* to identify essential habitat(s) associated with the species' occurrence. Using the specific functional habitats described earlier and outlined in Strayer (2008) and Newton et al. (2008) as a guide, this approach will focus on examining geomorphic, chemical, and thermal characteristics of *A.*

*heterodon* habitat. Thus, I have two broad objectives for the project:

1. Predict *A. heterodon* potential distribution at the landscape scale.
2. Identify essential geomorphic, chemical, and thermal habitats influencing *A. heterodon* occurrence at local scales.

The following chapters are arranged as four manuscripts to be submitted for publication. Chapters 2 and 3 address the first objective of building a predictive model for *A. heterodon*. The focus is on the Maryland Coastal Plain where a long history of agriculture, population expansion, and increasing groundwater withdrawals (Foresman et al. 1997; Benitez and Fisher 2004; Jantz et al. 2005; Fisher et al. 2006) threaten *A. heterodon* populations. Once found in several sites in the Choptank River basin on the Delmarva Peninsula, *A. heterodon* is now largely absent from the basin. However, recent discovery of *A. heterodon* in Herring Run, a small tributary of the Choptank River, provides hope that other undiscovered mussel populations might exist. Thus, there is need for model results that could be used to target future surveys towards streams with the greatest chance of containing the mussel.

Chapter 2 focuses on identifying biological surrogates for *A. heterodon*; fish or mussel species that would indicate an increased or decreased likelihood for *A. heterodon* to be present. A stream segment database was created for the Maryland Coastal Plain that contains landscape features known to influence the abundance,

distribution, and assemblage structure of unionids such as land cover and land use (Gagnon et al. 2006; Hopkins 2009), bedrock geology (Arbuckle and Downing 2002; McRae et al. 2004; Weber and Schwarz 2011), and soil characteristics (Hopkins 2009; Weber and Schwartz 2011). Unique pairings of mussel and fish sample sites were made and linked to a stream segment. Community analyses were conducted across the Maryland Coastal Plain and within a subset of these sites found within river systems containing *A. heterodon*. A combination of hierarchical cluster analysis and indicator species analysis determined mussel community structure and mussel and fish species associated with each cluster. Nonmetric multidimensional scaling identified landscape variables associated with the community structure. Specific questions addressed were:

Q<sub>1</sub>. What is the mussel structure for Maryland Coastal Plain streams and within river systems where *A. heterodon* occur?

Q<sub>2</sub>. Are there biological surrogates (mussel or fish species) for mussel assemblages; *A. heterodon* in particular?

Q<sub>3</sub>. What landscape factors best explain community structure?

The focus of Chapter 3 is on predicting potential suitable habitat for *A. heterodon*. The stream segment database was also used for modeling and the results from the community analyses guided the modeling process. Currently among the best models for predicting occurrence of species with very small sample sizes (Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008), maximum entropy was used to develop a predictive model to determine the suitability of *A. heterodon* macrohabitat for stream segments in the Coastal Plain. The overall question addressed was:



Q4. Can landscape features predict the occurrence of *A. heterodon* in the Maryland Coastal Plain?

Chapters 4 and 5 each address the second objective of identifying essential habitats and constraints to the species at a sub-segment scale. Chapter 4 focuses on using range-wide field-measurements to identify a potential thermal limit associated with the distribution of *A. heterodon*. The mussel has been associated with cold groundwater seeps and upwellings (Briggs et al. 2013). Deep groundwater tends to be markedly colder than shallow groundwater since it reflects recharge during winter and spring months rather than via storm events throughout the year (Tóth 1963). Thus, if *A. heterodon* inhabits cold water, it may be limited to reaches that have intermediate to deep groundwater contributions. Paired air/water temperatures were sampled in *A. heterodon* reaches from New Hampshire to North Carolina to address the following questions:

Q5. Can range-wide in situ stream temperatures identify a potential thermal limit for *A. heterodon*?

Q6. Can air-water temperatures and regression relationships be used to identify stream groundwater sources?

The focus of Chapter 5 is on identifying factors that control the spatial distribution of *A. heterodon* in Flat Brook, a tributary to the upper Delaware River, where a sharp change in gradient roughly corresponds to the upstream limit of *A. heterodon* occurrence. This suggests that geomorphic characteristics (bed grain size, fluid shear stress, bed mobility, etc.) may explain its distribution however, changes in stream gradient may also reflect geological or geomorphological boundaries that

influence flow regimes, groundwater contributions to streams, and stream water chemistry (Tóth 1963; Tóth 1970; Boxall et al. 2008). Thus, chemical and geomorphic samples were taken along the length of Flat Brook to address the following questions:

Q<sub>7</sub>. Is the spatial distribution of *A. heterodon* in Flat Brook constrained by the physical stream habitat (bed stability)?

Q<sub>8</sub>. Is the spatial distribution of *A. heterodon* in Flat Brook constrained by local water chemistry (e.g., waters saturated with respect to aragonite)?

Chapter 6 is a synthesis of the information provided in the preceding Chapters. It discusses how the results of Chapters 2 and 3 can be combined to predict suitable stream segments for *A. heterodon* in the Maryland Coastal Plain (Objective 1). Results of Chapters 4 and 5 contribute toward identifying essential geomorphic, thermal, and chemical habitat across the species' range (Objective 2). The Chapter concludes by discussing implications of the results in terms of the *A. heterodon* recovery plan.

## Chapter 2: Mussel community structure, biological surrogates, and landscape associations in the Maryland Coastal Plain

### 2.1 Abstract

At-risk species are in the most need of predictive distribution modeling however these species are among the most difficult to model. Habitats with similar environmental pressures should contain species with similar adaptations or attributes, and these species could serve as biological surrogates for other species in predictive modeling. I examined freshwater mussel community structure to identify biological surrogates (mussel or fish species) for the federally endangered dwarf wedgemussel, *Alasmidonta heterodon*, within the Maryland Coastal Plain. Hierarchical agglomerative cluster analysis and indicator species analysis divided the bivalve community into six clusters in the Maryland Coastal Plain. A second series of analyses within a subset of Coastal Plain rivers that contain *A. heterodon* divided the bivalve into five clusters. *A. heterodon* defined its own cluster, which was not associated with other mussel species. Three fish species (redfin pickerel, shield darter, and ironcolor shiner) were significant indicators of the *A. heterodon* cluster, yet were not suitable surrogate species due to incompatible habitat or their rarity. Ordination results suggested that ecoregion, land cover, bedrock and surficial geology, air temperature, and location within the stream network are associated with mussel community structure. These results suggest that habitat-based rather than biological surrogate-based models may be better predictors of *A. heterodon* distributions within the Maryland Coastal Plain.

## 2.2 Introduction

Species distribution modeling is an important technique used in the conservation and management of rare or endangered species. Due to their narrow geographical distributions, specialized habitat requirements, and low population sizes, however, these species present significant challenges for distribution modeling (Lomba et al. 2010). The distribution and abundance of a species has a functional relationship to habitat conditions and resources that occur at various spatial scales (Guisan and Thuiller 2005). Therefore, habitats with similar environmental pressures should contain species with similar attributes or adaptations and community structure (Poff 1997). This suggests that individual taxa or taxonomic groups could serve as biological surrogates in predictive species modeling; the presence of one species makes it more or less likely for another species to be present. For example, plant species composition can be used as a surrogate for water beetle species composition in Ireland (Gioria et al. 2010) and beaver distribution can serve as a surrogate for amphibian habitat in Alberta (Stevens et al. 2007). I examined freshwater mussel community structure to identify potential biological surrogates (mussel or fish species) to enhance predictive habitat modeling of an endangered mussel species.

Both biological (e.g., fish species) and environmental conditions affect freshwater mussel distributions (Strayer 2008). Most freshwater mussel species have a parasitic life-stage on host fish, with the number and species of fish hosts unique to each mussel species (Zale and Neves 1982; Michaelson and Neves 1995; Gray et al. 2002; Douda et al. 2012; Lellis et al. 2013). Long-distance dispersal may occur during this parasitic life stage and can be dependent on fish movement (Strayer 2008).

Therefore, mussel distributions may be patterned according to specific fish host distribution, abundance, and/or environmental requirements (Watters 1992; Vaughn 1997; Haag and Warren 1998; Vaughn and Taylor 2000; Rashleigh and DeAngelis 2007; Schwalb et al. 2013). Although mussel larval dispersal can require host fish, subsequent mussel growth and reproduction may be dependent on fine-scale habitat conditions and processes that can limit species distribution and abundance (Strayer 1999; Vaughn and Taylor 2000; Gangloff and Feminella 2007; Allen and Vaughn 2010; Maloney et al. 2012; Strayer and Malcolm 2012). These fine-scale data are often not available on a regional scale, therefore distribution modeling of mussel species or assemblages has been more successful using landscape-scale habitats (Hopkins 2009; Weber and Schwartz 2011; Atkinson et al. 2012). Incorporating both fish distributions and landscape variables into a predictive framework can enhance models of mussel community structure (Vaughn and Taylor 2000; Schwalb et al. 2013) and, potentially, individual mussel species.

Community analyses often define distinct assemblages of taxa and identify habitats influencing taxa assemblages (Ilmonen et al. 2009; Haag 2010; Pérez-Quintero 2013). Scientists have evaluated freshwater mussel community structure (Sepkoski and Rex 1974; Horsak and Hajek 2003; Haag 2010; Zigler et al. 2012; Pérez-Quintero 2013) and identified spatial or environmental characteristics underlying mussel assemblages (Baldigo et al. 2003; Walsh et al. 2007a; Atkinson et al. 2012; Pérez-Quintero 2013). Biological associations have focused on whether fish distributions, particularly of fish hosts, determine mussel community structure (Haag and Warren 1998; Vaughn and Taylor 2000; Schwalb et al. 2013). These community-

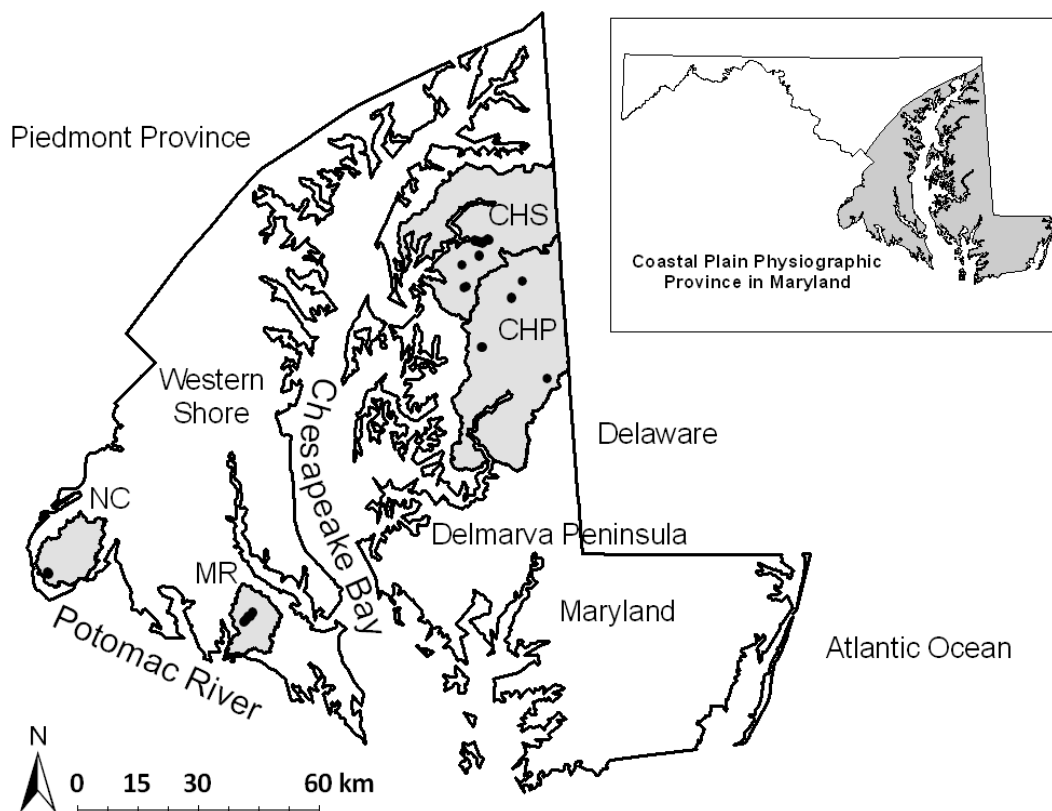
level associations have not been used to evaluate the distribution of individual species.

My objective was to determine whether freshwater mussel community structure could be used to identify biological surrogates (mussel or fish species) for the federally endangered dwarf wedgemussel, *Alasmidonta heterodon*, within the Maryland Coastal Plain (MCP). I addressed the following questions: 1) What is the mussel community structure for MCP streams and for the subset of streams in river systems where *A. heterodon* occur? 2) Are there biological surrogates (mussel or fish species) for various mussel assemblages; *A. heterodon* in particular? and 3) What landscape factors best explain mussel community structure?

### 2.3 Methods

#### 2.3.1 Study Area

In Maryland, *A. heterodon* appears to be restricted to the MCP (Maryland Department of Natural Resources, unpublished data). The Coastal Plain is bordered by the Piedmont Province on the west and the Atlantic Ocean on the east and is divided by the Chesapeake Bay into the Western Shore and the Delmarva Peninsula (Fig. 2.1). *A. heterodon* are currently found in four river systems, two in the Western Shore (Nanjemoy Creek and McIntosh Run) and two in the Delmarva Peninsula (Chester and Choptank; Fig. 2.1). All the rivers are in regions of low relief and wide floodplains, although elevations and stream gradients are higher in the Western Shore than Delmarva Peninsula.



**Figure 2.1** The location of *A. heterodon* (circles) within four Maryland Coastal Plain basins (shaded). Nanjemoy (NC) and McIntosh (MR) basins are in the Western Shore and the Chester (CHS) and Choptank (CHP) basins are in the Delmarva Peninsula.

### 2.3.2 Biological Databases

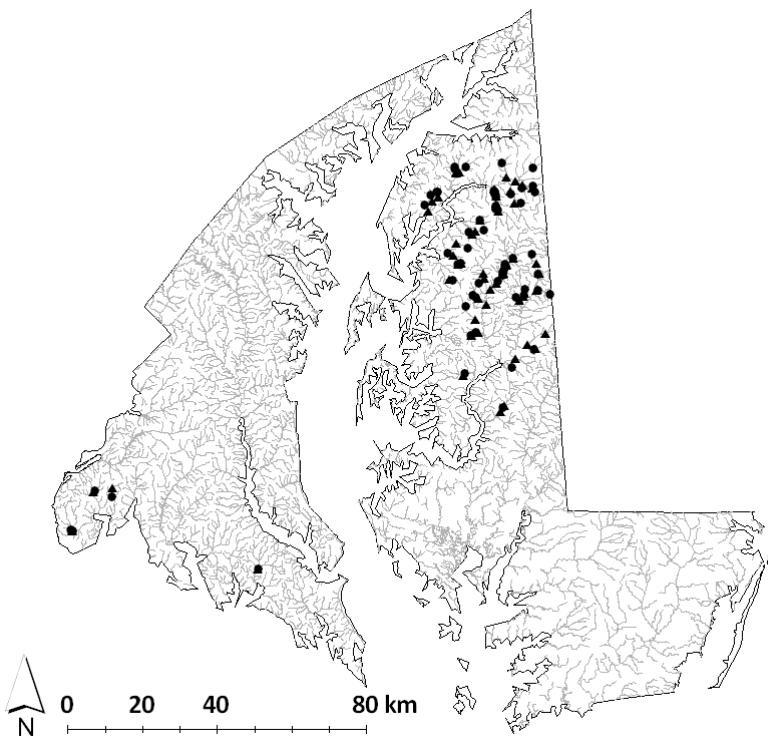
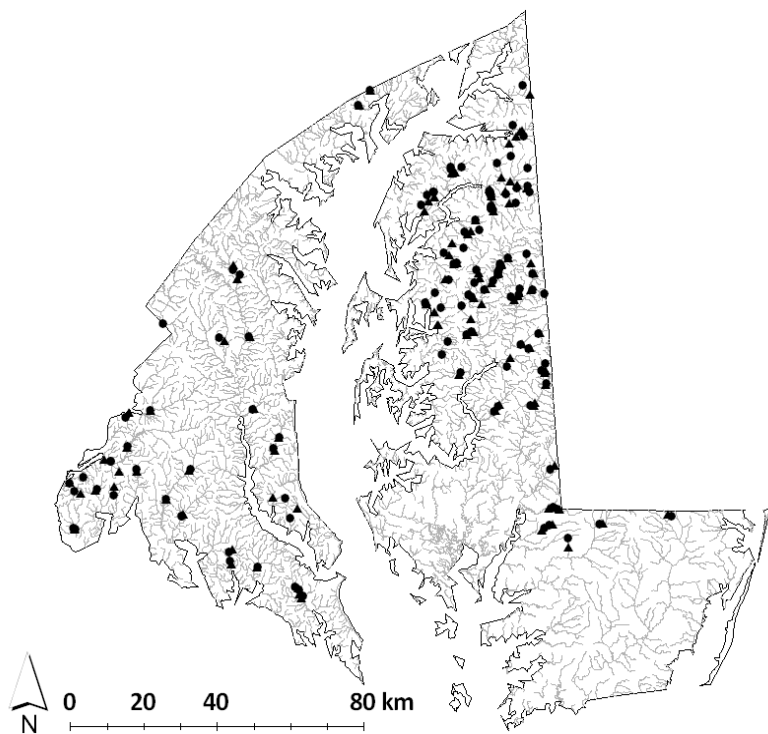
Community analyses used existing mussel and fish databases. Mussel community data came from the Maryland Natural Heritage Program freshwater mussel database. Data collection was from 1983 to 2007 and identified 19 species of bivalves (Table 2.1; Maryland Department of Natural Resources, unpublished data). I coded sites for analyses by recording each species as present or absent. Presence was identified by a record of a live animal, dead shell, or textual indication of presence (e.g., “abundant”); absence was assigned to all other entries. Sites were queried at two scales, the MCP and the subset of MCP streams found in the four systems that

contained *A. heterodon*. The finer scale dataset was used to narrow the range of environmental and, possibly, community heterogeneity to that found in *A. heterodon* river systems. This could potentially identify different biological communities and bivalve-landscape associations than found in the broader MCP which could be of use in predictive modeling. To identify mussel communities and limit the effect of rare species, only those mussel species found in  $\geq 2\%$  of the sites were used. This generated a database of 123 sites/13 species for the entire MCP and of 69 sites/9 species for the *A. heterodon* rivers (Table 2.1; Fig. 2.2). The 69 sites are a subset of the 123 MCP sites.

**Table 2.1** Scientific and common names of freshwater bivalves found within the Maryland Coastal Plain. Bolded species were found in  $\geq 2\%$  of the Coastal Plain sites and used in the broader scale community analyses. Species followed by a ‘\*’ were found in the subset of river systems that contain *A. heterodon* and included in the finer-scale community analyses.

<b>Scientific Name</b>	<b>Common Name</b>
<i>Alasmidonta heterodon</i>	<b>Dwarf wedgemussel*</b>
<i>Alasmidonta undulata</i>	<b>Triangle floater*</b>
<i>Anodonta implicata</i>	<b>Alewife floater*</b>
<i>Corbicula fluminea</i>	<b>Asian clam*</b>
<i>Elliptio complanata</i>	<b>Eastern elliptio*</b>
<i>Elliptio fisheriana</i>	<b>Northern lance*</b>
<i>Elliptio lanceolata</i>	<b>Yellow lance*</b>
<i>Elliptio producta</i>	<b>Atlantic spike</b>
<i>Lampsilis cardium</i>	Plain pocketbook
<i>Lampsilis cariosa</i>	Yellow lampmussel
<i>Lampsilis radiata</i>	<b>Eastern lampmussel</b>
<i>Leptodea ochracea</i>	<b>Tidewater mucket</b>
<i>Ligumia nasuta</i>	Eastern pondmussel
<i>Pyganodon cataracta</i>	<b>Eastern floater*</b>
<i>Pyganodon cataracta X</i>	Eastern floater X
<i>Rangia</i>	Common rangia
<i>Sphaeridae</i>	Peaclam; Fingernail clam
<i>Strophitus undulatus</i>	<b>Creeper*</b>
<i>Utterbackia imbecillis</i>	<b>Paper pondshell</b>





**Figure 2.2** The paired fish (circles) and mussel (triangles) sites used in the community analyses in A) the entire Maryland Coastal Plain and B) in the subset of river systems that contain *A. heterodon*.

Fish community data came from the Maryland Biological Stream Survey (MBSS; MD Department of Natural Resources), which provides a record of fish abundances. The database covers the years 1994 to 2004 and contains 90 fish species (MD Department of Natural Resources, unpublished data). I identified the MBSS fish site closest to each mussel site, allowing only unique pairings to ensure independence of sample sites. A mussel site with *A. heterodon* was given priority for linkage, followed by proximity to the closest fish site. Approximately 67% of the mussel-fish pairings were on the same or adjacent stream segments. To limit the effect of extremely rare species, community structure was evaluated using fish species present in  $\geq 5\%$  of the fish sites, resulting in 123 sites/32 species in the entire MCP and 69 sites/30 species in *A. heterodon* rivers (Fig. 2.2).

### 2.3.3 Environmental Databases

The stream segment database was developed from the National Hydrography Dataset Plus (NHDPlus; U.S. Environmental Protection Agency 2006), which was augmented by creating and incorporating land cover, land use, and geology layers; parameters that have previously been associated with the assemblage structure of mussels (Arbuckle and Downing 2002; McRae et al. 2004; Gagnon et al. 2006; Hopkins 2009; Weber and Schwarz 2011). The NHDPlus includes a stream network based on the 1:100,000 National Hydrography Dataset. Stream segments are contiguous, unbranched linear features that start and stop at decision points along the stream network (e.g., at the confluence of two streams/rivers). The NHDPlus contains hierarchical datasets for: stream segment, catchment (local area draining into each segment), and cumulative watershed (cumulative area draining into the bottom of

each segment). From the available attributes I selected those related to segment size, stream network position, streamflow, and climate.

Bedrock and surficial geology were obtained from the U.S. Geological Survey (Clawges and Price 1999; Dicken et al. 2005). I obtained land cover and impervious surfaces from the 2001 National Land Cover Database and Omernick Level III ecoregions from the Environmental Protection Agency (Yang et al. 2002; U.S. Environmental Protection Agency 2003; Homer et al. 2007). Water table depth, soil permeability, available water capacity, and organic matter data were obtained from the State Soil Geographic Database (U.S. Department of Agriculture 2008). I generated catchment and cumulative flowline values for these datasets with the Catchment Attribute Allocation & Accumulation Tool (CA3T version 1.009; U.S. Environmental Protection Agency 2008). All shapefiles were clipped to the study area and converted into 30 m grids (NAD83 projection) for use in the CA3T.

Stream crossings and blockages were incorporated at the catchment scale. Blockage data came from The National Inventory of Dams dataset (U.S. Army Corp of Engineers 2008) and the Maryland Department of Natural Resources (unpublished data). County level stream crossing data came from the 2000 Census Tiger/Line data (U.S. Census Bureau 2001) and were intersected with the NHDPlus stream network to produce point coverages of stream crossings. The number of blockages and total stream crossings (road and railroad) in each local catchment were determined using Hawth's Analysis Tools for ArcGIS (version 3.27; Beyer 2004). A summary of database attributes can be found in Table 2.2. Each mussel sample site was associated

with the closest stream segment using linear referencing in ArcGIS (version 9.2, ESRI, Redlands).

**Table 2.2** Hierarchical attributes in the stream segment database. Data are at three scales: segment (S), catchment (local area draining into the stream segment; L) or cumulative watershed (cumulative area draining into each segment; C). The code used for each variable follows its name in the attribute column. Classification and description of the land cover attributes is taken from the 2001 National Land Cover Dataset.

Attribute and Code	Description	Scale
Slope (m/m); S	Slope of segment	S
Length (km); L	Length of segment	S
Stream order; SO	Strahler stream order of the segment from the NHDPlus	S
Maximum elevation (m); MAE	Maximum elevation of segment (smoothed)	S
Minimum elevation (m); MIE	Minimum elevation of segment (smoothed)	S
Mean annual flow (cfs); MAF	Mean annual flow at bottom of segment calculated by the unit runoff method	C
Mean annual velocity (fps); MAV	Mean annual velocity at bottom of segment computed by Jobson method	C
Incremental flow (cfs); IF	Incremental flow for the segment as computed by the unit runoff method	C
Temperature (°C*10); MAT	Mean annual air temperature	L,C
Precipitation (mm); MAP	Mean annual precipitation	L,C
Area (sq.km); DA	Cumulative drainage area	C
Blockages (#); B	Dams, culverts, etc.	L
Stream crossings (#); SC	Road and railroad crossings	L
Open water (%); OW	Area classified as open water, generally with less than 25% cover of vegetation/land cover.	L,C
Developed, open space (%); DOS	Area classified as developed open space, including areas with some constructed materials but mostly vegetation (law grasses). Impervious surfaces are generally < 20% of the total cover.	L,C
Developed, low intensity (%); DLI	Area classified as developed, low intensity, including areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 20-49% of the total cover.	L,C
Developed, medium intensity (%); DMI	Area classified as developed, medium intensity, including areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 50-79% of the total cover.	L,C
Developed, high intensity (%); DHI	Area classified as developed, high intensity, including areas where people reside or work in high numbers. Impervious surfaces account for 80-100% of the total cover.	L,C
Barren land (%); BL	Area classified as rock, sand, or clay where vegetation generally accounts for <15% of total cover.	L,C
Deciduous forest (%); DF	Area classified as deciduous forest: areas dominated by trees where 75% or more of the tree species shed foliage simultaneously in response to seasonal change.	L,C

Evergreen forest (%); EF	Area classified as evergreen forest: areas dominated by trees where 75% or more of the tree species maintain their leaves all year. Canopy is never without green foliage.	L,C
Mixed forest (%); MF	Area classified as mixed forest with areas dominated by trees where neither deciduous nor evergreen species represent more than 75% of the cover present.	L,C
Pasture/hay (%); PH	Area classified as pasture/hay: areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops. Pasture/hay vegetation accounts for >20% of total vegetation.	L,C
Cultivated crops (%); CC	Area classified as cultivated crops: areas used for the production of annual crops (corn, soybeans, vegetables, tobacco, and cotton), perennial woody crops (orchards and vineyards), or land being actively tilled. Crop vegetation accounts for >20% of total vegetation.	L,C
Woody wetlands (%); WW	Area classified as woody wetlands: areas where forest or shrubland vegetation accounts for >20% of the vegetative cover and the soil or substrate is periodically saturated with or covered with water.	L,C
Emergent herbaceous wetlands (%); EHW	Area classified as emergent herbaceous wetlands: areas where perennial herbaceous vegetation accounts for >80% of the vegetative cover and the soil or substrate is periodically saturated with or covered with water.	L,C
Impervious surfaces (%); IS	Area classified as impervious surfaces	L,C
Backshore deposits (%); BD	Area classified as backshore deposits	L,C
Floodplain & alluvium terraces (%); FAGT	Area classified as floodplain and alluvium gravel terraces	L,C
Loam (%); LOAM	Area classified as loam; texture variable, ranging from sand to clay, mostly non-swelling clay mineral, kaolinite	L,C
Tertiary and Quarternary-aged gravels (%); TQG	Area classified as upper Tertiary and Quarternary-aged gravels	L,C
Micaceous residuum (%); MRC	Area classified as Micaceous residuum; clay, mostly kaolinite	L,C
Massive kaolinitic clay (%); MKC	Area classified as clay residuum; mostly massive kaolinitic	L,C
Miocene (%); MIO	Area classified as Miocene	L,C
Paleocene (%); PAL	Area classified as Paleocene	L,C
Eocene (%); EO	Area classified as Eocene	L,C
Pleistocene (%); PLE	Area classified as Pleistocene	L,C
Upper Cretaceous (%); UC	Area classified as Upper Cretaceous	L,C
Lower Cretaceous (%); LC	Area classified as Lower Cretaceous	L,C
Ultramafic rocks (%); UR	Area classified as ultramafic rocks	L,C
Paleozoic maric intrusives (%); PMI	Area classified as Paleozoic maric intrusives	L,C
Cambrian eugeosynclinal (%); CE	Area classified as Cambrian eugeosynclinal	L,C
Cambrian volcanics (%); CV	Area classified as Cambrian volcanics	L,C
Orthogneiss (%); OR	Area classified as orthogneiss	L,C
Middle Atlantic Coastal Plain (%); MACP	Area classified in Mid-Atlantic Coastal Plain ecoregion	L,C
Northern Piedmont (%); NP	Area classified in Northern Piedmont ecoregion	L,C
Southeastern Plains (%); SP	Area classified in Southeastern Plains ecoregion	L,C

Water table depth (ft); WTD	Average depth to the water table	L,C
Soil permeability (in/hr); PERM	Average soil permeability	L,C
Available water capacity (inches/in); AWC	Average available water capacity	L,C
Organic matter (% by weight); OM	Average organic matter	L,C

#### 2.3.4 Data Analyses

Mussel community structure was identified by hierarchical agglomerative cluster analysis (Lance and Williams 1967). Each cluster analysis used flexible beta as the linkage method (with  $\beta = -0.25$ ) and a Sørensen (Bray-Curtis) distance measure. Flexible beta is a space-conserving method that allows for user control of its space-distorting properties; setting  $\beta = -0.25$  generates results similar to Ward's method, but is compatible with the Sørensen distance measure commonly used in biological community analyses (Legendre and Legendre 1998; McCune and Grace 2002). For each scale (MCP and the subset of MCP rivers with *A. heterodon*) a series of cluster analyses were performed across a large number of cluster levels and indicator species analysis was used to identify the best cluster level (PC-ORD© version 5, MjM Software Design, Gleneden Beach, OR).

Indicator species analysis (ISA; Dufrêne and Legendre 1997) combines information on the concentration of species abundance and faithfulness of occurrence within a particular group (e.g., cluster groupings or habitat types) to generate indicator values (IVs) for each species in each group (McCune and Grace 2002). Both abundance and binary data can be used for ISA (Dufrêne and Legendre 1997; Bakker 2008). These IVs range from 0 (not indicative) to 100 (highly indicative), with the highest IV for each species indicating cluster membership. Statistical significance of the IV is tested using a Monte Carlo method. An ISA was conducted at multiple

clustering levels and the average of the maximum indicator values over all species was calculated. The cluster level that maximized the indicator value was chosen as the best level of community structure and the appropriate indicator species assigned to each cluster for that level (Walsh et al. 2007b). Mussel clusters were identified across the entire MCP and in the subset of sites found in the four systems that contained *A. heterodon*. To identify fish species indicative of each mussel cluster, the abundance of each fish species at each site was used in an ISA of the final mussel clusters at each scale. Those species with a maximum indicator value with  $P \leq 0.05$  were identified as indicators for the corresponding cluster (in both the mussel and fish analyses).

Nonmetric multidimensional scaling (NMS) was used to identify associations between mussel clusters and landscape features. I conducted an NMS analysis using the mussel community data sets used for the cluster analyses. To ensure data independence, only unique pairings of mussel and stream segments were allowed. Where multiple mussel sites occurred on a stream segment, priority was given to sites with *A. heterodon* occurrence. This procedure reduced the number to 101 (entire MCP) and 51 (subset of region in *A. heterodon* rivers) sites/segments for analysis. An NMS was performed at each scale using the slow and thorough autopilot mode with the following options: a Sørensen distance measure; maximum number of axes = 6; a random starting configuration; 250 runs with real data; maximum number of iterations = 500; and a stability criterion of 0.00001 (PC-ORD© version 5, MjM Software Design, Gleneden Beach, OR). The number of dimensions chosen for the final solution minimized stress and produced a stable solution. A non-parametric

Spearman correlation was used to identify landscape features associated with each ordination axis (R version 2.7.2, R Foundation for Statistical Computing, Vienna, Austria). Mussel cluster assignments were overlaid onto each ordination plot for visual analysis.

## 2.4 Results

### 2.4.1 Mussel Community Structure

Community structure for mussels within the entire MCP was best described with six clusters (Table 2.3; Fig. 2.3a). *Pyganodon cataracta* ( $IV = 43.0$ ) and *Leptodea ochracea* ( $IV = 6.2$ ; NS) formed cluster 1 and *Anodonta implicata* ( $IV = 96.9$ ), *Lampsilis radiata* ( $IV = 10.2$ ; NS), and *Utterbackia imbecillis* ( $IV = 9.9$ ; NS) formed cluster 2. Two *Elliptio* clusters were formed, cluster 3 with *Elliptio complanata* ( $IV = 24.0$ ) and *Elliptio producta* ( $IV = 8.3$ ; NS) and cluster 4 with *Elliptio fisheriana* ( $IV = 51.9$ ), *Alasmidonta undulata* ( $IV = 16.1$ ), and *Elliptio lanceolata* ( $IV = 16.1$ ; NS). The invasive bivalve *Corbicula fluminea* formed cluster 5 ( $IV = 64.0$ ) and *A. heterodon* ( $IV = 84.7$ ) with *Strophitus undulatus* ( $IV = 15.8$ ; NS) formed cluster 6.

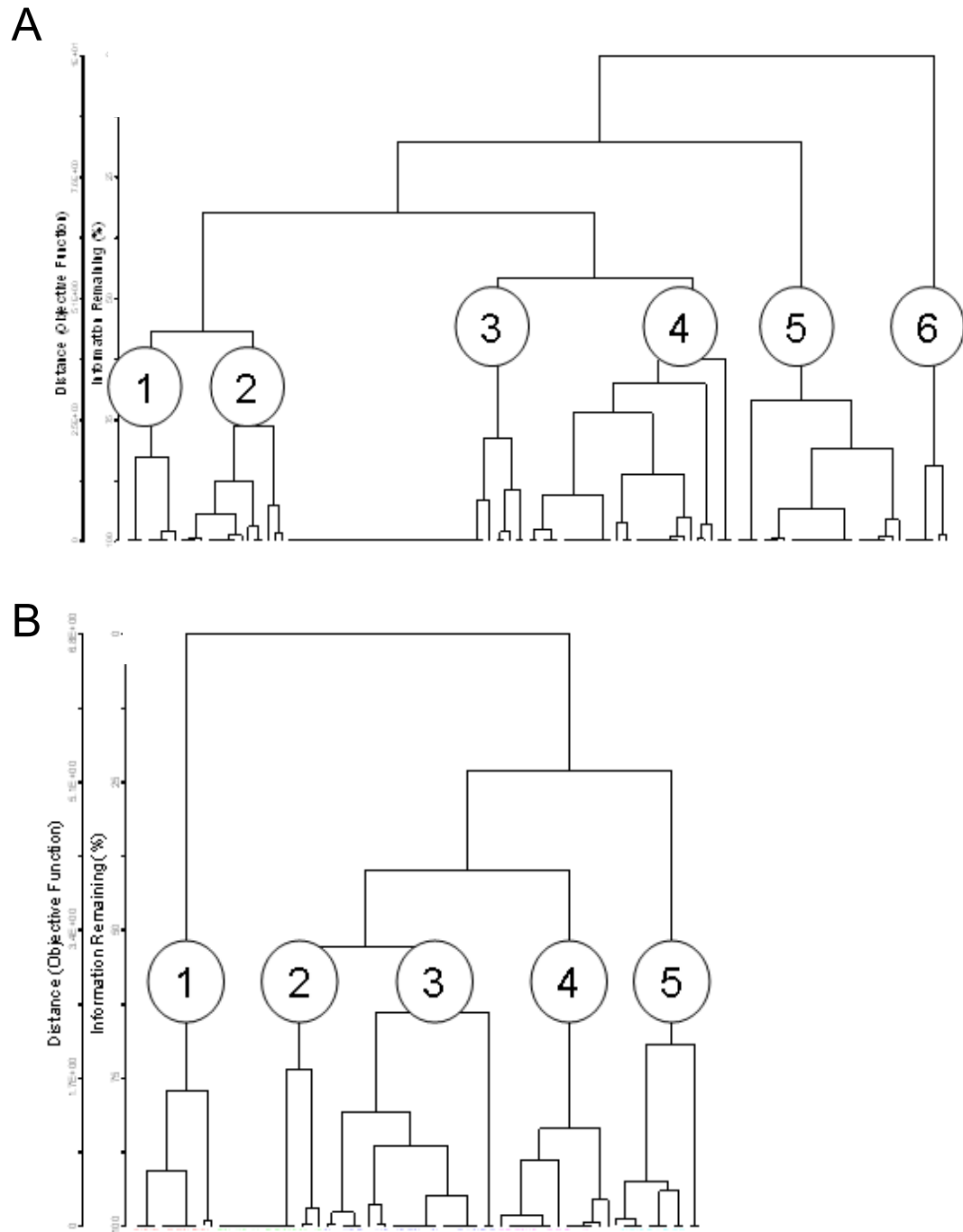
Mussel community structure within the subset of river systems containing *A. heterodon* was best described with five clusters that resembled those of the larger Coastal Plain (Table 2.3; Fig. 2.3b). Cluster 1 consisted of *A. heterodon* ( $IV = 87.5$ ) and *S. undulatus* ( $IV = 8.7$ ; NS). Two *Elliptio* clusters were identified: *E. complanata* ( $IV = 25.8$ ) and *E. lanceolata* ( $IV = 16.3$ ; NS) formed cluster 2 and *E. fisheriana* ( $IV = 51.1$ ) and *A. undulata* ( $IV = 23.8$ ) formed cluster 3. Cluster 4 consisted solely of *C.*



*fluminea* ( $IV = 68.7$ ). Cluster 5 consisted of *P. cataracta* ( $IV = 75.0$ ) and *A. implicata* ( $IV = 25.8$ ).

**Table 2.3** Mussel assemblages and fish indicators found across the entire Maryland Coastal Plain and in the subset of river systems containing *A. heterodon*. Mussel significance was determined using  $P \leq 0.05$ . Only fish indicators significant at  $P \leq 0.05$  are shown.

Group	# Sites	Mussel Indicator	<i>IV</i>	<i>P</i>	Fish Indicator	<i>IV</i>	<i>P</i>
Coastal Plain							
1	7	<i>Pyganodon cataracta</i>	43.0	0.0004	<i>Gambusia holbrooki</i>	48.5	0.0002
		<i>Leptodea ochracea</i>	6.2	NS	<i>Ameiurus nebulosus</i>	38.5	0.0200
					<i>Lepomis cyanellus</i>	22.9	0.0264
2	14	<i>Anodonta implicata</i>	96.9	0.0002			
		<i>Lampsilis radiata</i>	10.2	NS			
		<i>Utterbackia imbecillis</i>	9.9	NS			
3	33	<i>Elliptio complanata</i>	24.0	0.0002			
		<i>Elliptio producta</i>	8.3	NS			
4	23	<i>Elliptio fisheriana</i>	51.9	0.0002			
		<i>Alasmidonta undulata</i>	16.1	0.0492			
		<i>Elliptio lanceolata</i>	16.1	NS			
5	19	<i>Corbicula fluminea</i>	64.0	0.0002			
6	5	<i>Alasmidonta heterodon</i>	84.7	0.0002	<i>Esox americanus</i>	42.3	0.0206
		<i>Strophitus undulatus</i>	15.8	NS	<i>Percina peltata</i>	27.9	0.0084
<i>A. heterodon</i> Rivers							
1	7	<i>Alasmidonta heterodon</i>	87.5	0.0002	<i>Notropis chalybaeus</i>	27.5	0.0054
		<i>Strophitus undulatus</i>	8.7	NS			
2	13	<i>Elliptio complanata</i>	25.8	0.0014			
		<i>Elliptio lanceolata</i>	16.3	NS			
3	14	<i>Elliptio fisheriana</i>	51.1	0.0002			
		<i>Alasmidonta undulata</i>	23.8	0.0088			
4	8	<i>Corbicula fluminea</i>	68.7	0.0002			
5	9	<i>Pyganodon cataracta</i>	75.0	0.0002			
		<i>Anodonta implicata</i>	25.8	0.0064			



**Figure 2.3** Mussel community structure within A) the entire Maryland Coastal Plain and B) in the subset of river systems that contain *A. heterodon*. Community structure for mussels within the Maryland Coastal Plain was best described with six clusters: 1) *Pyganodon cataracta*; 2) *Anodonta imbecilis*; 3) *Elliptio complanata*; 4) *Elliptio fisheriana*; 5) *Corbicula fluminea*; and 6) *A. heterodon*. Mussel community structure within river systems containing *A. heterodon* was best described with five clusters: 1) *A. heterodon*; 2) *E. complanata*; 3) *E. fisheriana*; 4) *C. fluminea*; and 5) *P. cataracta*. The mussels indicated are the predominant one in their respective cluster (i.e., had the largest indicator value).

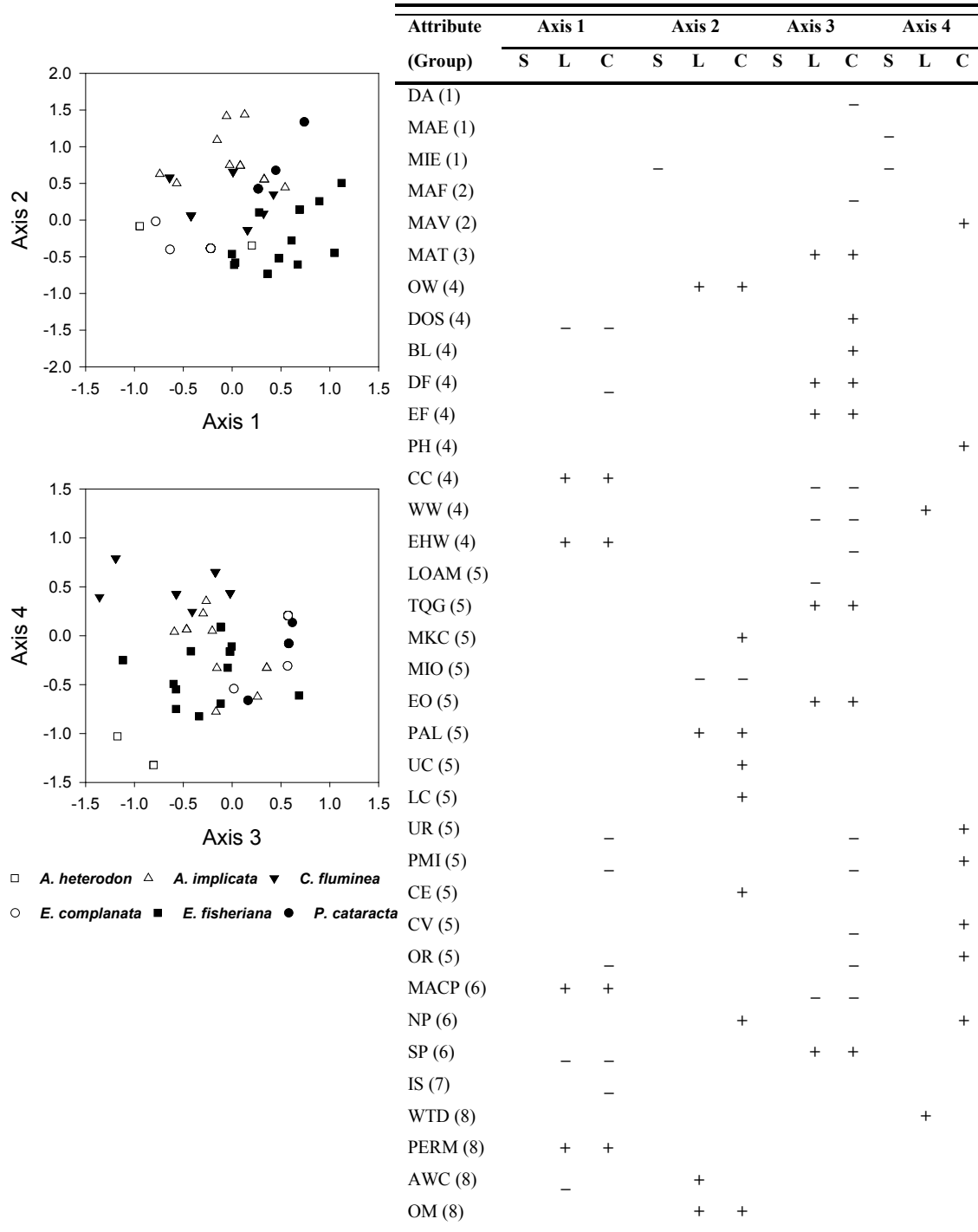
In each cluster, one species had a much larger indicator value than the other species in the cluster. That species will represent the cluster throughout the remainder of the paper (e.g., *A. heterodon* cluster).

#### 2.4.2 Fish Indicators of Mussel Species or Assemblages

The majority of fish species were not significant indicators of mussel clusters (at  $P \leq 0.05$ ; Table 2.3). In the Coastal Plain, five fish species were indicative of two mussel clusters (Table 2.3). *Gambusia holbrooki* (mosquitofish;  $IV = 48.5$ ), *Ameiurus nebulosus* (brown bullhead;  $IV = 38.5$ ), and *Lepomis cyanellus* (green sunfish;  $IV = 22.9$ ) were indicative of the *P. cataracta* cluster. *Esox americanus* (redfin pickerel;  $IV = 42.3$ ) and *Percina peltata* (shield darter;  $IV = 27.9$ ) were indicative of the *A. heterodon* cluster in the MCP. In the *A. heterodon* rivers, *Notropis chalybaeus* (ironcolor shiner;  $IV = 27.5$ ) was indicative of the *A. heterodon* cluster. *Etheostoma olmstedi* (tessellated darter) is a known host for *A. heterodon* (Michaelson and Neves 1995) and was a non-significant indicator of the *A. heterodon* cluster in the Coastal Plain.

#### 2.4.3 Mussel Assemblage Associations with Landscape Features

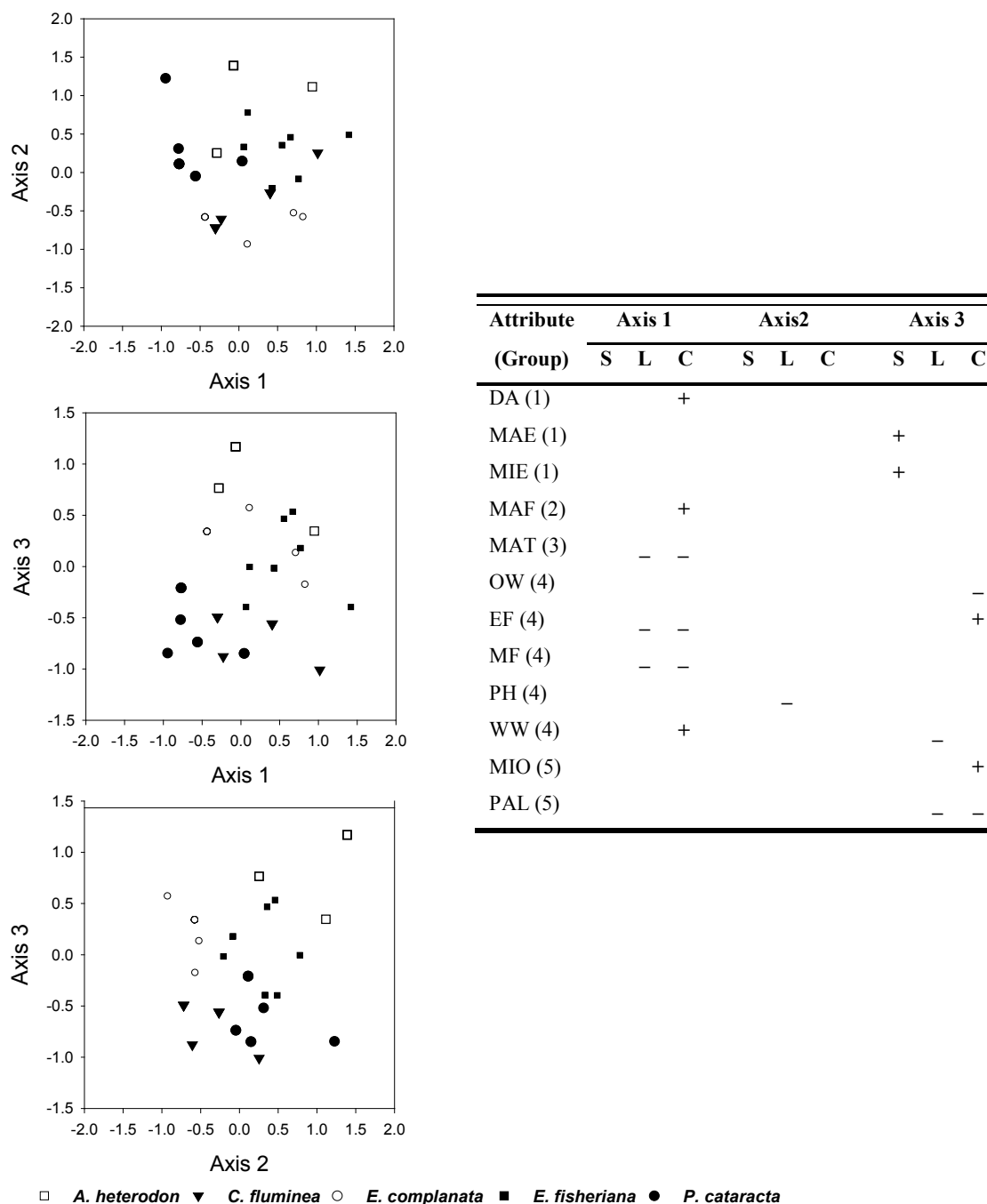
*Coastal Plain.*— The 4-dimensional solution was the best solution (a subset of plots is shown in Fig. 2.4). The final stress of the 4-dimensional solution was 7.398 with a final instability of  $< 10^{-4}$  over 278 iterations. Ordination axes were strongly correlated with land cover, bedrock and surficial geology, soil characteristics, mean annual air temperature, and ecoregion (Fig. 2.4). All axes indicated a general separation between ecoregions, primarily between the Delmarva Peninsula and Western Shore. Axis 1 separated communities according to land cover; Axis 2



**Figure 2.4** Ordination plots for mussel communities across the Maryland Coastal Plain. Mussel with largest indicator value in cluster is shown. The table shows significant attributes associated with each axis ( $P \leq 0.05$ ). Positive (+) or negative (-) signs indicate the direction of the relationship. Attributes are at three scales: segment (S); catchment (local area draining into segment (L); or cumulative watershed (cumulative area draining into segment (C). Attribute codes and descriptions are provided in Table 2.2. Attribute groups are numbered as follows: 1) drainage area/elevation; 2) flow/velocity; 3) temperature; 4) landuse/cover; 5) surficial/ bedrock geology; 6) ecoregion; 7) impervious surfaces; and 8) soil characteristics.

separated sites according to bedrock geology (Miocene sediments versus older-aged rocks; Fig. 2.4). Axis 3 separated sites according to development, land cover, surficial and bedrock geology, ecoregion, and Delmarva or Western Shore position (Fig. 2.4). Axis 4 indicated sites in the Northern Piedmont ecoregion with pasture/hay and woody wetland land cover with older bedrock geology (Fig. 2.4).

The *E. complanata* cluster was predominantly associated with the Southeastern Plains ecoregion in the Western Shore (Fig. 2.4). Sites within this cluster were generally warm with a mix of forested, low intensity residential, and barren lands, underlain by Miocene and older-aged sediments. The *P. cataracta*, *A. implicata*, and *C. fluminea* clusters were associated with open water and older-aged sediments. *P. cataracta* was associated with Paleocene-aged sediments in the Northern Piedmont ecoregion, cultivated croplands with permeable soils and emergent wetlands in the Coastal Plain ecoregion, and sites with warmer air temperatures, Tertiary and Quaternary gravels, and a mix of land covers in the Southeastern Plains ecoregion (Fig 2.4). *A. implicata* was primarily associated with the Paleocene-aged sediments in the Northern Piedmont ecoregion and *C. fluminea* with a mix of wetland and agricultural lands in the Northern Piedmont and Coastal Plain ecoregions (Fig. 2.4). The *E. fisheriana* and *A. heterodon* clusters were both strongly associated with agricultural lands and wetland areas in the Coastal Plain ecoregion (Fig. 2.4) The *E. fisheriana* cluster was found only on the Delmarva Peninsula in sites with permeable soils, while the *A. heterodon* cluster was associated with loam deposits and higher elevations (Fig. 2.4).



**Figure 2.5** Ordination plots for mussel communities in the subset of Maryland Coastal Plain river systems that contain *A. heterodon*. The mussels shown are the predominant one in the cluster. Significant attributes associated with each axis ( $P \leq 0.05$ ) are shown in the table. Positive (+) or negative (-) signs indicate the direction of the relationship. Attributes are at three scales: segment (S); catchment (local area draining into segment (L); or cumulative watershed (cumulative area draining into segment (C). Attribute codes and descriptions are provided in Table 2.2. Attribute groups are numbered as follows: 1) drainage area/elevation; 2) flow; 3) temperature; 4) landuse/ landcover; and 5) bedrock geology.

*A. heterodon rivers*. — The 3-dimensional solution was the best solution (Fig. 2.5). The final stress of the 3-dimensional solution was 11.56 with a final instability of  $< 10^{-4}$  over 165 iterations. Ordination axes were strongly correlated with land cover, bedrock geology, temperature, and location within the stream network (Fig. 2.5). Axis 1 separated forested from wetland sites (Fig. 2.5). Axis 2 was negatively correlated with pasture/hay lands, while Axis 3 separated open water sites underlain by Paleocene, often glauconitic, sediments from higher-elevation forested sites with Miocene sediments (Fig. 2.5).

The *P. cataracta* and *C. fluminea* clusters were associated with open water or woody wetland areas with Paleocene-aged sediments (Fig. 2.5). The *E. complanata* cluster was associated with pasture/hay lands. The *E. fisheriana* cluster was associated with sites having larger drainage areas and woody wetlands, while the *A. heterodon* was associated with non-pasture/hay lands, forests, higher elevations, and Miocene-aged sediments (Fig. 2.5).

## 2.5 Discussion

Community analyses were performed to identify biological and landscape surrogates to enhance predictive modeling of *A. heterodon* distribution within the MCP. Both the entire MCP and the subset of river systems containing *A. heterodon* exhibited similar mussel assemblages. The primary difference was the joining of *P. cataracta* and *A. implicata* into a single cluster at the finer scale (*A. heterodon rivers*) and the loss of the majority of species deemed not-significant at the broader scale (MCP). Mussel assemblages were associated with landscape variables occurring at three scales: segment, local catchment, and cumulative watershed.

### 2.5.1 Mussel Community Structure and Landscape Associations

*P. cataracta* and *A. implicata* generally clustered together. Both species lack hinge teeth (Martin 1997; Strayer and Jinka 1997) and can be difficult to distinguish from one another. I found *P. cataracta* and *A. implicata* clusters in watersheds with open water (defined as having less than 25% cover of vegetation/land cover), often associated with agricultural or wetland areas. These species can “float” on soft muddy and silty substrates, and both can occur in ponds and lakes (Martin 1997; Locke et al. 2003). *P. cataracta* is tolerant of warm water temperatures, low dissolved oxygen, and eutrophic conditions and in rivers it is found in natural or manmade impoundments (Dimock and Wright 1993; Locke et al. 2003). *A. implicata* can occur in coastal ponds near tidally influence waters (Martin 1997).

The invasive clam *C. fluminea* is found in many major U.S. waterways. I found *C. fluminea* in its own cluster associated with open water areas in agricultural or wetland settings underlain by pre-Miocene rocks. The species is taxonomically different from the freshwater mussel species in the MCP. Its rapid growth, early sexual maturity, short life span, high fecundity, extensive dispersal capacities, and tolerance of human-modified streams create a successful invader (McMahon 2002). *C. fluminea* can quickly recover after disturbances (McMahon 1999). In contrast, native mussel populations recover slowly after habitat disturbances, which make them susceptible to human activities (McMahon and Bogan 2001; Sethi et al. 2004; Strayer et al. 2004).

*E. complanata* was not associated with any other mussel species and had the lowest *IV* score among the major mussel indicator species (*IV* = 24.0) suggesting a



lack of faithfulness to the cluster. Widespread species such as *E. complanata*, generally have the highest indicator values when all sites are in one group, with indicator values decreasing as the number of clusters increases (Dufrêne and Legendre 1997). Considered a habitat generalist, it was the species most strongly associated with a mix of land-use types within the Southeastern Plains ecoregion and tended toward larger streams with pasture/hay within *A. heterodon* rivers. *E. complanata* communities were also associated with large watersheds in the Delaware and Susquehanna River basins and have been predicted to occur in large streams throughout the Atlantic Slope (Strayer 1993; Walsh et al. 2007a). *E. complanata* is a member of the subfamily Amblesminae which was associated with forested riparian zones in southwestern Ontario while *E. complanata* communities were associated with forested watersheds in the Delaware River basin (Morris and Corkum 1996; Walsh et al. 2007a). The species has also been found in low gradient portions of rivers with adjacent wetlands in a tributary of the upper Connecticut River (E. Nedeau, unpublished data).

The second *Elliptio* cluster consisted of *E. fisheriana* and *A. undulata*. This cluster was associated with high elevation agricultural watersheds with wetlands. *E. fisheriana* communities in the Susquehanna and Potomac River basins were associated with forested landscapes and sandstone, shale, and calcareous sedimentary rocks (Walsh et al. 2007a). In my study, *E. fisheriana* was found only in the Delmarva Peninsula, an area with a long agricultural history (Benitez and Fisher 2004). Walsh et al. (2007a) associated the *E. fisheriana* community with dams and nutrient point sources. The species is one that can regulate its rate of oxygen

consumption which might allow it to survive in impoundments or eutrophic areas (Chen et al. 2001). *A. undulata* can tolerate standing water and can be found in a variety of habitats, including impoundments associated with dams (Strayer 1993; Nedeau 2008).

*A. heterodon* was not significantly associated with any other mussel species. Across the MCP the *A. heterodon* cluster was associated with higher elevation sites within the Coastal Plain ecoregion, cultivated crop and wetland land uses, loamy soils, and a mix of rock-types. Within the subset of this region found in *A. heterodon* rivers, the cluster was also associated with Miocene-aged sediments draining forested, rather than pasture/hay lands. *A. heterodon* generally occurs in low gradient reaches with fine sediment (sand), moderate depths, and slow to moderate flows that are temporally stable (Strayer and Ralley 1993; Michaelson and Neves 1995; Maloney et al. 2012; W. Lellis, USGS, unpublished data). *A. heterodon* distributions have also been associated with low calcium concentration (Strayer 1993). Within the low relief Coastal Plain, *A. heterodon* are primarily found in Tertiary sediments composed of well drained upland deposits, suggesting that geology might be a controlling factor (Preston 2000; Schmidt 1993). Within this setting, the species could occur where suitable local stream chemistry and morphology are maintained.

#### 2.5.2 Biological Surrogates

Only two mussel clusters were associated with fish species: the *P. cataracta* cluster across the MCP and the *A. heterodon* cluster at both scales. *G. holbrooki*, *A. nebulosus*, and *L. cyanellus* were indicative of the *P. cataracta* cluster. All three fish species are found in pools and backwaters in creeks and streams, as well as in ponds,

lakes, and reservoirs (Jenkins and Burkhead 1993). *A. nebulosus* is tolerant of low pH (< 5; Schofield and Driscoll 1987). *G. holbrooki* is found in the lowlands, usually over muddy or sandy substrates, and can occur in inhospitable environments such as warm springs, near-anaerobic conditions, and brackish waters with salinities up to 25‰ (Hardy 1978; Jenkins and Burkhead 1993; Nordlie and Mirandi 1996). *P. cataracta* is able to survive in warm, eutrophic conditions with low dissolved oxygen (Dimock and Wright 1993), thus these fish species could be potential surrogate species.

*E. americanus* and *P. peltata* were indicative of the *A. heterodon* cluster across the MCP, whereas only *N. chalybaeus* was indicative of the cluster in the subset of the region found in *A. heterodon* rivers. *E. americanus* occupies sloughs, drainages ditches, backwater areas of faster moving streams, and sluggish streams and thrives in darkly stained waters of low pH (Jenkins and Burkhead 1993). These habitats are not conducive to *A. heterodon* survival. Although it is one of the most widespread species of the *Percina* genus, *P. peltata* is uncommon in Maryland and *N. chalybaeus* is listed as an endangered species (Jenkins and Burkhead 1993; Maryland Natural Heritage Program 2010; Ciccotto and Stranko 2011). Both species are insectivores, inhabit low gradient, clear creeks, use substrate of sand to fine gravel for egg development, and are intolerant of stream degradation (Jenkins and Burkhead 1993; Hall et al. 1996). These life-history characteristics suggest that the two species may inhabit a habitat niche similar to *A. heterodon*, but their rarity within the MCP makes them unsuitable surrogates for *A. heterodon*.

### 2.5.3 Conclusion

I did not find *A. heterodon* to be significantly associated with other mussel species in the MCP. *E. olmstedii* is a known host for *A. heterodon* (Michaelson and Neves 1995), but was non-significantly associated with the *A. heterodon* cluster possibly due to its widespread distribution in the MCP (Maryland Department of Natural Resources, unpubl. data). Two significant indicators of the *A. heterodon* cluster were *P. peltata* and *N. chalybaeus*. Their rarity makes them unsuitable surrogates for predicting *A. heterodon* distribution. While the species are not known hosts of *A. heterodon*, they may be associated with the cluster due to use of a similar habitat niche which suggests that the three species may have declined from a loss of essential habitat. These results suggest that landscape models using habitat-based surrogates that incorporate the geologic, geographic, and land use characteristics of a locale and its drainage area might be preferable to models using biological surrogates for predicting *A. heterodon* distributions within the MCP.

## Chapter 3: Using maximum entropy to predict suitable habitat for the endangered dwarf wedgemussel in the Maryland Coastal Plain

### 3.1 Abstract

Species distribution modeling is needed for the conservation of rare and endangered species. I used a machine learning approach (maximum entropy) to model occurrences and suitable habitat for the federally-endangered dwarf wedgemussel, *Alasmodonta heterodon*, in Maryland's Coastal Plain watersheds. Landscape-scale predictors (e.g., land cover, land use, soil characteristics, geology, and climate) were used to predict the suitability of individual stream segments for *A. heterodon*. The best model contained variables at three scales: minimum elevation (segment scale), percent Tertiary deposits, low intensity development, and woody wetlands (local catchment), and percent low intensity development, pasture/hay agriculture, and average depth to the water table (cumulative watershed). Despite a very small sample size due to *A. heterodon*'s rarity, cross-validated prediction accuracy was 91%. Most predicted suitable segments occur in watersheds not known to contain *A. heterodon*. This identification provides opportunities for new discoveries or potential (re)introductions.

### 3.2 Introduction

Species distribution modeling is useful for many conservation purposes, such as identifying habitat for rare and endangered species. Predicting suitable habitat at the landscape scale is difficult due to ecosystem complexity, disparities in the

effective scale of environmental variables, and method of collection of species data (Huston 2002). Rare species may occur in sparse and fragmented populations that are difficult to locate. Models based on these small populations may have little predictive power or be non-transferable to other systems (Strayer 2008). Known distributions of rare species often provide the only available data to: (1) identify suitable habitat to guide surveys for undiscovered populations and (2) forecast potential impacts of human activities and global change on species habitat. I used species distribution models to identify suitable habitat for a federally endangered freshwater mussel, *Alasmidonta heterodon*.

Previous attempts to predict unionid occurrence have used linear-response models (e.g., regression models and discriminant analyses) that were statistically significant but had low predictive power (Strayer 1993; Strayer and Ralley 1993; Arbuckle and Downing 2002). The underlying assumptions of a linear response and multivariate normal distributions in these models are often not met in species-environment relationships (Strayer and Ralley 1993; De'ath and Fabricius 2000; McCune and Grace 2002; Gotelli and Ellison 2004). Modeling techniques that incorporate nonlinear relationships have been used to quantify bivalve-habitat relationships (Gray et al. 2005) and often have greater predictive power than linear models (Steuer et al. 2008; Zigler et al. 2008; Hopkins 2009). Maximum entropy (maxent) modeling is a non-linear method particularly suited for species distribution modeling where presence-only species data are available (Hernandez et al. 2006; Pearson et al. 2007). Therefore, it could be suitable for modeling distributions of freshwater mussel species (Weber and Schwartz 2011; Wilson et al. 2011).

Maxent is a machine learning approach that incorporates the maximum-entropy principle; estimating a target distribution by finding the distribution that is closest to uniform (i.e., maximum entropy) subject to given constraints (Jaynes 1957). The application of the method to species distribution modeling has been described from both machine learning (Phillips et al. 2006) and statistical (Elith et al. 2011) viewpoints. Maxent uses species occurrence data and environmental data derived from a geographic information system (GIS) to predict suitable habitat for a species. Environmental data is typically supplied as grids of pixels (i.e., environmental conditions in a cell; Phillips et al. 2006), but vector-based data (i.e., environmental data associated with a stream segment) can also be used (Elith et al. 2011).

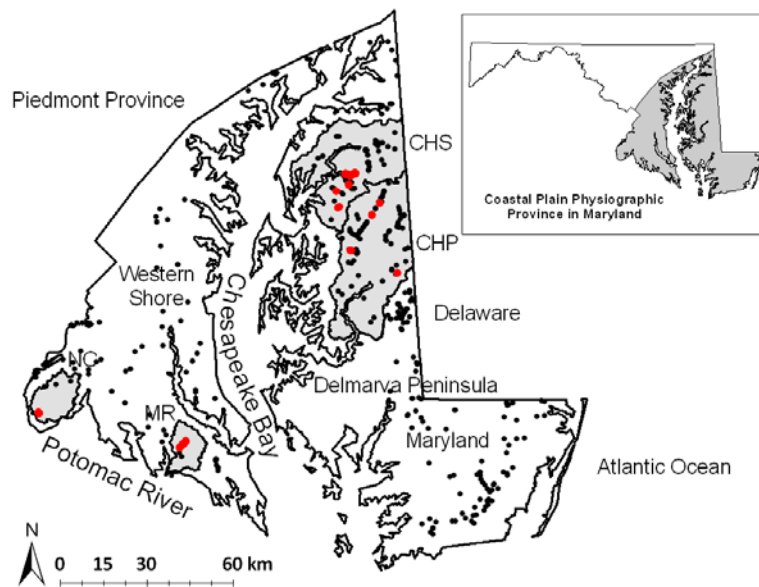
*A. heterodon* is endemic to Atlantic Slope drainages and populations are declining due to stream impoundments and channel alteration, pollution, and likely other, unknown factors (U.S. Fish and Wildlife Service 1993, 2007; Locke et al. 2003). The mussel is difficult to find due to its small size, tendency to close quickly in response to shadows or movement, typically sparse population densities, and its fragmented distribution (Strayer et al. 1996; W.A. Lellis, U.S. Geological Survey, unpublished data). Locating additional populations of the species is constrained by the effort required to conduct snorkel surveys of all streams within its range, but predictive modeling may help prioritize streams for sampling. The Coastal Plain of Maryland has a long history of agriculture development, human population expansion, and groundwater withdrawals (Hamilton et al. 1991; Benitez and Fisher 2004; Fisher et al. 2006) and identifying suitable stream reaches for *A. heterodon* is important for both conservation planning and for directing targeted sampling. Using a

maxent approach, my objective was to determine if landscape variables could predict suitable habitat for *A. heterodon* in the Maryland Coastal Plain.

### 3.3 Methods

#### 3.3.1 Study Area

The study was conducted in the Maryland Coastal Plain, part of the Coastal Plain physiographic province that extends from South Carolina to New Jersey and supports populations of *A. heterodon* (Maryland Department of Natural Resources, unpublished data). The Coastal Plain comprises roughly half of Maryland and is divided into two sections (Western Shore and the Delmarva Peninsula) separated by the Chesapeake Bay (Fig. 3.1). The Coastal Plain is underlain by Cretaceous and



**Figure 3.1** Freshwater mussel sample sites in the Maryland Coastal Plain used in maximum entropy modeling. Red circles indicate the location of *A. heterodon* (presence data) and black circles show mussel sample locations within the Coastal Plain (background data). The four shaded basins have *A. heterodon*; Nanjemoy (NC) and McIntosh (MR) in the Western Shore and the Chester (CHS) and Choptank (CHP) in the Delmarva Peninsula.



younger sedimentary units composed of gravel, sand, silt, clay, and shells (Schmidt 1993; Shedlock et al. 1999) that are important aquifers and confining beds (Hamilton et al. 1991). The main source of water in the Coastal Plain is groundwater (Schmidt 1993). Agriculture is the dominant land use in the Delmarva Peninsula, largely associated with animal production (Shedlock et al. 1999). Occurring largely in well drained soils, agricultural lands are interspersed with woodlands based on local differences in soil, geomorphic features, and hydrologic characteristics (Shedlock et al. 1999). Many streams in the mid-to-lower Delmarva Peninsula are low-gradient and bordered by pond-like backwaters, marshes, and swamps, however wetlands can also be found in poorly drained, forested parts of the central uplands (Jenkins and Burkhead 1993; Tiner and Burke 1995; Shedlock et al. 1999). Major urban centers (Baltimore and Washington D.C.) are found along the Piedmont-Coastal Plain boundary; counties in the western Coastal Plain are the most rapidly urbanizing counties in Maryland with urbanization generally decreasing from north to south (Foresman et al. 1997; Jantz et al. 2005). Stream acidity varies from acidic with  $\text{pH} < 6$  (blackwaters) to neutral or alkaline ( $\text{pH} > 7$ ) for streams draining deposits with significant calcium carbonate shells (Hamilton et al. 1991). *A. heterodon* are documented in two Western Shore streams draining into the Potomac River (Nanjemoy Creek and McIntosh Run) and in the Choptank and Chester Rivers in the mid to upper Delmarva Peninsula (Fig. 3.1). The Western Shore streams are underlain by shell-rich Formations with Quaternary deposits (Cleaves et al. 1968). The Delmarva streams also contain Quaternary deposits (Cleaves et al. 1968), and are low-gradient streams with headwater wetland regions (Norton and Fisher 2000). *A.*

*heterodon* is found in the non-tidal regions of these four rivers (Maryland Department of Natural Resources, unpublished data).

### 3.3.2 Biological Database

*A. heterodon* occurrence data are part of the Maryland Natural Heritage Program freshwater mussel database that includes data collected from 1983 to 2007 (Maryland Department of Natural Resources, unpublished data). Of the 446 sites surveyed for freshwater mussels in the Coastal Plain, *A. heterodon* was found in 41 sites (Fig. 3.1). Multiple sampling methods, field crews, and data recording methods were employed throughout the time period covered by the database. Therefore, to maximize the number of sites for analysis, species occurrence was coded as present or absent. Presence was assigned where a record of a live/dead animal, shell, or some other indication of presence (character or code; e.g., “present”) was provided. To identify characteristics for sites currently inhabited by the species I omitted six sites where *A. heterodon* has not been located since the early 1990’s. This reduced the number of sites with *A. heterodon* to 35.

### 3.3.3 Stream Segment Database

The maximum entropy modeling program (MaxEnt; Phillips et al. 2006; Phillips and Dudík 2008) requires as input both the location of known species occurrences and some form of environmental background data. Both these datasets need to cover the same spatial extent. Therefore, I used environmental data from all sites within the Maryland Coastal Plain where mussel surveys have been conducted to develop and test the model and then used the model to predict suitable habitat across the entire Maryland Coastal Plain.

For the environmental data, I created a stream segment database based on the National Hydrography Dataset Plus (NHDPlus; U.S. Environmental Protection Agency 2006) with additional landscape layers such as land cover, land use, geology, and soil characteristics that are known to influence the abundance, distribution, and assemblage structure of unionids (Arbuckle and Downing 2002; McRae et al. 2004; Gagnon et al. 2006; Hopkins 2009; Weber and Schwarz 2011). The NHDPlus dataset includes a stream network based on the 1:100,000 National Hydrography Dataset. In this network, stream segments are contiguous, unbranched linear features that start and stop at decision points along the stream network (e.g., at the confluence of two streams/rivers). Stream segments may vary in size but are unique within the stream network. The NHDPlus contains hierarchical datasets for the stream segment, catchment (local area draining into each segment), and watershed (cumulative area draining into the bottom of each segment). From the available attributes I selected for use those related to stream size and position in the stream network, as well as attributes relating to discharge and climate.

I obtained land cover, impervious surface, and canopy density data from the 2001 National Land Cover Database (Yang et al. 2002; Homer et al. 2007). Bedrock geology for Maryland was obtained from the U.S. Geological Survey (Dicken et al. 2005). Water table depth, soil permeability, available water capacity, and organic matter data were obtained from the State Soil Geographic Database (U.S. Department of Agriculture 2008). I generated catchment and cumulative watershed values for these datasets with the Catchment Attribute Allocation & Accumulation Tool (CA3T version 1.009; U.S. Environmental Protection Agency 2008). All shapefiles were

clipped to the study area and converted into 30m grids (NAD83 projection) for use in the CA3T.

Each sample site was associated with the closest stream segment using linear referencing in ArcGIS (version 9.2, ESRI, Redlands). The 35 sites with *A. heterodon* were found on 12 individual stream segments which served as the *A. heterodon* occurrence input layer. Background data would usually be drawn at random from the Maryland Coastal Plain, however, occurrence data is often spatially biased (Phillips et al. 2009). Differences between the resulting environmental bias and the random representation of the environmental conditions in the modeled region can produce inaccurate models (Phillips et al. 2009). A solution to this problem is to account for the bias associated with survey data by using background data with a similar bias such as survey data for a similar fauna (Phillips et al. 2009). Thus, for background data I used all sites within the Maryland Coastal Plain where mussel surveys have been conducted (regardless of whether mussels were found), which provided an input of 257 individual stream segments. Environmental covariates associated with these input datasets consisted of 56 hierarchical variables for each stream segment (Table 3.1).

**Table 3.1** Hierarchical attributes used as input into the maximum entropy modeling. Data are at three scales: segment (S), catchment (local area draining into the stream segment; L) or watershed (cumulative area draining into each segment; C). The code used for each variable follows its name in the attribute column. Classification and description of the land cover attributes is taken from the 2001 National Land Cover Dataset.

Attribute and Code	Description	Scale
Slope (m/m); S	Slope of segment	S
Length (km); L	Length of segment	S
Pathlength (km); PL	Distance from segment's downstream end to its terminal segment's downstream end	S
Stream order; SO	Strahler stream order of the segment from the NHDPlus	S

Maximum elevation (m); MAE	Maximum elevation of segment (smoothed)	S
Minimum elevation (m); MIE	Minimum elevation of segment (smoothed)	S
Mean annual flow (cfs); MAF	Mean annual flow at bottom of segment calculated by the unit runoff method	C
Mean annual velocity (fps); MAV	Mean annual velocity at bottom of segment computed by Jobson method	C
Temperature (°C*10); MAT	Mean annual air temperature	L,C
Precipitation (mm); MAP	Mean annual precipitation	L,C
Area (sq.km); DA	Drainage area	L,C
Open water (%); OW	Area classified as open water, generally with less than 25% cover of vegetation/land cover.	L,C
Developed, open space (%); DOS	Area classified as developed open space, including areas with some constructed materials but mostly vegetation (law grasses) Impervious surfaces are generally < 20% of the total cover.	L,C
Developed, low intensity (%); DLI	Area classified as developed, low intensity, including areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 20-49% of the total cover.	L,C
Developed, medium intensity (%); DMI	Area classified as developed, medium intensity, including areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 50-79% of the total cover.	L,C
Developed, high intensity (%); DHI	Area classified as developed, high intensity, including areas where people reside or work in high numbers. Impervious surfaces account for 80-100% of the total cover.	L,C
Barren land (%); BL	Area classified as rock, sand, or clay where vegetation generally accounts for <15% of total cover.	L,C
Deciduous forest (%); DF	Area classified as deciduous forest: areas dominated by trees where 75% or more of the tree species shed foliage simultaneously in response to seasonal change.	L,C
Evergreen forest (%); EF	Area classified as evergreen forest: areas dominated by trees where 75% or more of the tree species maintain their leaves all year. Canopy is never without green foliage.	L,C
Mixed forest (%); MF	Area classified as mixed forest with areas dominated by trees where neither deciduous nor evergreen species represent more than 75% of the cover present.	L,C
Pasture/hay (%); PH	Area classified as pasture/hay: areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops. Pasture/hay vegetation accounts for >20% of total vegetation.	L,C
Cultivated crops (%); CC	Area classified as cultivated crops: areas used for the production of annual crops (corn, soybeans, vegetables, tobacco, and cotton), perennial woody crops (orchards and vineyards), or land being actively tilled. Crop vegetation accounts for >20% of total vegetation.	L,C
Woody wetlands (%); WW	Area classified as woody wetlands: areas where forest or shrubland vegetation accounts for >20% of the vegetative cover and the soil or substrate is periodically saturated with	L,C

	or covered with water.	
Emergent herbaceous wetlands (%); EHW	Area classified as emergent herbaceous wetlands: areas where perennial herbaceous vegetation accounts for >80% of the vegetative cover and the soil or substrate is periodically saturated with or covered with water.	L,C
Impervious surfaces (%); IS	Area classified as impervious surfaces	L,C
Canopy density (%); CD	Area classified as tree canopy	L,C
Tertiary deposits (%); TD	Area classified as Tertiary-aged deposits	L,C
Quaternary deposits (%); QD	Area classified as Quaternary-aged deposits	L,C
Water table depth (ft); WTD	Average depth to the water table	L,C
Soil permeability (in/hr); PERM	Average soil permeability	L,C
Available water capacity (inches/in); AWC	Average available water capacity	L,C
Organic matter (% by weight); OM	Average organic matter	L,C

### 3.3.4 Data Analysis

MaxEnt uses environmental data from a subset of sites within the geographic area of interest (i.e., background sample) and presence records to create a probability distribution of: (1) the density of environmental covariates where the species is present and (2) the density of environmental covariates of the background sample. Out of the many possible distributions of environmental covariates at the presence sites, the model selects the one that is most similar to the distribution in the landscape (i.e., background sample), effectively minimizing the relative entropy between the two distributions. This is achieved under the constraint that the value of each covariate in the probability distribution is close to its mean across all locations with observed presences. MaxEnt fits the model on features that are transformations of the covariates (linear, product, quadratic, hinge, threshold, or categorical), therefore, complex relationships can be modeled (Phillips et al. 2006; Elith et al. 2011). Overfitting is avoided by regularization, a form of model selection that trades off model fit and model complexity, essentially fitting a penalized maximum likelihood

model (Phillips and Dudík 2008; Elith et al. 2011). MaxEnt provides a logistic output; an estimate of probability of suitable conditions between 0 and 1 (Phillips 2006).

The form of regularization used by MaxEnt accommodates correlated variables so the pre-processing of environmental datasets to select a few dominant axes (e.g., using Principal Components Analysis) was unnecessary (Elith et al. 2011). Thus, the input dataset consisted of all 56 variables associated with the individual stream segments at mussel survey locations. I used the model results to predict potential habitat across the entire Maryland Coastal Plain. I used all feature types (linear, product, quadratic, hinge, threshold, and categorical) and the default settings in MaxEnt to fit the model to the data (i.e., train the model) and a 10-fold cross-validation to estimate model performance and uncertainty (i.e., test the model). Variable importance was determined by a jackknife cross-evaluation procedure that quantifies the explanatory information of each variable when it is used in isolation and the information lost when it is omitted from a model. I used a combination of variable importance and the area under the curve (AUC) of the receiver-operating characteristic (ROC) plot to identify the best models (Phillips 2006; Wilson et al. 2011). Predicted probabilities from the final models were linked to a shapefile in R (version 2.7.2, R Foundation for Statistical Computing, Vienna, Austria) and displayed in ArcGIS following the methods outlined in Elith et al. (2011).

### 3.4 Results

#### 3.4.1 Model Selection

All candidate models had better than random predictions of suitable *A. heterodon* habitat (Table 3.2). The full model had the lowest cross-validated AUC

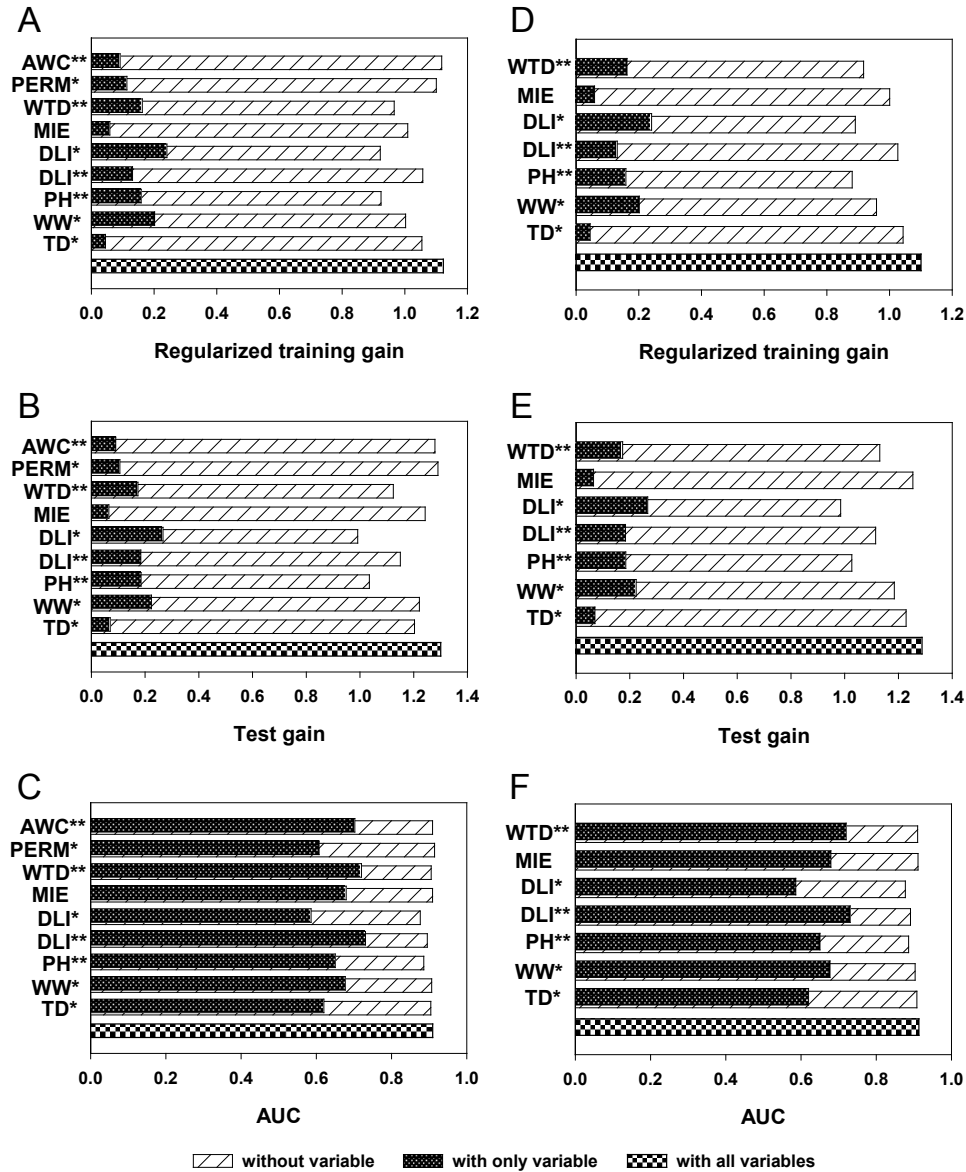
(56 variables;  $0.743 \pm 0.200$ ; Table 3.2). Model reduction to 25 variables increased the AUC to  $0.767 \pm 0.182$  and retained many variables related to geology, land use/land cover, location, stream size, and soil characteristics. Removing % barren lands in the cumulative watershed and % deciduous forest in the local catchment from the model increased the cross-validated AUC to  $0.802 \pm 0.150$  (Table 3.2). Further removal of % barren land and % pasture hay in the local catchment and path length increased the AUC to  $0.835 \pm 0.167$  (Table 3.2). The greatest increase in the cross-validated AUC (of 0.045 to  $0.880 \pm 0.083$ ) came from eliminating % open water in the local catchment and stream order to produce the 18 variable model (Table 3.2). Eliminating % open water, % woody wetlands, and % Tertiary deposits in the cumulative watershed and % developed open space and % emergent herbaceous wetlands in the local catchment to generate a 13 variable model increased the AUC to  $0.903 \pm 0.075$  (Table 3.2). Subsequently removing medium and high intensity development and mixed forests from the model further increased the AUC to  $0.909 \pm 0.068$  (Table 3.2).



**Table 3.2** MaxEnt models for *A. heterodon* suitability in the Maryland Coastal Plain. The variables in each model, AUC of the training model, and average AUC (with standard deviation) of the cross-validated model are shown. One asterisk (\*) behind a variable signifies a catchment-scale variable (local area draining into the stream segment) while a double asterisk (\*\*) indicates a cumulative watershed variable (cumulative area draining into the stream segment). The definition for the variable codes are as follows: average available water capacity (AWC); average soil permeability (PERM); average water table depth (WTD); minimum elevation of the segment (MIE); % open water (OW); % developed, open space (DOS); % developed, low intensity (DLI); % developed, medium intensity (DMI); % developed, high intensity (DHI); % barren land (BL); % deciduous forest (DF); % mixed forest (MF); % pasture/hay (PH); % woody wetlands (WW); % emergent herbaceous wetlands (EHW); pathlength (PL); stream order (SO); % Tertiary deposits (TD).

Model	Training AUC	Cross-Validated AUC
full model (56 variables)	0.967	0.743 ± 0.200
(25 variables) AWC**, PERM*, WTD**, MIE, OW*, OW**, DOS*, DLI*, DLI**, DMI*, DMI**, DHI**, BL*, BL**, DF*, MF**, PH*, PH**, WW*, WW**, EHW*, PL, SO, TD*, TD**	0.958	0.767 ± 0.182
(23 variables) AWC**, PERM*, WTD**, MIE, OW*, OW**, DOS*, DLI*, DLI**, DMI*, DMI**, DHI**, BL*, MF**, PH*, PH**, WW*, WW**, EHW*, PL, SO, TD*, TD**	0.958	0.802 ± 0.150
(20 variables) AWC**, PERM*, WTD**, MIE, OW*, OW**, DOS*, DLI*, DLI**, DMI*, DMI**, DHI**, MF**, PH**, WW*, WW**, EHW*, SO, TD*, TD**	0.955	0.835 ± 0.167
(18 variables) AWC**, PERM*, WTD**, MIE, OW**, DOS*, DLI*, DLI**, DMI*, DMI**, DHI**, MF**, PH**, WW*, WW**, EHW*, TD*, TD**	0.955	0.880 ± 0.083
(13 variables) AWC**, PERM*, WTD**, MIE, DLI*, DLI**, DMI*, DMI**, DHI**, MF**, PH**, WW*, TD*	0.945	0.903 ± 0.075
(9 variables) AWC**, PERM*, WTD**, MIE, DLI*, DLI**, PH**, WW*, TD*	0.943	0.909 ± 0.068
(7 variables) WTD**, MIE, DLI*, DLI**, PH**, WW*, TD*	0.944	0.914 ± 0.073

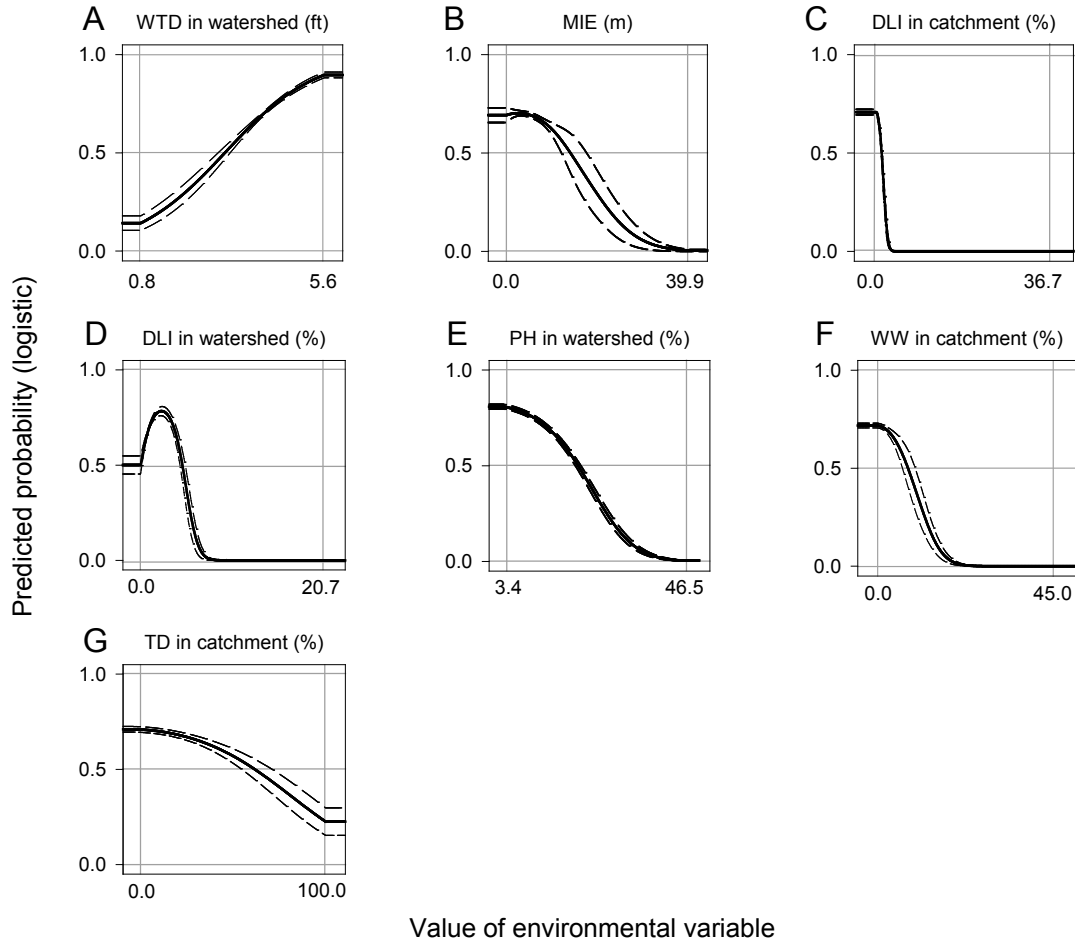
The variable reduction process can be illustrated by reduction of the 9-variable model to the final 7-variable model (AUC to  $0.914 \pm 0.073$ ; Table 3.2). Variable importance plots quantify the explanatory information of each variable when it is used in isolation and the information lost when it is omitted from the model. Gain is an indication of goodness of fit with higher gain and AUC values having better fit and accuracy, respectively. Examination of the variable importance plots for the 9-variable model indicates that available water capacity and soil permeability provide some information in isolation (AWC\*\*, PERM\*; dark bars; Fig. 3.2a), however the model shows little or no reduction in gain or AUC when either variable is omitted (difference between tiled and hatched bars; Fig. 3.2b, c). Omitting any of the remaining 7 variables reduces the gain and weakens the model (Fig. 3.2). The cross-validated AUC increased slightly with a reduction from a 9 to 7-variable model ( $0.909 \pm 0.068$  to  $0.914 \pm 0.073$ , respectively; Table 3.2). In the final model, the amount of low intensity development in the local catchment was the most important variable in training the model (DLI\*; Fig. 3.2d). Local low intensity development had the most useful information in isolation whereas the amount of pasture hay agriculture in the cumulative watershed had the most information that was not already explained by the other variables (PH\*\*; Fig. 3.2d). In model testing, low intensity development in the local catchment had the most useful information in isolation as well as the most information that was not already explained by the other variables (Fig. 3.2e). However, the AUC plot shows low intensity development in the cumulative watershed (DLI\*\*; followed closely by the average depth to the water table in the cumulative watershed, WTD\*\*) to be the most effective single variable for predicting *A. heterodon* occurrence (Fig. 3.2f). Thus, local low intensity development helps obtain a good fit to the training data, but low intensity development in the cumulative watershed (and possibly average depth to water table) may be more transferable to other systems.



**Figure 3.2** Variable importance plots for variables in the 9-variable (A-C) and 7-variable (D-F) models. Each plot quantifies the explanatory information of each variable when it is used in isolation (length of the dark bar) and the information lost when it is omitted from the model (decrease in gain: difference between tiled and hatched bars). Gain is an indication of goodness of fit with higher gain and AUC values having better fit and accuracy, respectively. The plots are for the training models (A, D) and the test models (B, C, E, F). Variables with longer dark bars (more information by itself) and shorter hatched bars (more information lost when variable omitted from the model) supply more explanatory information to the model. The definition for the variable codes are as follows: average available water capacity (AWC); average soil permeability (PERM); average water table depth (WTD); minimum elevation of the segment (MIE); % developed, low intensity (DLI); % pasture/hay (PH); % woody wetlands (WW); % Tertiary deposits (TD). One asterisk (\*) behind a variable signifies a catchment-scale variable (local area draining into the stream segment) while a double asterisk (\*\*) indicates a cumulative-watershed variable (cumulative area draining into the stream segment).

### 3.4.2 Variable Response

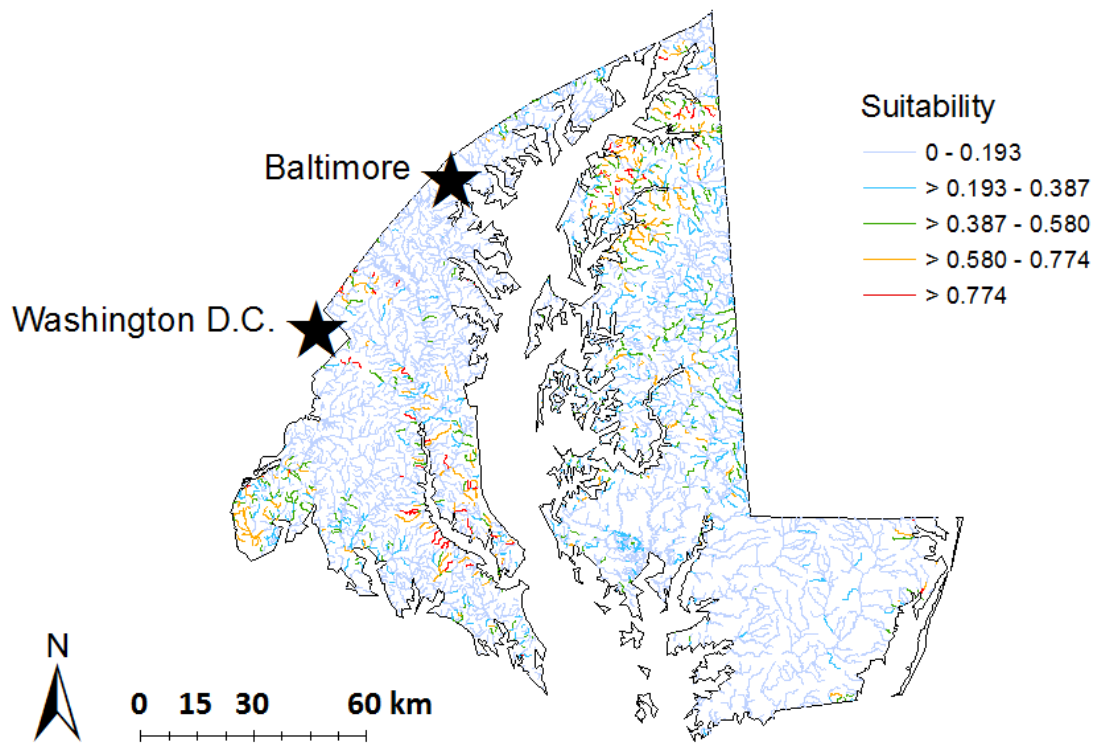
Marginal response curves indicate how the logistic prediction changes for values of each environmental variable. For these calculations, all other variables are set to their average value over the set of presence localities. Results of the model indicate that habitat suitability increases with increasing average depth to the water table in the cumulative watershed (Fig. 3.3a). Suitability decreases sharply in stream segments with elevations > 5 m (Fig 3.3b). Habitats with low intensity development in the local catchment and cumulative watershed were generally unsuitable (Fig. 3.3c, d). Suitability declines sharply between values of ~0.5 - 3% local low intensity development (Fig. 3.3c). In the cumulative watershed, suitability peaks at ~2.5% low intensity development and declines sharply with increasing levels of development to ~7.6% (Fig. 3.3d). Habitat suitability declines dramatically between values of 13 - 35% pasture/hay land cover in the cumulative watershed (Fig. 3.4e). Suitability decreases as woody wetlands increases from 2 to 17% (Fig. 3.3f). Local catchments containing a large proportion of Tertiary-aged sediments were generally unsuitable habitats for *A. heterodon* (~ 50%; Fig 3.3g).



**Figure 3.3** Marginal response of *A. heterodon* to changes in each model variable. The y-axis is the predicted probability of suitable conditions (logistic output) with all other variables set to their average value over the set of presence localities. The mean response  $\pm 1$  standard deviation are shown. The variable codes are as follows: A) average water table depth (WTD); B) minimum elevation of the segment (MIE); C) % low intensity development (DLI; catchment); D) % low intensity development (DLI; watershed); E) % pasture/hay (PH); F) % woody wetlands (WW); and G) % Tertiary deposits (TD).

### 3.4.3 Predicted Suitable Habitat

The MaxEnt model results were integrated into the GIS database to generate a suitability map for *A. heterodon* in the Maryland Coastal Plain. Suitability was arbitrarily grouped by equal intervals for display purposes. More highly suitable segments were predicted around the Nanjemoy basin in the south-western tip of the Western Shore, along the Patuxent River flowing into Chesapeake Bay, and within and north of the Chester River basin in the upper Delmarva Peninsula (Fig. 3.4). Most of these more highly suitable segments, however, are not known to contain *A. heterodon* (Maryland Department of Natural Resources, unpublished data).



**Figure 3.4** Final *A. heterodon* suitability predictions for Maryland Coastal Plain streams. The groupings were arbitrarily defined using equal intervals for display purposes. Suitability increases from 0 (light blue) to 1 (red).

### 3.5 Discussion

#### 3.5.1 Model Performance

Previous studies indicate that maximum entropy has out-performed other methods for habitat prediction at low sample sizes ( $\leq 10$ ; Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008), and thus was considered to be an appropriate modeling approach for *A. heterodon*.

My final MaxEnt model had a high cross-validated prediction accuracy of 0.91, which is an improvement on previous models for *A. heterodon*, but is slightly lower than other models for rare and endangered freshwater mussels (AUC=0.97, Hopkins 2009; AUC between 0.923 and 0.967, Weber and Schwartz 2011; AUC=0.970, Wilson et al. 2011).

Model accuracy tends to increase with sample size (Stockwell and Peterson 2002; Wisz et al. 2008), thus I expected to have a lower AUC than the other models due to the small sample size. When using presence-only datasets, higher AUC values can be obtained when absences are selected from a very large area (Wisz et al. 2008). Constraining the extent of my study area to the Maryland Coastal Plain, the region most likely to contain *A. heterodon* based on survey data, likely resulted in more conservative AUC estimates (Edren et al. 2010).

#### 3.5.2 Species-Environment Relationships

Earlier attempts to model *A. heterodon* habitat linked the species to microhabitat features such as water depth, current speed, and substrate type; but low predictive power in the resulting models suggested that physical microhabitat data might be of limited use for predicting the species' occurrence (Strayer and Ralley 1993). Use of macrohabitat factors (those affecting distribution at a scale of 1 to 10 km) were useful predictors of the distributions of several mussel species in the northern Atlantic Slope, but their predictive power varied widely (Strayer 1993). My MaxEnt model results suggest that stream characteristics at multiple spatial scales may influence *A. heterodon* occurrence, which is

similar to recent findings for other mussel species (Hopkins 2009; Weber and Schwartz 2011).

One hydrogeomorphic characteristic influenced suitability for *A. heterodon*; minimum elevation of the stream segment. In a study of the Neversink River, N.Y., *A. heterodon* was also associated with lower elevations (Baldigo et al. 2003). Streambed gradient decreases with elevation and *A. heterodon* are associated with low gradient reaches in streams of the upper Delaware River and the Maryland Coastal Plain (Ashton 2010; W.A. Lellis, U.S. Geological Survey, unpublished data). These low gradient streams may have stable streambeds that can serve as refuges during high flows (Strayer 1999; Strayer and Ralley 1993; Maloney et al. 2012).

I found suitable habitat for *A. heterodon* to have little low intensity development in either the catchment or cumulative watershed. Similarly, within the Maryland Coastal Plain, *A. heterodon* were found in sites with significantly less impervious surfaces than sites without the mussel (Ashton 2010). Between 1990 and 2000 the Chesapeake Bay watershed lost agricultural and forested lands to low intensity development at the outskirts of urban areas (Jantz et al. 2005). Development is often accompanied by reduced groundwater and baseflow, increased surface runoff, greater volume storm flows that peak more rapidly, increased channel erosion, and degraded water quality (Wolman 1967; Dunne and Leopold 1978; Nelson and Palmer 2007; Schiff and Benoit 2007), all conditions associated with reduced mussel survival and species richness (Gangloff et al. 2009; Allen and Vaughn 2010; Brown et al. 2010; Galbraith et al. 2010; Peterson et al. 2011). Thus, further development within catchments deemed suitable for *A. heterodon* could pose a threat to both known and unknown populations.

The suitability of streams for *A. heterodon* decreased with increasing Tertiary deposits in the local catchment. Underlying geology was also a factor associated with the rare Rabbitsfoot mussel (*Quadrula cylindrinca*) at the subcatchment level (Hopkins 2009).



Deposits within the Tertiary Period encompass many layers, from the older Paleocene to the younger Pliocene, with an accompanying array of sediments, land covers, and water chemistries (Hamilton et al. 1991; Schmidt 1993). The Paleocene layer is a glauconite- and pyrite-rich formation that can generate groundwater high in iron and acidity (Böhlke et al. 2007). This layer tends to have more relief than younger Tertiary and Quaternary deposits where *A. heterodon* are found (Schmidt 1993; Maryland Natural Resources, unpublished data). These unconsolidated deposits allow precipitation to penetrate and become stored in the sandy layers that are the aquifers in the region (Schmidt 1993). I also found *A. heterodon* suitability to increase with depth to the water table. Where water moves through deposits containing shells or cement, dissolution of calcium carbonate in the sediments produces calcium bicarbonate-type water with a high pH (Chapelle 1983; Hamilton et al. 1991). When this groundwater is discharged to the stream, calcium carbonate precipitation can occur which is needed for mussel growth and reproduction (Pynnönen 1991). This is consistent with Strayer's (1993) suggestion that *A. heterodon* distributions are correlated with some factor associated with calcium concentrations. Many of the deposits containing carbonate shells are found in Miocene-aged sediments (a younger Tertiary layer; Schmidt 1993).

I also found *A. heterodon* suitability to decrease with the amount of pasture/hay lands in the cumulative watershed. Corn, soybeans, and small grains are the major crops in the region with differences in cropping systems (i.e., tilled croplands versus pasture or hay lands) largely associated with different types of animal agriculture (Shedlock et al. 1999; Sims and Coale 2002). To optimize soil pH for specific crops, carbonate minerals are often applied to maintain or increase soil pH (i.e., agricultural liming; Goulding and Blake 1998). These carbonates are very soluble, thus any liming activities in the watershed can alter water chemistry toward calcium bicarbonate-type water (Oh and Raymond 2006), which might increase suitability for *A. heterodon* (C. Campbell and K. Prestegard, unpublished data). Liming is usually reserved for cultivated (tilled) crops. Pasture and hay are often grown on

poorer soils that are not usually limed and thus would not receive the water chemistry changes associated with liming.

Within Maryland, wetland habitats are commonly found in the Coastal Plain; particularly in the lower Delmarva Peninsula (Tiner and Burke 1995). Woody wetlands contribute to the organic acids characteristic of blackwater Coastal Plain streams (Morgan and Good 1988). Low pH can cause shell dissolution and mortality in older mussels (Kat 1982) while extended periods of acidic conditions can cause sublethal effects, such as increased sensitivity to contamination (Pynnönen 1995) and decreased glochidial viability (Huebner and Pynnönen 1992). *A. heterodon* sites generally have a significantly higher pH than sites without the mussel (Ashton 2010). In addition, a primary host of *A. heterodon*, the tessellated darter (*Etheostoma olmstedii*; Michaelson and Neves 1995), is intolerant of high acidity and does not occur in blackwater streams with low pH (Jenkins and Burkhead 1993). *A. heterodon* may tolerate some standing water conditions, but the mussel generally prefers slow to moderate flow velocities (Michaelson and Neves 1995).

### 3.5.3 Model Predictions and Utility

Ecological niche models are exploratory models that predict potential habitat based on the similarity between unknown habitat and known habitat (O’Conner 2002). These models rely on the assumption that a species is in at least pseudo-equilibrium with its environment (Guisan and Thuiller 2005). Temporal and spatial ecosystem dynamics, biotic interactions, and human modifications create conditions where this assumption of equilibrium may not be valid. As a result, individuals of a species are not always found in suitable habitat and may be found in sites with some unsuitable characteristics. For example, land conversion from forest to farmland in the Maryland Coastal Plain began in the 1600’s with the arrival of European settlers (Benitez and Fisher 2004) and continues today as forest and farmland are converted to accommodate increasing urban and exurban sprawl (Foresman et al. 1997;

Fisher et al. 2006). This legacy of modifications to the landscape and streamscape make it impossible to know the original distribution of *A. heterodon*, if it currently exists in favored habitats, or if current populations are relicts on their way to extirpation. Although my analysis is necessarily correlational and not causative, the models allow segment-level predictions within streams from large spatial extents.

Although many of the suitable stream segments fall outside basins known to contain *A. heterodon*, I view such sites as opportunities for new discoveries. For example, only 19 out of 462 (~4.1%) stream segments in the two upper suitability groupings on the map (arbitrarily defined) have been sampled for freshwater mussels, and few have targeted *A. heterodon*, which can be harder to find than most other mussel species when not targeted (W.A. Lellis, U.S. Geological Survey, unpublished data). Thus, these logistic predictions could provide a foundation for a prioritized sampling scheme for the species in the Maryland Coastal Plain. For example, the predicted habitat suitabilities could be stratified and random segments selected from each strata for sampling as follows: 40 highly suitable, 20 moderately suitable, and 10 unsuitable. Sampling in this manner would allow for the potential discovery of unknown *A. heterodon* populations, the validation of the MaxEnt model, and the collection of data for further model calibration. In a similar manner, resource managers intimately familiar with these streams could also use these stratifications to identify individual stream segments that show potential for species' (re)introduction. In addition, results from the model may be applied to other Coastal Plain areas within the range of *A. heterodon*.

The model identified variables that affect habitat suitability for *A. heterodon* at the stream segment scale. Although *A. heterodon* are likely not responding to these variables *per se*, this information can suggest co-varying abiotic or biotic variable(s) that could be controlling the species' distribution (Strayer 2008). I found the amount of local and cumulative low intensity development to be important in fitting the model and for transferring the results to other systems. In addition, other work in the Coastal Plain found *A. heterodon* in

sites with significantly less impervious surfaces than sites without the mussel (Ashton 2010). These results suggest that some factor(s) associated with development could provide unsuitable conditions for *A. heterodon*. Urbanization is associated with increased volume of runoff, flood peaks, erosion, and sedimentation (Wolman 1967; Leopold 1968). Channel incision and increased cross-sectional areas increase bankfull channel capacity and nearbed shear stresses during high flow events (Booth 1990; Gangloff and Feminella 2007). *A. heterodon* are typically found in fine sediments with moderate depths and slow to moderate flows that are temporally stable (Strayer and Ralley 1993; Michaelson and Neves 1995; Maloney et al. 2012). Thus, the decrease in hydraulic and bed stability accompanying urbanization may be a determinant factor of the low suitability of developed reaches for *A. heterodon* in the Coastal Plain. Increases in human development also results in reduced groundwater recharge, groundwater levels, and baseflow (Leopold 1968) and the model identified depth to the water table as another variable that could be useful for transferring model results to other areas. The water table depths associated with *A. heterodon* in the Coastal Plain are consistent with calcium bicarbonate-type water with a high pH (Hamilton et al. 1991); conditions favorable for calcium carbonate precipitation (Chapelle 1983).

Urban and exurban sprawl will continue to tax stream ecosystems in the region, therefore work is needed to identify if and how bed instability and water chemistry or quality affect *A. heterodon* viability. Bed stability has already received attention (Strayer and Ralley 1993; Strayer 1999; Maloney et al. 2012), however little is known about the chemical requirements for *A. heterodon* and would be a fruitful area for future research. Results of these studies could then refine model predictions and guide resource management and restoration priorities toward safeguarding those ecosystem processes most likely to affect habitat vital for *A. heterodon* persistence.

## Chapter 4: A field-based potential thermal limit for *Alasmidonta heterodon*, an endangered freshwater mussel, and regional differences in underlying thermal regimes

### 4.1 Abstract

Identifying essential aquatic habitat characteristics that limit or support mussel populations is needed to develop strategies to sustain at-risk populations under continued climate and land-use change. Temperature is a constraint to the distribution of many aquatic taxa. I examined if field temperature measurements can identify a potential thermal limit for *Alasmidonta heterodon* and if air-water temperatures and regression relationships can be used to identify preferred groundwater sources. Paired air-water temperature sensors were placed in *A. heterodon* reaches throughout the species range during the summer of 2011. August stream water temperature maxima for 2011 suggested a realized thermal limit of 29°C for *A. heterodon*. All sites with < 1°C diurnal variation in stream temperature were in the south. In addition, 95<sup>th</sup> percentile rates of water temperature change in southern sites were approximately half of those for northern sites. Slope-intercept plots from air-water regressions at each site suggest a range of shallow to deep groundwater flow contributions to streamflow. This simple grouping of sites masks the higher water temperature variability observed for a given air temperature in the southern sites. This suggests that hydrological processes are more important in the thermal regimes of southern sites than in northern sites. Identifying a potential thermal limit for *A. heterodon*, as

well as differentiating thermal regimes across the species' range, provides valuable information to better guide conservation activities.

#### 4.2 Introduction

Freshwater mussels are among the most imperiled freshwater fauna (Lydeard et al. 2004). Identifying essential aquatic habitat characteristics that limit or support mussel populations is needed to develop strategies to sustain at-risk populations under continued land use and climate change (Lydeard et al. 2004; Strayer et al. 2004). Mussel habitat has been characterized with various physical, chemical, and biological attributes (Strayer and Ralley 1993; Di Maio and Corkum 1995; Johnson and Brown 2000; McLain and Ross 2005). These habitat characterizations, however, are not sufficiently species-specific to guide endangered species reintroductions or to set resource management priorities (Strayer 2008). Temperature tolerance limits, however, may constrain the spatial distribution of many aquatic taxa (Sweeney and Vannote 1978; Milner et al. 2001; Brazner et al. 2005; Isaak et al. 2010). The existence and use of thermal niches may influence mussel species performance and community structure in rivers (Spooner and Vaughn 2008; Spooner and Vaughn 2009; Galbraith et al. 2010). Mussel populations living near their thermal tolerance limits may be susceptible to extirpation if stream temperatures rise (Pandolfo et al. 2010; Ganser et al. 2013). In this paper, I examine whether in situ stream temperature measurements can identify a thermal limit for a federally endangered freshwater mussel.

The dwarf wedgemussel, *Alasmodonta heterodon*, is a species in decline throughout much of its range along the Atlantic Coast of the United States due to

impoundments, pollution, channel alteration, and siltation (U.S. Fish and Wildlife Service 1993, 2007; Locke et al. 2003). *A. heterodon* populations occur in distinct, widely separated, low density patches along stream reaches (Strayer et al. 1996). Previous habitat analyses suggest that *A. heterodon* prefer fine sediment, moderate channel depths, and slow to moderate velocities (Strayer and Ralley 1993; Michaelson and Neves 1995; Maloney et al. 2012). In the upper Delaware River basin, *A. heterodon* has been associated with low gradient reaches, stable streambeds, and water chemistry close to saturation with respect to aragonite (Maloney et al. 2012; W. Lellis, unpublished data; C. Campbell, unpublished data). Little is known about the thermal limits of *A. heterodon*, however, the species has been associated with cool groundwater seeps in the upper mainstem Delaware River (Briggs et al. 2013). In situ evaluation of stream temperature regimes for this species have not been conducted. Therefore, I designed this study to evaluate whether range-wide in situ stream temperatures can identify a potential thermal limit for *A. heterodon*.

Water temperature has been demonstrated to influence freshwater mussel reproduction, growth, heart rate, behavior, and species coexistence (Bauer 1992; Heinricher and Layzer 1999; Galbraith and Vaughn 2009; Spooner and Vaughn 2009; Galbraith and Vaughn 2011; Archambault et al. 2014; Ganser et al. 2013). Thermal tolerance data is limited to a small number of native freshwater mussels, ~15 species (Dimock and Wright 1993; Pandolfo et al. 2010; Galbraith et al. 2012; Archambault et al. 2014; Ganser et al. 2013), including only one endangered species (*Lampsilis abrupta* (Say); Archambault et al. 2014; Ganser et al. 2013). These data indicate that susceptibility to high temperatures varies by species and life stage (Pandolfo et al.

2010; Galbraith et al. 2012; Ganser et al. 2013). Heart rate generally increases with increasing temperature until a critical thermal threshold is reached (Pandolfo et al. 2009) beyond which heart rate either remains stable or declines (Braby and Somero 2006). Temperature thresholds can also control the onset and cessation of growth (Goewert et al. 2007; Negishi and Kayaba 2010). Thermal regimes are cues for timing of gamete development (Galbraith and Vaughn 2009) and altered thermal regimes can disrupt the freshwater mussel reproductive cycle, inhibiting successful reproduction (Heinricher and Layzer 1999; Galbraith and Vaughn 2009).

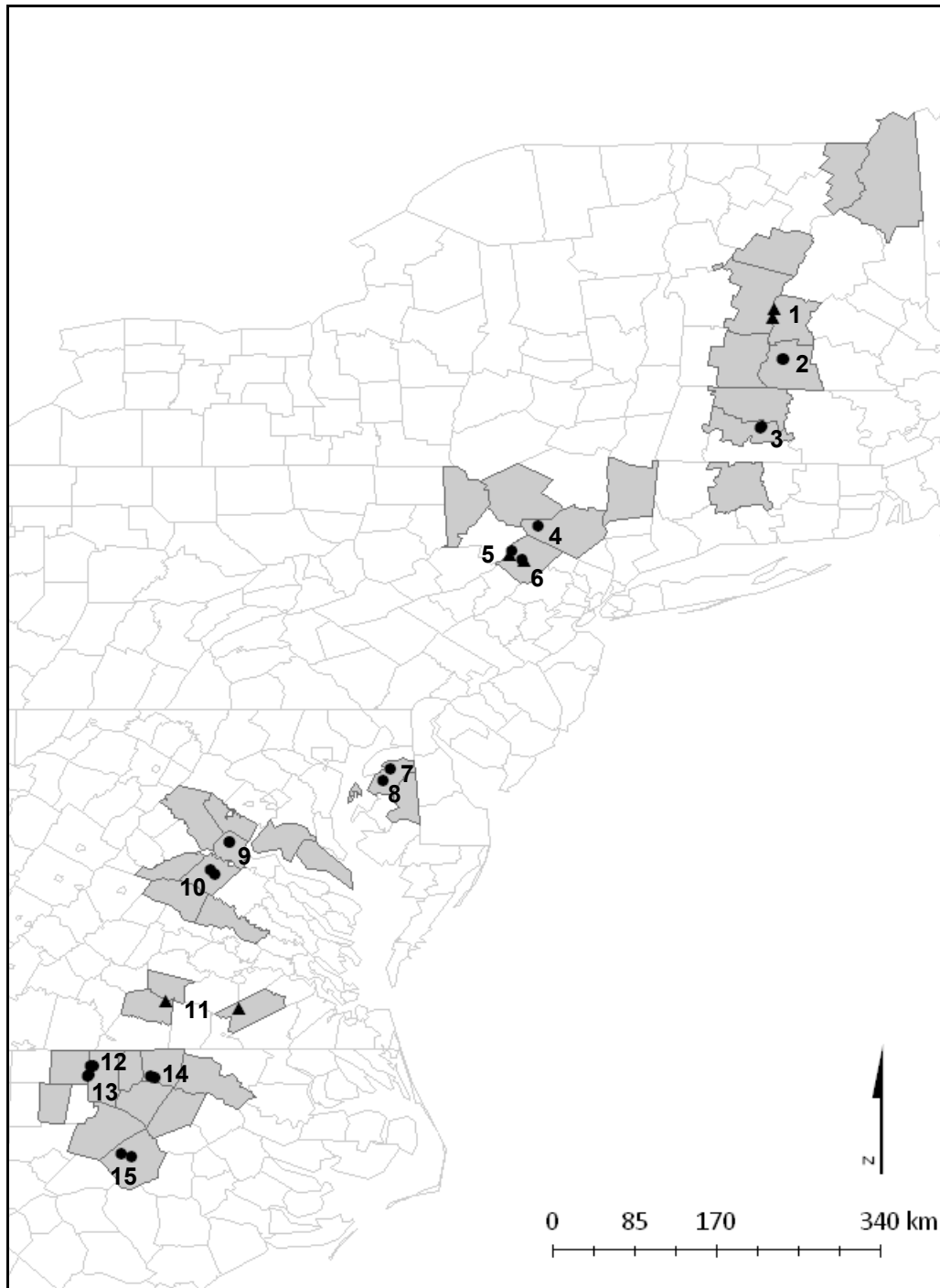
Stream temperature is influenced by source water temperature, air temperature, discharge, shading, and stream residence time (Edinger et al. 1968; Gu et al. 1998; Bogan et al. 2003). During base flow conditions, only groundwater sources contribute to stream flow, but these water sources may be from local to regional flow systems (Tóth 1970; Bogan et al. 2003). Stream baseflow temperature, temperature variability, and other water quality parameters can be affected by groundwater sources or the mixing of water from multiple sources (Tóth 1963, Tóth 1970, Caissie 2006). Thus, the use of cool groundwater seeps by *A. heterodon* (Briggs et al. 2013) could provide thermal and geochemical refugia. I investigated field-based temperature usage of *A. heterodon* by testing two hypotheses: 1) the thermal limit for *A. heterodon* can be estimated by sampling in situ stream temperatures throughout the species' range; and 2) sources of water to baseflow in *A. heterodon* reaches can be estimated from air to water temperatures and regression relationships, and these data will indicate intermediate to deep groundwater sources, particularly for streams in the southern extent of *A. heterodon*'s range.



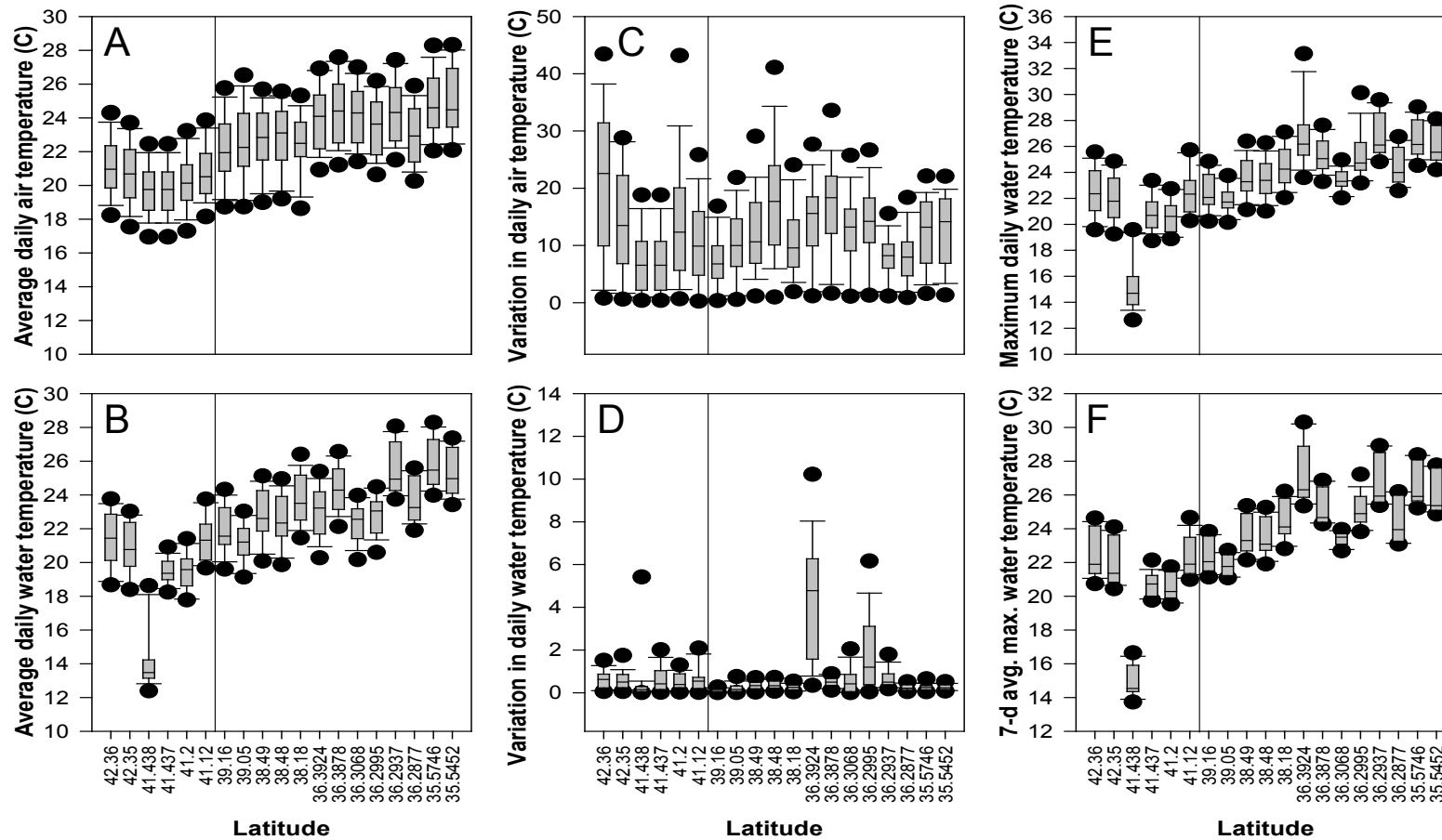
### 4.3 Methods

#### 4.3.1 Study Area

The current Atlantic Slope range of *A. heterodon* extends from the upper Connecticut River basin in New Hampshire south to the Neuse River basin in North Carolina (U.S. Fish and Wildlife Service 1993, 2007; Fig. 4.1). This range encompasses a latitudinal-based air temperature gradient that influences stream temperature distributions (Fig. 4.2a, b). Stream temperature was sampled in 15 streams that span the current range of the species (Fig. 4.1). These streams are located in four drainage systems: 1) the Connecticut River basin (Connecticut River, VT/NH; the Ashuelot River, NH; and Fort River, MA); 2) the Delaware River basin (Neversink River, NY; Flat Brook, NJ; and Paulins Kill, NJ); 3) the Chesapeake basin (Browns Branch, MD; Three Bridges Branch, MD; Aquia Creek, VA; and Po River, VA); and 4) south Atlantic coastal rivers draining into the Albemarle-Pamlico Sound (Chowan River (Nottoway River, VA), Tar River (Shelton Creek, Cub Creek, and Shocco Creek; NC), and Neuse River (Swift Creek, NC)). Streams in the Connecticut and Delaware River basins I consider northern streams; the rest are southern streams.



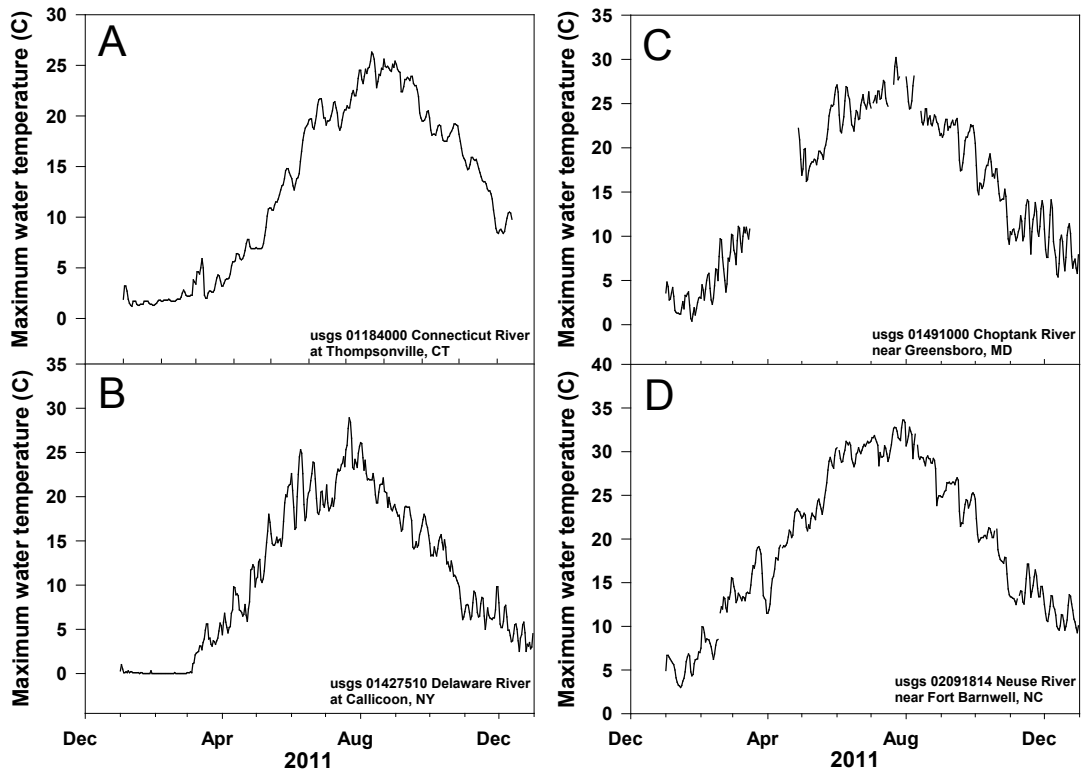
**Figure 4.1** Fifteen streams where temperatures were sampled within the range of *A. heterodon*. The gray areas are counties where the mussel has been recorded. The black dots represent the *A. heterodon* reaches where loggers were recovered and the triangles represent the reaches where loggers were lost. They are as follows (from north to south): 1 = lower Connecticut River mainstem; 2 = Ashuelot River; 3 = Fort River; 4 = Neversink River; 5 = Flat Brook; 6 = Paulins Kill; 7 = Browns Branch; 8 = Three Bridges Branch UT1; 9 = Aquia Creek; 10 = Po River; 11 = Nottoway Creek; 12 = Shelton Creek; 13 = Cub Creek; 14 = Shocco Creek; 15 = Swift Creek.



**Figure 4.2** Water and air temperature ( $^{\circ}\text{C}$ ) for the time interval July 30 to August 31, 2011 for *A. heterodon* stream reaches arranged by latitude. Box plots indicate: (A) average daily air temperature, (B) average daily water temperature, (C) daily variation in air temperature, (D) daily variation in water temperature, (E) average maximum daily water temperature, and (F) 7-day moving average maximum water temperature. Whiskers indicate the 10<sup>th</sup> and 90<sup>th</sup> percentiles while the dots indicate the 5<sup>th</sup> and 95<sup>th</sup> percentiles. The vertical line separates northern (left) from southern (right) sites.

#### 4.3.2 Selection of Sampling Interval for Air and Water Temperatures

Annual stream temperature data monitored by the U.S. Geological Survey at stream sites throughout the region indicate that annual water temperature maxima occur near the end of July into August for rivers in the study region (Fig. 4.3; data available at: <http://waterdata.usgs.gov/nwis/sw>). Therefore, a stream and air temperature monitoring program designed to obtain maximum temperatures targeted this time interval. Temperature monitoring was conducted in summer 2011. I later evaluated whether the sampled year was representative of recent climatic conditions.



**Figure 4.3** Select USGS 2011 daily maximum temperature data for four gaging stations that span the *A. heterodon* streams sampled.

#### 4.3.3 Field Temperature Monitoring Procedures

Air and water temperatures were monitored with Onset HOBO® Pendant combined temperature sensors and data loggers (Onset Computer Corporation, Pocasset, MA) that were calibrated in the laboratory with three temperatures that spanned expected field values. Sensor resolution was 0.10°C at 25°C with an accuracy of  $\pm 0.47^\circ\text{C}$  (Onset Computer Corporation, Pocasset, MA). Paired air and water temperature sensors and loggers were placed in each study reach. Two reaches with *A. heterodon* were monitored in 13 of the 15 study streams; one reach was monitored in the other 2 streams. Stream water temperature sensors were secured to rebar and placed at the substrate surface. Air temperature sensors were secured to a branch in a nearby tree, at a distance of  $\sim 2 - 3$  m above the ground surface. Temperature data were recorded at 20 minute intervals over a period of 87 days. This time interval was sufficient to detect differences in thermal regimes across sites. Sensor emplacement was performed by volunteers from state agencies, federal agencies, and universities. Initial placement occurred between June 17 and July 29, 2011; prior to the annual stream temperature maximum. One site on the Po River and both Ashuelot River sites were downstream of dams, which likely affected baseflow temperatures (Erickson and Stefan 2000). Therefore, these sites were excluded from data analysis because they were unlikely to provide stream water source temperature information. High discharge events in late summer 2011 caused the loss of several temperature monitors: one site in Flat Brook, one site in the Paulins Kill, and both sites along the Connecticut River mainstem and the Nottoway River; this reduced the dataset to 12 streams. The reduced study region extends from Massachusetts to North

Carolina and includes streams with watershed areas between 7 and 778 km<sup>2</sup> (Fig. 4.1).

#### 4.3.4 Data Analysis

*Daily variation in stream temperature*—Diurnal variations in stream temperature are influenced by water source temperatures, air temperatures, and stream shading. Stream and water temperature data were evaluated by constructing box plots of: a) moving averages of 1, 3, 5, and 7-day intervals, b) variations in temperature over the same intervals, and c) maximum temperature for the same intervals. I also examined the rate of change of stream temperature at each site (change temperature / change time) using a common 20 minute time step. Cumulative probability analysis was performed on the stream temperatures for each stream site. For all these analyses, I used data for the time interval of July 30 to August 31, 2011.

*Annual temperature maximum*—Maximum stream temperature was operationally defined as the 95<sup>th</sup> percentile for the period July 21 to August 31, 2011. I evaluated the 95<sup>th</sup> percentile temperature for both the aggregate dataset for the entire region and for individual sites using the R software program (version 2.7.2; R Foundation for Statistical Computing, Vienna, Austria). Upper limit estimates for individual sites were obtained by calculating the 95<sup>th</sup> percentile of water temperature at each site over the 42 day sampling period. The aggregate dataset was used in a bootstrapping analysis to estimate the range-wide thermal maximum for *A. heterodon* streams. The aggregate 95<sup>th</sup> percentile was bootstrapped 10,000 times from random subsets of 3,024 observations (the typical dataset length for each stream).

Observations were sampled with replacement. Maximum temperature was estimated by calculating the mean and 95% confidence interval of these 10,000 values.

*Air-water linear regression analysis*—Linear regression analysis of air to water temperature data have been used to define the strength of this relationship and to characterize groundwater sources to stream baseflow (Bogan et al. 2003; O’Driscoll and DeWalle 2006; Kelleher et al. 2012). The strength of the relationship between air and water temperature usually increases with the time interval used to generate average air and water temperatures (Bogan et al. 2003; Kelleher et al. 2012). I determined the average mean temperatures for 1-, 3-, 5-, and 7-day moving windows for the time period of July 30 to August 31, 2011. For each data set, water temperature was regressed against the corresponding air temperature:  $T_w = mT_a + b$ , where  $T_w$  is the water temperature,  $T_a$  is the air temperature,  $m$  is the slope of the relationship, and  $b$  is the  $y$ -intercept. The time interval that generated the highest  $R^2$  values for air-water regressions were used in further analyses (Table 4.1).

The slope,  $m$ , and  $y$ -intercept,  $b$ , in the air-water regression equations for each stream reach were used to evaluate possible sources of stream baseflow following the procedures outlined in Bogan et al. (2003). Stream reaches with temperatures dominated by heat exchange with the atmosphere tend to have high regression slopes and small  $y$ -intercepts. Smaller regression slopes indicate stable baseflow temperatures, which are associated with intermediate to regional groundwater flow to the stream (Erickson and Stefan 2000; Bogan et al. 2003). The  $y$ -intercepts could represent recharge temperatures or average groundwater temperatures for regional or intermediate flow systems (Bogan et al. 2003).

**Table 4.1** Coefficients of the air-water linear regressions for *Alasmidonta heterodon* reaches across the Atlantic Slope. Sites are arranged from north to south. Only those used in the temperature analyses are provided. The last row provides the results of the regression combining all sites.

Site	1-day			3-day			5day			7-day		
	$R^2$	Slope	Intercept	$R^2$	Slope	Intercept	$R^2$	Slope	Intercept	$R^2$	Slope	Intercept
Fort1	0.585	0.720	6.183	0.705	0.861	0.264	0.765	0.954	1.318	0.853	1.063	-0.988
Fort2	0.620	0.669	7.012	0.707	0.786	4.639	0.755	0.895	2.377	0.827	1.008	0.024
Neversink1	0.083	-0.352	21.160	0.089	-0.385	21.750	0.079	-0.351	20.970	0.083	-0.352	21.160
Neversink2	0.433	0.325	13.090	0.509	0.375	12.070	0.586	0.443	10.730	0.736	0.466	10.280
LittleFlat	0.698	0.548	8.448	0.785	0.610	7.228	0.824	0.656	6.311	0.861	0.667	6.102
PaulinsKill	0.669	0.654	7.757	0.745	0.766	5.431	0.787	0.832	4.074	0.876	0.873	3.226
Browns	0.834	0.648	7.629	0.882	0.687	6.778	0.915	0.742	5.553	0.958	0.774	4.827
ThreeBrid	0.784	0.465	10.740	0.833	0.466	10.730	0.883	0.473	10.550	0.942	0.478	10.430
Aquia1	0.798	0.694	6.987	0.857	0.784	4.907	0.909	0.895	2.349	0.952	0.963	0.790
Aquia2	0.776	0.693	6.722	0.862	0.801	4.263	0.895	0.890	2.219	0.943	0.966	0.469
Po2	0.732	0.663	8.943	0.808	0.777	6.357	0.883	0.884	3.952	0.943	0.930	2.933
Shelton1	0.930	0.774	4.397	0.964	0.830	3.029	0.980	0.839	2.819	0.984	0.855	2.423
Shelton2	0.734	0.585	10.020	0.847	0.692	7.368	0.901	0.733	6.340	0.924	0.767	5.552
Cub1	0.896	0.631	7.982	0.933	0.675	6.954	0.958	0.690	6.615	0.972	0.708	6.189
Cub2	0.775	0.568	8.635	0.852	0.625	7.253	0.898	0.633	7.055	0.918	0.659	6.431
Shocco1	0.804	0.723	8.034	0.913	0.861	4.645	0.941	0.894	3.823	0.954	0.911	3.443
Shocco2	0.724	0.637	9.060	0.851	0.798	5.348	0.886	0.843	4.292	0.904	0.873	3.609
Swift1	0.778	0.664	9.412	0.893	0.785	6.370	0.919	0.800	5.989	0.938	0.814	5.668
Swift2	0.838	0.626	9.687	0.924	0.707	7.648	0.950	0.715	7.455	0.960	0.726	7.175
Combined	0.602	0.953	0.805	0.654	1.063	-1.673	0.685	1.132	-3.225	0.698	1.166	-3.988



*Comparison of 2011 data with 30-year average August air temperature*

*data*—August air temperature data for 2011 were compared with 30-year (1981-2010) average August temperature data using spatially distributed data obtained from PRISM (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 10 Jul 2012). These data were converted from an ASCII grid into a floating raster and values extracted for cells containing my sample sites. These data are reported as  $t_{\text{mean\_Aug}}$  in Table 4.2. Each site-specific 30-year mean air temperature value was used in the site-specific air-water regression equations to calculate the 30-year mean August water temperature for each site (water at  $t_{\text{mean\_Aug}}$ ; Table 4.2).

Comparisons between the long-term average water temperature and the observed 2011 temperatures were made for each site by subtracting the predicted 30-year average water temperature from the 7-day maximum. To compare the 30-year mean air temperature at each site to the air temperature associated with a potential thermal threshold, the air-water regressions developed for each site were used to estimate the air temperature needed to bring the water to any identified thermal threshold.

**Table 4.2** Temperature metrics for *Alasmidonta heterodon* reaches across the Atlantic Slope. Sites are arranged from north to south. Only those used in the temperature analyses are provided. All temperatures are in °C. Definitions of column headings are as follows: 95<sup>th</sup> percentile temperature (Q95); rate of temperature change in the 95<sup>th</sup> percentile temperature per hour ( $\Delta Q95$ ); 30-year mean August air temperature ( $t_{\text{mean\_Aug}}$ ; PRISM 2012); site-specific 30-year mean August water temperature calculated using the 30-year mean air temperature in air-water regression equations (water at  $t_{\text{mean\_Aug}}$ ); difference between the 30-year mean water temperature and the observed 7-day maximum in 2011 (diff 7d  $t_{\text{mean}}$ ); temperature needed to bring the water to a 29°C thermal threshold using air-water regressions developed for each site (air at 29°C).

Site	Q95	$\Delta Q95$ (°C/hr)	Maximum water temperature				$t_{\text{mean\_Aug}}$	Water at $t_{\text{mean\_Aug}}$	Diff 7d $t_{\text{mean}}$	Air at 29°C
			1-day	3-day	5-day	7-day				
Fort1	24.31	0.65	25.64	25.23	24.79	24.70	21.14	21.48	3.22	28.21
Fort2	23.63	0.63	24.98	24.68	24.18	24.17	21.27	21.46	2.71	28.75
Neversink1	18.65	0.46	19.66	19.14	17.77	16.74	21.16	13.72	3.03	---
Neversink2	22.32	0.81	23.50	23.14	22.54	22.35	21.16	20.13	2.21	40.20
LittleFlat	22.35	0.55	22.81	22.47	22.15	21.84	20.94	20.06	1.78	34.34
PaulinsKill	25.46	0.55	25.73	25.64	25.29	24.81	21.10	21.64	3.17	29.53
Browns	25.73	0.18	25.18	24.78	24.42	23.92	24.24	23.58	0.34	31.24
ThreeBrid	24.25	0.27	23.89	23.74	23.23	22.80	24.28	22.03	0.77	38.87
Aquia1	26.26	0.38	26.75	26.23	25.82	25.49	24.01	23.91	1.58	29.29
Aquia2	25.99	0.37	26.74	26.21	25.71	25.40	24.01	23.66	1.74	29.53
Po2	27.13	0.47	27.51	27.13	26.68	26.34	24.24	25.46	0.88	28.04
Shelton1	26.94	2.10	34.36	31.79	31.76	30.33	24.57	23.44	6.89	31.07
Shelton2	27.11	0.49	27.70	27.41	27.03	26.87	24.65	24.45	2.42	30.59
Cub1	24.24	0.55	25.37	24.28	24.08	23.95	24.68	22.69	1.26	34.26
Cub2	25.27	1.55	30.21	28.87	27.44	27.55	24.68	23.66	3.89	32.23
Shocco1	28.87	0.58	29.87	29.27	28.99	28.93	25.06	26.26	2.67	28.07
Shocco2	25.94	0.28	27.15	26.40	26.25	26.19	25.07	25.49	0.70	29.09
Swift1	28.52	0.29	29.58	28.68	28.45	28.40	25.44	26.37	2.03	28.67
Swift2	27.89	0.28	28.26	27.92	27.81	27.80	25.58	25.74	2.06	30.07

#### 4.4 Results

##### 4.4.1 Average Daily Temperature and Daily Temperature Variations

Average daily water temperatures generally tracked with air temperatures and increased from northern to southern sites (Fig. 4.2a, b). Daily water temperature variations were markedly lower than air temperature variations and neither were simple functions of latitude (Fig. 4.2c, d). Diurnal water temperature variance data showed three behaviors: 1) sites with  $< 1^{\circ}\text{C}$  diurnal variation in stream temperature; 2) sites with  $1 - 2^{\circ}\text{C}$  of variation in stream temperature; and 3) sites with  $> 5^{\circ}\text{C}$  variation in stream temperature. All 9 sites with  $< 1^{\circ}\text{C}$  diurnal variation in stream temperature were south of the Delaware River basin (Fig. 4.2d). These consisted of 5 sites in the Chesapeake basin (Browns Branch, Three Bridges Branch, Aquia River, and Po River) and 3 draining into Abermarle-Pamlico Sound (Shocco Creek and Swift River). Both sites in the Fort River (Connecticut River basin), 3 sites in the Delaware River (Neversink River, Flat Brook and Paulins Kill), and 3 sites draining into the Abermarle-Pamlico Sound (Shelton Creek, Cub Creek, and Shocco Creek) had  $1 - 2^{\circ}\text{C}$  of diurnal variation (Fig. 4.2d). Two sites in the latter basin (Shelton Creek and Cub Creek) and one site in the Delaware River basin (Neversink River) had  $> 5^{\circ}\text{C}$  variation in diurnal temperature (Fig. 4.2d).

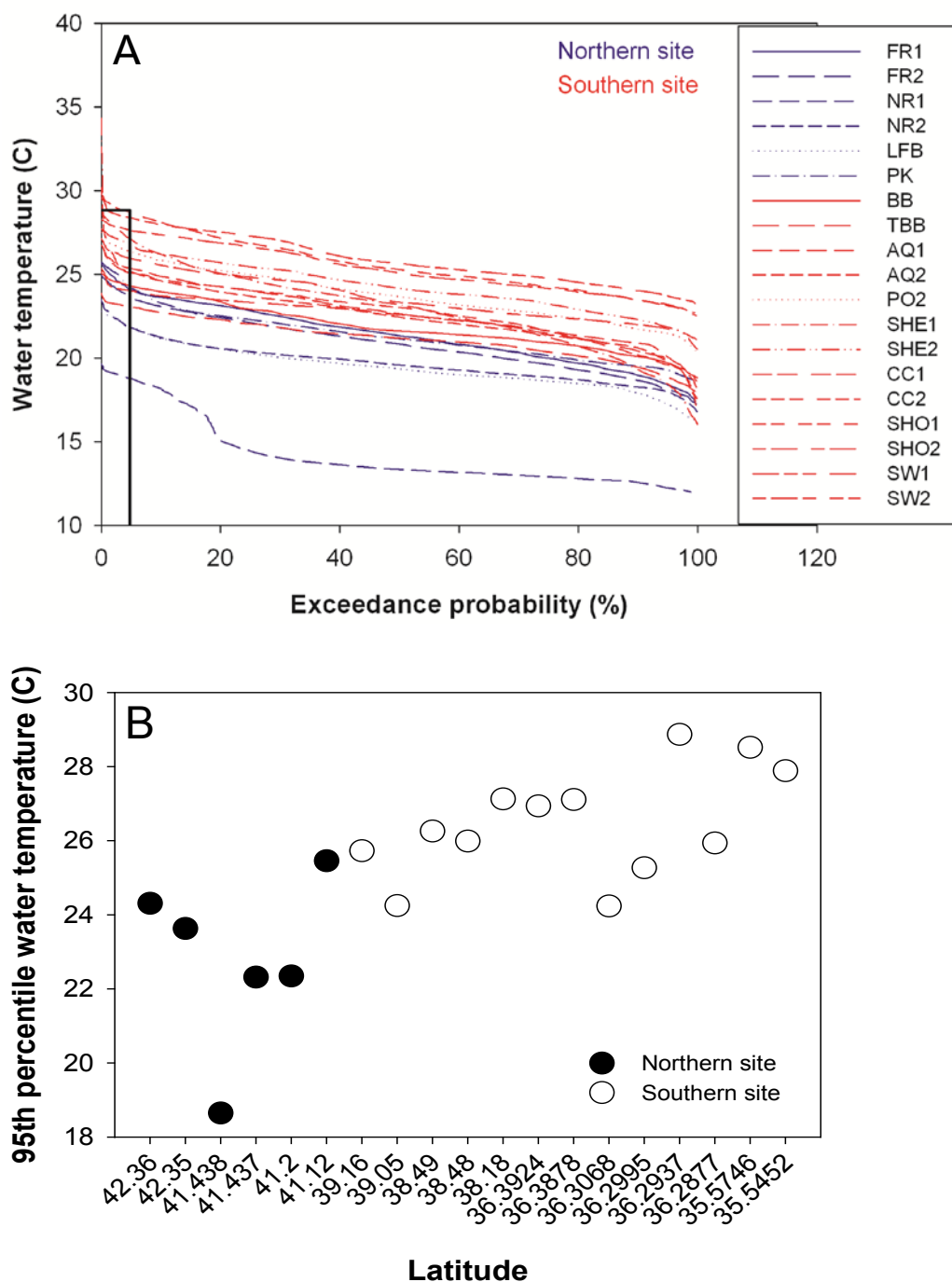
##### 4.4.2 Water Temperature Maxima

Water temperature maximum were evaluated using mean maximum temperature data and the upper 95<sup>th</sup> percentile data for both individual sites and aggregated data. Daily, 3-, 5-, and 7-day mean maximum water temperatures

calculated for each site in 2011 indicate a general increase in daily maxima with decreasing latitude (Table 4.2; Fig. 4.2e). Mean maximum water temperature decreased with increasing time interval (1 to 7-day; Fig. 4.2e, f; Table 4.2).

The cumulative probability analyses of August temperature data indicate that sites have similar distributions of water temperature, but with different mean and maximum values (Fig. 4.4a). The Neversink River site (NR1), however, had markedly colder temperatures and a different temperature distribution than the other sites (Fig. 4.4a). The two Maryland sites in the Chesapeake basin (Browns Branch, BB, and Three Bridges Branch, TBB) resembled the northern sites (Fig. 4.4a). The warmest temperature which was exceeded 5% of the time was  $\sim 28.9^{\circ}\text{C}$  (Fig. 4.4a).

The 95<sup>th</sup> percentile water temperatures varied considerably among sites, ranging from  $18.7^{\circ}\text{C}$  in the Neversink River, NY to  $28.9^{\circ}\text{C}$  in the Shocco River, NC (Table 4.2). The bootstrapped upper 95<sup>th</sup> percentile for aggregated site data was  $27.1^{\circ}\text{C}$ . Across sites, the median 95<sup>th</sup> percentile was  $25.7^{\circ}\text{C}$  (mean  $25.3^{\circ}\text{C}$ ). Plotting the 95<sup>th</sup> percentiles by latitude identified a potential thermal threshold of  $\sim 29^{\circ}\text{C}$  (Fig. 4.4b).



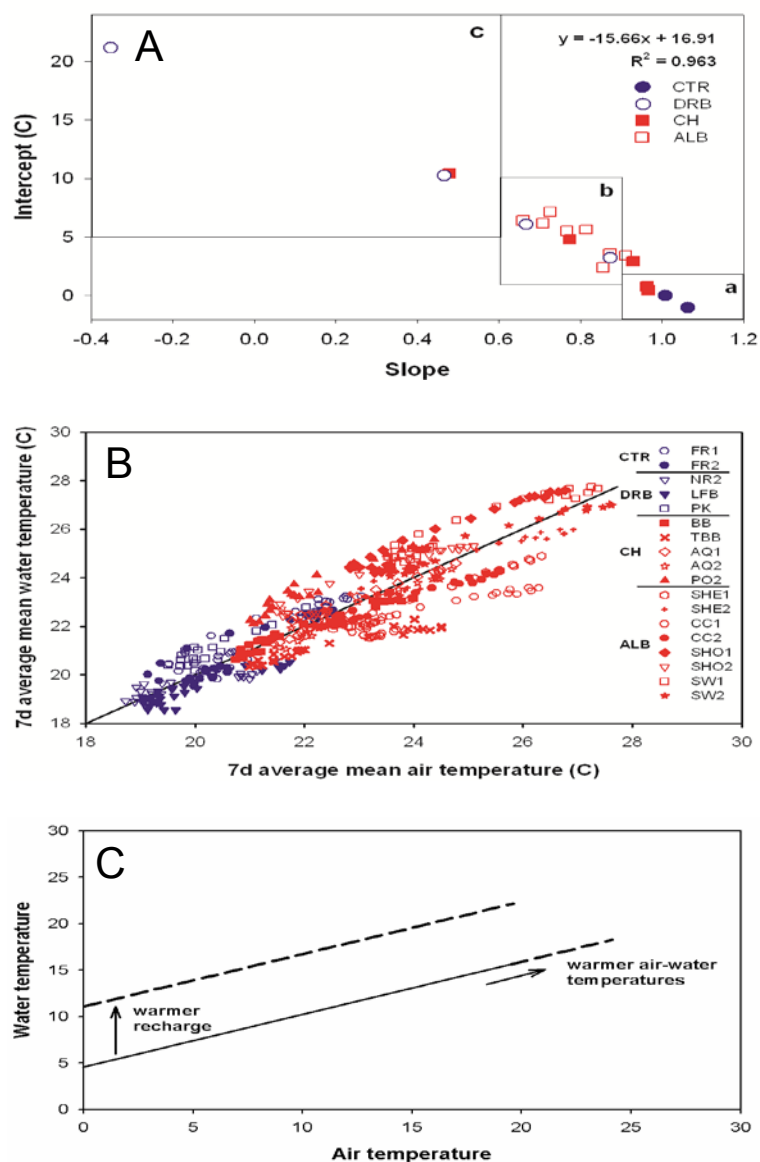
**Figure 4.4** Plots showing (A) temperature exceedance and (B) 95<sup>th</sup> percentile water temperatures. Streams in (A) are arranged north to south with the following codes: FR1 = Fort1; FR2 = Fort2; NR1 = Neversink1; NR2 = Neversink2; LFB = LittleFlat; PK = PaulinsKill; BB = Browns; TBB = ThreeBrid; AQ1 = Aquia1; AQ2 = Aquia2; PO2 = Po2; SHE1 = Shelton1; SHE2 = Shelton2; CC1 = Cub1; CC2 = Cub2; SHO1 = Shocco1; SHO2 = Shocco2; SW1 = Swift1; and SW2 = Swift2. The horizontal line in (A) indicates the temperature at a 5% exceedance.

Most of the stream sites exhibited a similar rate of temperature change ( $^{\circ}\text{C} / \text{hr}$ ); however, one site in Shelton Creek and one site in Cub Creek had markedly larger rates of temperature change than the other sites (Shelton1 and Cub2; Table 2). The 95<sup>th</sup> percentile rate of change averaged  $0.61^{\circ}\text{C} / \text{hr}$  (std. dev. 0.11) for the northern sites and  $0.60^{\circ}\text{C} / \text{hr}$  (std. dev. 0.55) for southern sites. If the two anomalous southern sites (Shelton1 and Cub2) are removed, the southern region actually indicates lower rates of water temperature change ( $0.38^{\circ}\text{C} / \text{hr}$  (std. dev. 0.12)).

#### 4.4.3 Air-Water Regression Equations and Characterization of Baseflow Sources

Air-water regression relationships were determined for each site and were used to evaluate water sources. The  $R^2$  values for the air-water temperature relationship increased for all sites as the time interval used to generate average air and water temperatures was increased (Table 4.1). Streams in the Delaware River basin exhibited the poorest relationship between stream temperature and air temperature for all exposure periods ( $R^2$  values from 0.47 to 0.64). In contrast, high  $R^2$  values for air-water regression equations were determined for the Albermarle-Pamlico and Chesapeake basins (0.78 to 0.95).

I used the slope and  $y$ -intercept obtained from 7-day mean air-water regression equations for each reach to create a plot of regression slope value versus  $y$ -intercept (Fig. 4.5a). Following Bogan et al. (2003), this plot was divided into three baseflow source regions. Region A contains sites with high slope values and low  $y$ -intercepts and includes stream reaches in the Fort River (MA; CTR) and Aquia Creek (VA; CH; Fig. 4.5a). Region A is interpreted by Bogan et al. (2003) to reflect shallow groundwater sources that are recharged during cold seasons. In contrast, region C



**Figure 4.5** (A) Relationship between slope and y-intercept resulting from the air-water regression equations. The diagram indicates three regions, C, B, and A, which can be interpreted as regions with high regional groundwater contributions, C, and declining deep groundwater contributions (B to A; Bogan et al. 2003). Sites are colored as northern (blue) or southern (red). Basin codes are as follows: CTR = Connecticut River basin; DRB = Delaware River basin; CH = Chesapeake basin; and ALB = Albermarle-Pamlico basin. (B) 7-day average mean air vs. water temperatures with colors indicating northern (blue) and southern (red) sites. Streams are arranged north to south with the following codes: FR1 = Fort1; FR2 = Fort2; NR2 = Neversink2; LFB = LittleFlat; PK = PaulinsKill; BB = Browns; TBB = ThreeBrid; AQ1 = Aquia1; AQ2 = Aquia2; PO2 = Po2; SHE1 = Shelton1; SHE2 = Shelton2; CC1 = Cub1; CC2 = Cub2; SHO1 = Shocco1; SHO2 = Shocco2; SW1 = Swift1; and SW2 = Swift2. The line indicates a 1:1 relationship between air and water. (C) A schematic of how climate change can affect the distribution seen in plot (B). Changes can include an increase in stream recharge temperature (increase in y-intercept) or an increase in both air and water temperatures (increase out the x and y axis).

sites (Neversink River (NY; DRB) and Three Bridges Branch (MD; CH)), show little variation in groundwater temperature with air temperature and have high  $y$ -intercepts (Fig. 4.5a). Following the approach of Bogan et al. (2003), these are interpreted to be sites of deep or regional groundwater contributions. Many of the sites, including most of the sites in the southern range, are in region B, which is interpreted to represent intermediate groundwater sources (Fig. 4.5a). These sources have higher  $y$ -intercepts and less variable groundwater temperatures. The range of  $y$ -intercept values, particularly for the summer region, could represent variable recharge temperatures.

Northern sites are identified in each of the three hydrological regions (Fig. 4.5a). Sites with 7-day mean maximum water temperatures  $< 23^{\circ}\text{C}$  are located in the northern region where air temperatures are lower (Fig. 4.5a, b). Region A contains sites with 7-day mean maximum temperatures between  $23 - 27^{\circ}\text{C}$  (Fig. 4.5a). Many of the southern sites have high air and water temperature data (Fig. 4.5a, b), but regression slope and intercept values that identify with intermediate groundwater source regions (Fig. 4.5a).

#### 4.4.4 Predicted Water Temperatures Based on 30-Year Mean August Air Temperatures

One of the issues with examining maximum stream temperatures with data from only one year is that the temperatures may not be representative of long-term data. Therefore, I used the air-water equations to estimate water temperatures for the 30-year average based on the mean August temperature from 1981 to 2010. The 7-day average air-water temperature relationships were generally strong (all sites south of the Delaware  $R^2 > 0.9$ ; Table 4.1) These relationships were used to predict water



temperatures for average August values. These water temperatures ranged from 20.06°C in Flat Brook to 26.37°C in the Swift River, NC (Table 4.2). The 7-day maxima obtained from 2011 data generally exceeded the average water temperatures by 0.34 to 3.89°C (Table 4.2).

The maximum water temperature data from 2011 indicated that all sites were below 29°C during the warmest month for 95% of the time. To determine how close each site was to this potential thermal maximum, I used reach-specific air-water temperature regression equations to calculate the air temperature required to obtain 29°C water temperatures in all reaches. These data suggest that air temperatures would have to rise 7 to 19°C for the month of August to exceed the potential maximum at the northern sites, and 3 to 10°C to exceed this maximum at the southern sites (Table 4.2). Chesapeake Bay sites were variable but overlapped these northern and southern values (Table 4.2).

#### 4.5 Discussion

Field data identified an August (annual maximum) stream water temperature maxima of 29°C for *A. heterodon* in 2011. This is an apparent lower temperature maximum than has been reported for three other co-occurring mussel species (*Alasmidonta varicosa*, *Elliptio complanata*, and *Strophitus undulatus*; Strayer and Ralley 1991; Baldigo et al. 2003), all of which have thermal limits > 29°C. Adults of the three species sampled from Pine Creek, Pennsylvania, had critical thermal maxima (a measure of thermal tolerance, in this study defined as the onset of extreme gaping) between 39.5°C and 42.7°C under acclimation temperatures of 15°C and 25°C (Galbraith et al. 2012). Artificially propagated *A. varicosa* (glochidia and

juveniles) had incipient lethal temperatures (an estimate of an organism's lethal temperature, in this study defined as the temperature that causes mortality in 50% of the population or LT50) that were slightly lower than found in Pine Creek (Pandolfo et al. 2010). LT50s were 38°C and 36.1°C (glochidia) and 35°C and 35.1°C (juveniles) at an acclimation temperature of 22°C and 27°C, respectively (Pandolfo et al. 2010).

These apparent differences in thermal tolerance among species may also be due to differences between field and laboratory studies. Laboratory results can be difficult to compare to field-based conditions due to: 1) difficulties in creating optimal conditions for growth and physiological functions in a laboratory environment (Ganser et al. 2013) and 2) the inability to account for the array of abiotic factors and biotic interactions which can influence field distributions (Beitinger and Fitzpatrick 1979; Shrode et al. 1982). Thermal niches of fish species and fish communities have been calculated from field temperature measurements and used as thermal maximum for species (Wehrly et al. 2003; Huff et al. 2005). Thus, the field-based threshold of 29°C could serve as a potential realized thermal limit for *A. heterodon* in Atlantic Coast basins of the U.S.

The 1-day to 7-day thermal maxima may not be as important to organisms as either the rate of temperature change or the temporal extent of daily fluctuations (Ganser et al. 2013). For example, brook and brown trout in Michigan and Wisconsin streams demonstrated decreased tolerance for mean and maximum temperatures as the exposure period increased from 1 to 63 days (Wehrly et al. 2007). Laboratory studies of juvenile freshwater mussels also showed decreased survival with increased

exposure time to high temperatures (Ganser et al. 2013). In my study, southern sites exhibited low diurnal temperature variability and maximum temperatures that were markedly greater than those in the northern sites; these characteristics combined would expose southern sites to longer durations of maximum temperature. All sites with  $< 1^{\circ}\text{C}$  diurnal variation in stream temperature were south of the Delaware River basin. When the two anomalous sites were removed, the 95<sup>th</sup> percentile rates of water temperature change in southern sites were approximately half of those for northern sites. Thus, although these sites respond to increases in average air temperature, they do not show rapid rates of temperature changes during the day. These data suggest that mussels that inhabit the southern portion of the range live in warmer waters, but they may tolerate these waters due to the slow increase in temperature throughout the summer months and the low diurnal variations in temperatures.

The graph of 7-day air and water temperatures (Fig. 4.5b) indicates that southern sites exhibit a wider range in water temperature for a given air temperature than the northern sites. This suggests a range of water sources, recharge temperatures, or mixtures of hydrological processes for these southern sites. Most of the southern sites are found in the intermediate region of the slope-intercept plot; these intermediate flow systems may have recharge temperatures that reflect seasonal recharge temperatures that may vary among the sites compared to deeper flow systems (Tóth 1963). In the southern portion of *A. heterodon*'s range, groundwater recharge primarily occurs during fall to winter months due to high evapotranspiration during summer months, although significant recharge could also occur during autumn

tropical storms or hurricanes, leading to heterogeneity in recharge temperatures and  $y$ -intercept values, which are suggested by Figure 4.5b.

It is possible that *A. heterodon* has developed behavioral adaptations to survive in warmer stream temperatures that are encountered in these southern systems. The mussel may seek out habitats that provide thermal refugia during the summer. Areas associated with groundwater springs, seeps, or upwellings can dampen extreme temperatures, creating refugia from excessive summer temperatures (Power et al. 1999). *A. heterodon* occurrences have been associated with groundwater seeps in the mainstem Delaware River (J. Cole, unpublished data). Discrete groundwater seeps can produce plumes with up to 9.5°C cooler water than the surrounding water column (Briggs et al. 2013). Juvenile and adult *A. heterodon* can also bury into the substrate (Strayer et al. 1996), which can be a behavioral adaptation to reduce exposure to disturbances and to prevent dislocation during high water events (Balfour and Smock 1995). This behavior could also have been an adaptation to seek cooler water that would provide relief from high water temperatures. Additional diffuse groundwater upwelling through the streambed influences streambed temperatures at the greater depths ( $\sim >0.06$  m) inhabited by juveniles (Briggs et al. 2013). These thermal characteristics can be partially controlled by fine-scale streambed topography (Briggs et al. 2013). Thus, it is possible that *A. heterodon* are occupying finer scale thermal niches than were evaluated with my reach-level analysis.

Temperature, except at its extremes, may act as a cue toward locating other resources that would enhance survival (Coutant 1987). For example, the intermediate to deep groundwater sources that can stabilize thermal regimes for relatively small

streams can also affect stream chemistry (Tóth 1963, Tóth 1970). Thus, it may be possible that groundwater chemistry, in addition to or instead of a thermal threshold, is a constraint to *A. heterodon* occurrence. Mussels need calcium carbonate for shell growth and reproduction (Pynnönen 1991). In Flat Brook, New Jersey, *A. heterodon* were found downstream of an abrupt change in water chemistry where waters became saturated with respect to aragonite (a form of calcium carbonate; C.A. Campbell, unpublished data). This change in water chemistry reflected changes in groundwater sources and it was also accompanied by a temperature change. Thus, the constraints of groundwater chemistry on population distributions should also be examined and the covariance of appropriate geochemical and thermal characteristics evaluated.

In contrast to the southern sites, less groundwater recharge occurs during winter months in the northern sites due to frozen ground. Groundwater recharge primarily occurs in the fall and during spring snowmelt. The August temperature data for the northern sites suggest that the northern climate keeps water temperatures cooler even for shallow groundwater systems. It is also possible that intermediate to deep groundwater sources in the north reflect glacial era groundwater recharge temperatures. Under the current climate, groundwater source is less important in these colder northern sites than for the southern sites. Shifts in the recharge period to late fall (due to tropical storms) and a decrease in the importance of snowmelt could result in warming of recharge temperatures for these northern sites.

An increase in recharge temperatures could adversely affect *A. heterodon* populations. The warmer groundwater temperatures could initially increase mussel heart rate and metabolism (Pandolfo et al. 2009), however once a critical thermal

limit is reached the heart rate can abruptly decrease and remain depressed (Braby and Somero 2006) to lower the metabolic rate and conserve energy (Ganser et al. 2013). It has been suggested that this decrease in heart rate can result from a behavioral response to stress (heart valve closure) that could be advantageous for short-term threats such as desiccation at high temperatures (Braby and Somero 2006). However, prolonged physiological thermal stress could lower the fitness and, ultimately, the survival of *A. heterodon*. Warmer recharge temperatures could also influence mussel reproduction. The number of accumulated degree days is a measure of the total amount of heat to which an organism has been subjected and has been associated with the timing of reproduction and gamete development (Galbraith and Vaughn 2009). If recharge temperatures are increased enough to alter thermal regimes, it could disrupt the reproductive cycle and inhibit successful reproduction (Heinricher and Layzer 1999; Galbraith and Vaughn 2009).

Water temperature increases accompanying climate change could influence *A. heterodon* in two ways. First, thermally stable sites in the southern portion of the *A. heterodon* range may rely on groundwater recharge during the winter. Changes in the timing of recharge accompanying climate change may increase recharge temperature (Fig. 4.5c). Temperatures causing up to 50% mortality can vary by as little as  $\sim 5^{\circ}\text{C}$  (Pandolfo et al. 2010). Therefore, small increases in maximum temperatures ( $\sim 2^{\circ}\text{C}$ ) can significantly increase mortality (Johnstone and Rahel 2003). Some of the southern sites appear to have water temperatures near the potential  $29^{\circ}\text{C}$  thermal limit for *A. heterodon*. Thus, warmer recharge temperatures could eliminate some southern streams as suitable habitat, potentially shrinking the species' range (Fig. 4.5c).

Second, groundwater temperatures are expected to track increases in mean annual air temperatures, lessening the cooling capacity of groundwater and shrinking or eliminating summer refugia (Meisner et al. 1988; Power et al. 1999). This would push *A. heterodon* sites outward in Fig. 4.5b (e.g., Fig. 4.5c), which would cause the thermal regimes to become more dependent on hydrological processes. Even though some cold water populations may eventually be lost, these new thermal regimes may not shrink the overall species' range. The loss of more thermally sensitive species may provide opportunities for the invasion and spread of nonnative species (Olden et al. 2006).

My results suggest that 29°C could serve as a potential realized thermal limit for *A. heterodon*. In the northern part of its range, *A. heterodon* occupy sites with a wide range of groundwater sources but cooler thermal regimes than southern populations and may be susceptible to thermal stress. In contrast, the southern, Coastal Plain sites have warmer thermal regimes created by intermediate flow regimes that have variable recharge temperatures probably dependent on the timing of recharge. This region has likely undergone changes to the thermal regime for thousands of years that have driven the species to develop behavioral adaptations that reduces thermal stress accompanying higher temperatures (Ganser et al. 2013). *A. heterodon*'s wide distribution across the Atlantic Slope might afford the species a high degree of genotypic or phenotypic plasticity or wide thermal tolerances if these populations can be maintained (Ganser et al. 2013). Assuming a thermal threshold of 29°C, my predictions indicated that a few southern sites may have a buffer of only ~3°C before climate alone would drive water temperatures over this limit. Urban and

suburban development threaten many Coastal Plain sites in the southern region and could affect temperature regimes (Nelson and Palmer 2007; Kaushal et al. 2010). The combined effects of climate change and urbanization could increase water temperatures into ranges that affect individual species and, potentially, community structure (Nelson and Palmer 2007; Nelson et al. 2009). Temperature can influence the ability of mussels to recover (i.e., turn upright, move, and burrow) following disturbances associated with conservation activities such as relocation, stocking, and status surveys (Waller et al. 1999). Thus, identifying a potential thermal limit for *A. heterodon*, as well as better understanding differences in thermal regimes across the species' range, provides valuable information to guide conservation activities.



## Chapter 5: Physical and chemical constraints limit the habitat window for an endangered mussel

### 5.1 Abstract

The complex life history and sessile nature of native freshwater mussels make them among the most imperiled North American freshwater taxa. Development of effective conservation and restoration strategies for mussels requires identification of physical and chemical constraints on the distributions of individual mussel species. I examined whether the spatial distribution of the endangered *Alasmidonta heterodon* in Flat Brook, a tributary of the upper Delaware River, was constrained by water chemistry (i.e., calcium availability), bed mobility, or both. *A. heterodon* populations were bracketed between upstream sites with dilute water chemistry and downstream sites with mobile bed substrates. Upstream reaches were unsaturated with respect to aragonite, while near the confluence water was saturated for aragonite during summer baseflow but channels are steep with high bed mobility. Variability in bed mobility and water chemistry along the length of Flat Brook create a “habitat window” for *A. heterodon* defined by bed stability (mobility index  $\leq 1$ ) and aragonite saturation (saturation index  $\geq 1$ ). This habitat window could expand or narrow due to land-use or climate changes that affect base-flow chemistry or flood magnitudes.

## 5.2 Introduction

Native freshwater mussels (families Margaritiferidae and Unionidae) are vital to the functioning of freshwater ecosystems, but are among the most imperiled of freshwater taxa (Lydeard et al. 2004; Strayer et al. 2004; Vaughn et al. 2004; Spooner and Vaughn 2006). Widespread declines in species ranges have been attributed to changes in chemical or physical habitats and to dams or other structures that inhibit upstream migration of fish hosts (Smith 1985; Bogan 1993a; Locke et al. 2003; Bogan 2008). The sedentary nature of adult mussels makes them particularly vulnerable to local habitat changes, including increases in bed mobility, water pollution, deposition of fine sediment, and other habitat alterations that are often associated with urbanization, agriculture, logging, and other land-use changes (McRae et al. 2004; Gangloff and Feminella 2007; Randhir and Hawes 2009). Climate change may alter river flow regimes and thus affect bed stability and water chemistry (Poff et al. 1997). Therefore, identification of the factors that constrain the distributions of individual mussel species is needed to develop effective conservation or restoration strategies.

Previous research indicates that mussels require bed stability but also a suitable range of stream velocities; fast enough to maintain oxygen levels, provide food, transport nutrients, and flush wastes, yet slow enough to enable settlement of juveniles (Layzer and Madison 1995; Hardison and Layze, 2001; Morales et al. 2006; Steuer et al. 2008; Strayer 2008; Allen and Vaughn 2010; Maloney et al. 2012). Unionid shells are composed of calcium carbonate minerals, primarily aragonite (Wilbur 1964). In the northeastern United States during late summer low flows,

evaporative concentration of solutes in water, photosynthetically-driven increases in pH, and warm water temperature all create conditions that may favor aragonite precipitation (Candy et al. 2011). For long-term sustainability, mussels must be able to produce shell during these favorable conditions and retain the carbonate during less favorable conditions.

I sought to identify physical and chemical habitat characteristics that constrain the distribution of the federally endangered dwarf wedgemussel (*Alasmodonta heterodon*) in Flat Brook, a tributary of the upper Delaware River. The species is in decline due to a suite of human activities (e.g., impoundments, pollution, channel alteration, and siltation; U.S. Fish and Wildlife Service 1993, 2007; Locke et al. 2003). Populations of *A. heterodon* generally occur in distinct, widely separated, low density patches in linear, unbranched sections of stream (Strayer et al. 1996). These sections typically consist of fine sediments with moderate depths and slow to moderate flows that are temporally stable (Strayer and Ralley 1993; Michaelson and Neves 1995; Maloney et al. 2012). *A. heterodon* distribution might also be related to some factor associated with calcium concentration (Strayer 1993). In Flat Brook, the range of *A. heterodon* is associated with a decrease in stream gradient (W. Lellis, U.S. Geological Survey, unpublished data). Changes in stream gradient reflect geological or geomorphological boundaries that influence geomorphic characteristics (bed grain size, fluid shear stress, bed mobility, etc.), flow regimes, groundwater contributions to streams, and stream water chemistry (Tóth 1963; Tóth 1970; Boxall et al. 2008).

I tested two hypotheses about the distribution of *A. heterodon* in Flat Brook:

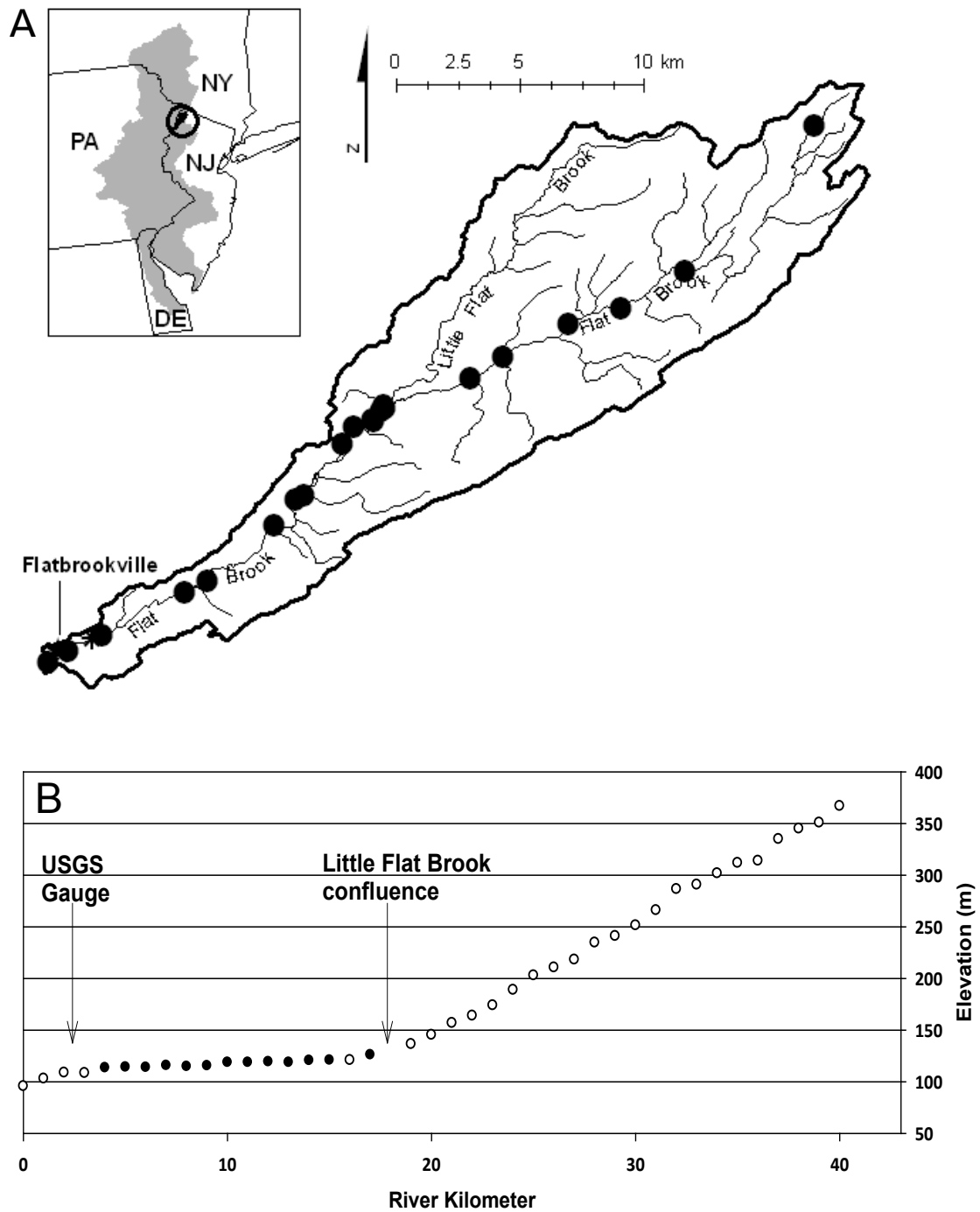
- 1) The spatial distribution of *A. heterodon* is constrained by the physical stream

habitat, therefore *A. heterodon* are found where bed substrate is stable; and 2) *A. heterodon* distributions are constrained by local water chemistry and are found where aragonite can be precipitated during summer low flow conditions.

### 5.3 Methods

#### 5.3.1. Study Area

Flat Brook is a 3<sup>rd</sup> order tributary to the Delaware River basin, the latter extending 35,224 km<sup>2</sup> into four states (Fig. 5.1a). The Delaware is undammed in its lower 531 km and supports migratory fishes such as the American eel (*Anguilla rostrata*), a host fish for *Elliptio complanata* (Lellis et al. 2013), which is the numerically dominant mussel species in the basin (W. Lellis, U.S. Geological Survey, unpublished data). The 166 km<sup>2</sup> Flat Brook basin is primarily forested and the water quality is considered unimpaired (Albert and Limbeck 2000). The basin is located in the Valley and Ridge province, and rock formations include the Shawangunk conglomerate and the carbonates, sandstone, and shale of the High Falls formation (Cook 1868). Flat Brook flows through surficial glacial tills in upstream reaches, but is incised through these sediments into Paleozoic sedimentary bedrock in downstream reaches likely in response to the post-glacial, meltwater-induced lowering of the Delaware River (Salisbury et al. 1902). Thus, the largest streambed gradients occur near the mouth (< river km 2.5). Upstream of river km 2.5, Flat Brook remains relatively flat until ~river km 21 where an abrupt increase in gradient occurs upstream of its major tributary, Little Flat Brook (20.4 km long), which enters Flat Brook at ~river km 17.8 (Fig. 5.1b). The gradient decreases near the headwaters (> river km 30) with an increase in surrounding wetland area. Average daily temperatures range from



**Figure 5.1** A) Flat brook watershed and its location within the Delaware River basin. Sites shown were sampled for geomorphology, water chemistry, or both. The location of the stream gage is indicated with an asterisk (\*). B) Longitudinal profile of Flat Brook showing the location of *Alasmidonta heterodon* (dark circles). Mussel qualitative survey data is aggregated at the kilometer-scale for display (W. Lellis, USGS, unpublished data).

-9 to 28°C and average annual rainfall and snowfall totals are 122 cm and 104 cm, respectively (National Weather Service). The 1.5 year recurrence interval discharge, my reference discharge for bankfull stage, is 34 m<sup>3</sup>/s at the U.S. Geological Survey Flat Brook gauge north of Flatbrookville, New Jersey (USGS Gauge number 01440000; Fig. 5.1). Three flood peaks occurred in 2011 (a snowmelt peak and 2 tropical storm peaks).

In 2006 and 2007, the U.S. Geological Survey qualitatively surveyed the entire 41.2 km Flat Brook (Fig. 5.1). The 205 contiguous sections were visually searched for a cumulative time of 17,467 minutes or approximately 7.1 hr/river km. *A. heterodon* were confined to the downstream, low gradient reaches of the stream (228 animals, CPUE 0.5 animals/hr; Fig. 5.1b; W. Lellis, U.S. Geological Survey, unpublished data). These results were comparable to an earlier (2001) U.S. Geological Survey qualitative survey, suggesting the distribution of *A. heterodon* was stable over time (W. Lellis, U.S. Geological Survey, unpublished data). Thus, I used the coordinates from the 2006/2007 surveys as a guide for sampling within and outside *A. heterodon* reaches. My goal was to determine if there was something unique about the geomorphic and geochemical habitats within this low gradient section of stream that makes it suitable for *A. heterodon*.

### 5.3.2. Geochemical Measurements and Calculations

I examined aragonite saturation indices to determine if calcium is available to mussels during the annual stream flow minimum, generally late August, a period with water temperature and pH maxima and high annual solute concentrations. Saturated water is conducive to aragonite precipitation and calcium is available to mussels,

while unsaturated waters are conducive to the dissolution of aragonite, thus mussel shells. The aragonite saturation index (SI) cannot be measured directly, but requires calculation of several variables: concentrations and chemical activities of  $\text{Ca}^{2+}$  and  $\text{HCO}_3^-$  and the chemical activities of  $\text{H}^+$  and  $\text{CO}_3^{2-}$ . I estimated concentrations by measuring specific conductance in the field, generating relationships between specific conductance and the concentrations of different parameters using U.S. Geological Survey National Water Quality Assessment Program (NAWQA) data, and using these relationships to estimate concentrations with my specific conductance measurements. I used a subset of my field data to test the reliability of the NAWQA relationships before using them to estimate concentrations for my remaining field data. These estimates were then used to calculate chemical activities and, subsequently, an aragonite SI.

Water chemistry was sampled on August 24, 2011 at 15 sites along Flat Brook, from upstream of the change in gradient (~river km 22.5) downstream to the mouth. Two sites were also sampled in downstream reaches of the main tributary, Little Flat Brook. Additionally, following baseflow recovery from floods associated with Tropical Storm Irene in early September, baseflow water chemistry was sampled October 22-23 at 13 sites: 10 that bracketed the changes in water chemistry observed in Flat Brook during the summer, one from the mouth of Little Flat Brook, and two groundwater samples from wells near Flat Brook. One spot measurement of pH, specific conductance (uS/cm), and temperature ( $^{\circ}\text{C}$ ) was made at each site with a YSI Professional Plus instrument (YSI Incorporated, Yellow Springs, OH, USA; Table 5.1). For October sampling, alkalinity was also measured at the stream with a semi-

quantitative test kit and, on samples that maintained their pH values, bicarbonate concentrations were measured by titration with a Hach digital titrator within 48 hours of field sampling. Calcium concentrations for October samples were also determined by Inductively Coupled Plasma Mass Spectrometry (ICP-MS).

Calculation of the SI for aragonite required several steps. First, baseflow water chemistry analyses from archived NAWQA data at Port Jervis, NY in 1998-1999 (upper Delaware; U.S. Geological Survey National Water Quality Assessment Data Warehouse available at: [http://cida.usgs.gov/nawqa\\_public/apex/f?p=136:1:0](http://cida.usgs.gov/nawqa_public/apex/f?p=136:1:0)) were used to develop relationships between specific conductivity and concentrations of  $\text{Ca}^{2+}$  and  $\text{HCO}_3^-$  and the ionic strength ( $I$ ) of the solution:

$$I = \frac{1}{2} \sum_{i=1}^n c_i z_i^2$$
 where  $c_i$  is the molar concentration of ion  $i$ ,  $z$  is the charge number of that ion, and the sum is taken over all ions in the solution. The resulting relationships are:

$$[\text{Ca}^{2+}] = 0.0808(SC) \quad R^2 = 0.99$$

$$[\text{HCO}_3^-] = 0.329(SC) \quad R^2 = 0.88$$

$$I = 0.000019(SC) \quad R^2 = 0.90$$

Where  $SC$  is specific conductivity in  $\mu\text{S}/\text{cm}$ , concentrations of calcium and bicarbonate are in  $\text{mg}/\text{L}$ , and ionic strength is in  $\text{moles}/\text{L}$ . To test these equations, I used my October field measurements of specific conductance to predict calcium and bicarbonate, then compared the predictions with corresponding lab measurements (Table 5.1). These equations were then used to estimate the ionic strength of each solution and concentrations of  $\text{Ca}^{2+}$  and  $\text{HCO}_3^-$  for the August field data (Table 5.1).



**Table 5.1** Field and analytical water chemistry data for sites in the Flat Brook basin in 2011.

River (km)	Specific Conductivity (uS cm <sup>-1</sup> )		pH		Ca (mgL <sup>-1</sup> )	Ca (mg L <sup>-1</sup> )	Ca (mgL <sup>-1</sup> )	HCO <sub>3</sub> <sup>-</sup> (mgL <sup>-1</sup> )	HCO <sub>3</sub> <sup>-</sup> (mgL <sup>-1</sup> )
	August	October	August	October	August (predicted)	October (predicted)	October (measured)	October (predicted)	October (measured)
0	189.7		8.56		<i>15.3</i>				
0.93	189.5		8.63		<i>15.3</i>				
2.51	189.3	173.9	8.56	8.46	<i>15.3</i>	<i>14.1</i>	14.3	57	58
6.66	194.9		8.33		<i>15.7</i>				
10.54	200.1		8.43		<i>16.2</i>				
12.5	201.8	162.1	8.45	8.3	<i>16.3</i>	<i>13.1</i>	12.9	53	59
15.29	199.3		8.4		<i>16.1</i>				
15.71	205.2	190.4	8.57	8.44	<i>16.6</i>	<i>15.4</i>	15.6	62	62
16.48	204.1		8.58		<i>16.5</i>				
17.17	199.5		8.64		<i>16.1</i>				
17.22	198.7		8.65		<i>16.1</i>				
17.77	247.6	290	8.56	8.86	<i>20</i>	<i>23.4</i>	22.8	95	93
17.93	88.7		7.72		<i>7.2</i>				
20.97	80	68.2	7.5	7.56	<i>6.5</i>	<i>5.5</i>	5.5	22	22
22.45	59.4	53.2	7.34	7.51	<i>4.8</i>	<i>4.3</i>	4.6	18	
25.06		50.1		7.6		<i>4.0</i>	4.2	16	13
27.05		49.3		7.46		<i>4.0</i>	4.2	16	
27.05*		252.3		8.05		<i>20.4</i>	19.8	83	90
30.08		41.5		7.27		<i>3.4</i>	3.4	14	18
41.04		26.7		7.34		<i>2.2</i>	3.3	8.7	
41.04*		150		7.2		<i>12.1</i>	14.0	49	65
17.85**	186.8	327.3	8.62	8.87		<i>26.4</i>	26.1	108	115
18.04**	326.3		8.65						

\*indicates a groundwater sample; \*\*indicates a Little Flat Brook site; italics indicate examples of Ca and HCO<sub>3</sub><sup>-</sup> concentrations predicted from equations given in text; measured values are not in italics

Next, I calculated chemical activities. Ionic strength was used in the Dubeye-Huckle equation to calculate activity coefficients ( $\gamma$ ) for  $\text{Ca}^{2+}$  and  $\text{HCO}_3^-$  for each water sample. Chemical activity of  $\text{Ca}^{2+}$  and  $\text{HCO}_3^-$  is the product of the activity coefficient and molar concentration. The activity of carbonate ( $\alpha\text{CO}_3^{2-}$ ) was calculated from bicarbonate and  $\text{H}^+$  activities by assuming equilibrium dissociation of bicarbonate according to the following equilibrium equation:

$K = (\alpha\text{H}^+ * \alpha\text{CO}_3^{2-}) / (\alpha\text{HCO}_3^-)$ , where  $K$  is the dissociation constant for the reaction (at the sample temperature),  $\alpha\text{H}^+$  is obtained from field pH measurements, and  $\alpha\text{HCO}_3^-$  was determined as defined above.

Finally, the SI for aragonite was calculated for each sample. SI is defined as the ratio of the ion activity product (IAP) to the solubility product for aragonite,  $K_{sp}(\text{aragonite})$ , which is adjusted for temperature:

$SI(\text{aragonite}) = (\alpha\text{Ca} * \alpha\text{CO}_3^{2-}) / K_{sp}(\text{aragonite})$ . Due to the wide range of values, the SI is expressed as the log (SI) and values  $> 0$  indicate saturated conditions. Field and analytical data for Flat Brook are presented in Table 5.1.

### 5.3.3. Geomorphic Characteristics and Determination of Bed Substrate Stability

Bed mobility was determined by calculating the ratio of bankfull dimensionless shear stress to critical dimensionless shear stress for the observed bed grain size distribution. This ratio can be used as a stability index that indicates potential streambed mobility at bankfull and higher flows. Data required for this analysis include field measurements of bankfull channel morphology (area, width, and depth), bed grain size distributions, and water surface gradient at each stream reach along Flat Brook. From these field measurements, the following hydraulic

parameters were calculated: hydraulic radius (area/perimeter), bankfull bed shear stress, bankfull dimensionless shear stress, critical dimensionless shear stress, and dimensionless shear stress ratio. Channel geomorphic measurements and bed stability were evaluated for the bankfull channel, the stage where flow is barely contained within the channel banks in most channels (Leopold et al. 1964; Gordon et al. 2004).

Channel morphology and streambed particle size distributions were measured at 10 reaches along the length of Flat Brook during August 2010 (Table 5.2). In each

**Table 5.2** Flat Brook geomorphic data (measured) and bankfull hydraulics (calculated).  $\tau_{bf}^*$  is bankfull dimensionless shear stress and  $\tau_{bf}^* / \tau_{crit}^*$  is the dimensionless shear stress ratio. For the latter, values approaching or  $>1$  indicate mobile bed sediments at bankfull discharge.

River (km)	Basin Area (km <sup>2</sup> )	Bankfull Width (m)	Bankfull Depth (m)	$\tau_{bf}^*$	$\tau_{bf}^* / \tau_{crit}^*$
0.11	171.55	21.48	0.83	0.092788	1.124851
2.51	168.15	19.67	0.74	0.025842	0.318471
5.79	161.60	19.27	1.19	0.069787	0.564754
6.66	158.98	17.03	0.93	0.067262	0.633228
12.50	144.94	17.28	0.81	0.02117	0.130372
15.29	139.40	14.49	0.85	0.028509	0.276233
15.71	131.64	17.82	0.85	0.015632	0.124508
20.97	75.61	16.95	0.74	0.113263	0.95579
30.08	23.39	7.28	0.42	0.00987	0.076612
41.04	2.23	4.93	0.37	0.056275	0.213923

reach, bankfull stage was identified, 10-15 measurements of depth were taken across the channel width, the area of each channel increment was calculated using the equation area = depth \* width, and the areas of each channel increment were summed to obtain channel cross sectional area. Channel morphology measurements were made

at three sites (riffle, pool, transition) in each reach. Reach-averaged values of width, depth, and area were obtained by averaging area and surface width for the three transects and calculating average depth using the equation  $\text{depth} = \text{area} / \text{width}$ . Pebble counts of ~100 surface particles across the channel width at each cross-section were measured (mm) and plotted as a cumulative grain size distribution from which the bed surface grain sizes (median, 84<sup>th</sup>, and 90<sup>th</sup> percentiles) were determined for each reach (Wolman 1954). The energy grade line represents the total head of the flow and its slope is the energy gradient which, at bankfull flow, is approximately equal to stream bed and water surface gradients, which were obtained from bed and water surface elevation surveys at 2 m intervals over a sequence of riffles and pools (10 channel widths) in five reaches (Prestegard 1983; Gordon et al. 2004). The small footprint and high repetition rates of discrete-return Light Detection and Ranging (lidar) systems results in a dense distribution of samples that can be used to create high resolution digital elevation models for watershed studies (Lefsky et al. 2002; Thoma et al. 2005; Cavalli et al. 2008; Hauer et al. 2009). Gradients generated from pre-processed lidar data for the lower Flat Brook (< river kilometer 21; obtained from the U.S. Geological Survey Leetown Science Center) were similar to the three surveyed bed gradients in this section and were used for energy gradients at unsurveyed sites.

Geomorphic data on these hydraulic and sediment parameters were used to calculate three different shear stresses. First, cross sectional-average bankfull bed shear stress ( $\text{N/m}^2$ ) was calculated as:  $\tau_{bf} = \rho_w g R S$ , where  $\rho_w$  is the density of water,  $g$  is gravitational acceleration,  $R$  is the hydraulic radius (area / perimeter), and  $S$  is

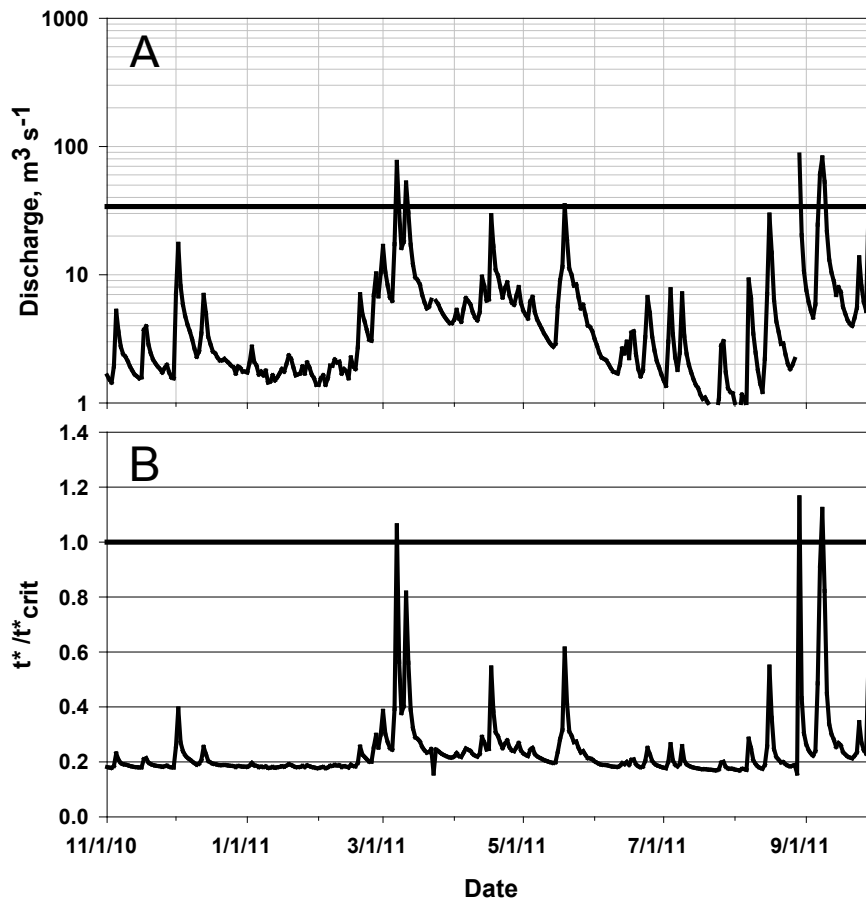
energy gradient (DuBoys 1879). Next, bankfull dimensionless shear stress, the ratio of bankfull bed shear stress to the grain resisting forces, was calculated as:

$$\tau_{bf}^* = \tau_{bf} / (\rho_s - \rho_w)gD,$$

where  $\tau_{bf}$  is the average bankfull bed shear stress,  $\rho_s$  is sediment density,  $D$  is grain diameter of the 84<sup>th</sup> percentile (m), and  $\rho_w$  and  $g$  were defined above (Shields 1936; Parker 1978). The bankfull bed mobility index (MI) was defined as the ratio of bankfull dimensionless shear stress to the critical shear stress required to move bed particles,  $\tau_{bf}^* / \tau_{crit}^*$  (dimensionless shear stress ratio). Most of the sites contained sediment mixtures with particles up to the size of large boulders so the critical dimensionless shear stress for particle motion is influenced by the organization of the large particles ( $D_{84}$  and larger), their size distribution, and the ratio of bed particle size to river width (Clancy and Prestegard 2006). Thus, critical dimensionless shear stress was calculated from a relationship defined for boulder-bed streams that considers effects of large particles  $\tau_{crit}^* = 0.054 (D_i / D_{90})^{-.737}$ , where  $D_i$  represents the size of a particle fraction of interest (here  $D_{50}$ ) and  $D_{90}$  is the diameter of the particle that is larger than 90% of the particles in the distribution (Lenzi et al. 2006). Finally, the MI was calculated for each site with MI values  $> 1$  indicating streambed mobility at high flows. Relevant data and calculations are provided in Table 5.2.

For the 2011 water year, the 3 floods  $>$  bankfull stage were used to evaluate predictions of the bed mobility index (Fig. 5.2a). Data for this evaluation were obtained from U.S. Geological Survey channel measurements (area and width) for a range of discharge values from low flow to above bankfull stage and my field surveys of bed and water surface elevations and particle size distributions at the U.S.

Geological Survey Flat Brook gauge. These data were used to calculate average depth (area / width) and bed shear stress,  $\tau_{bf} = \rho_w g R S$ , for each measured discharge event. The shear stress values were plotted against discharge to develop a predictive relationship between discharge and fluid shear stress. This relationship was used to calculate bed shear stress,  $\tau$ , dimensionless shear stress,  $\tau^*$ , and dimensionless shear stress ratios,  $\tau^* / \tau^*_{crit}$ , as a function of discharge during 2011, which were compared with field evidence for recent bed mobility (October 2011) and my bed MI (Fig. 5.2b).



**Figure 5.2** A) Discharge during the 2011 water year at the USGS Flatbrookville gauge showing 3 major flood events. The reference discharge for bankfull stage is indicated by a bold horizontal line. B) Dimensionless shear stress ratios, which indicate that bed material should have been mobilized during all three major 2011 flood events. The threshold for bed mobility (MI = 1) is indicated by a bold horizontal line.

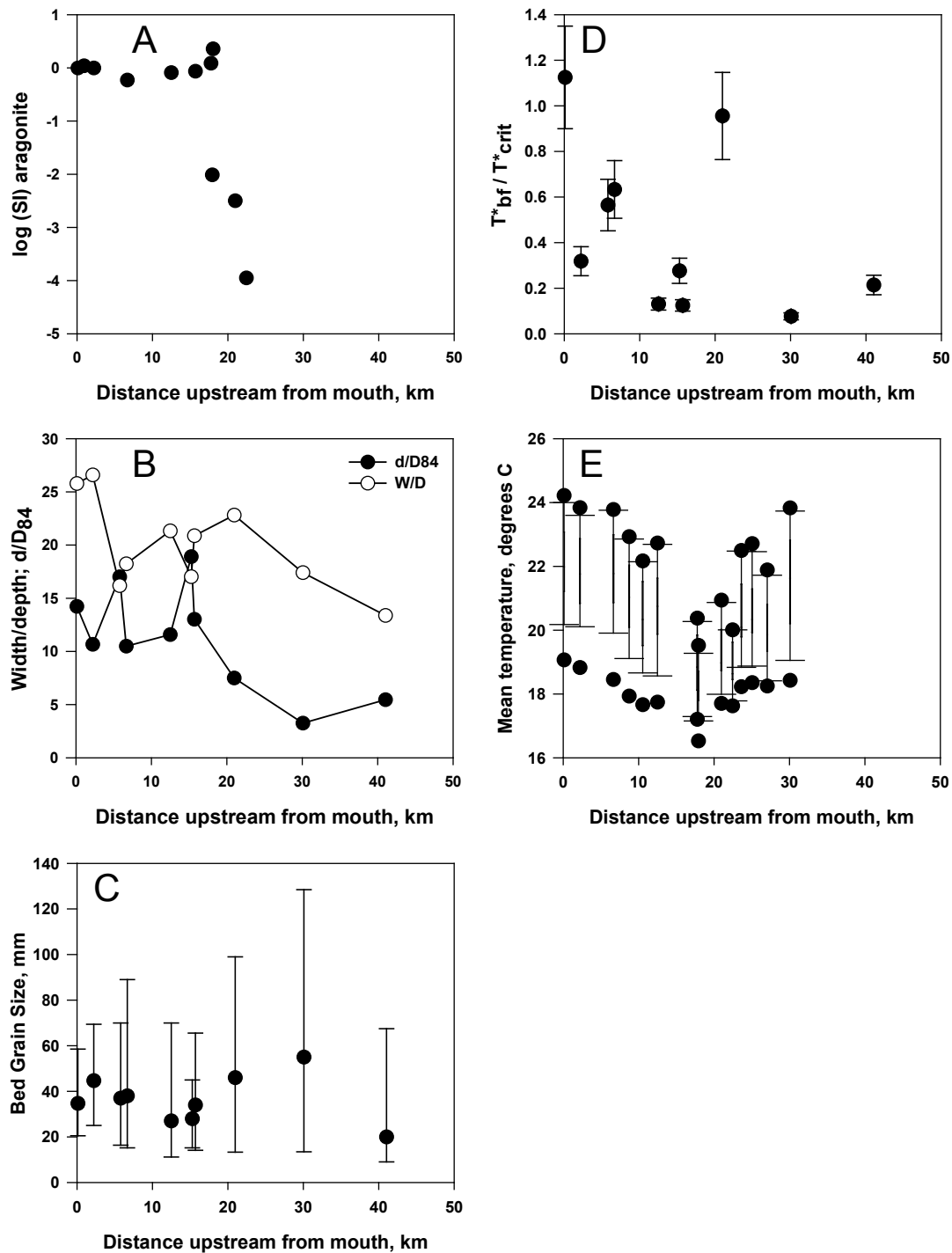
## 5.4 Results

### 5.4.1. Spatial Variations in Water Chemistry

August and October water chemistry data both indicate a longitudinal pattern of dilute upstream waters and an abrupt increase in specific conductance, pH, alkalinity, and calcium below the junction with Little Flat Brook (river km 17.8; Table 5.1). Upstream of river km 17.8, log (SI) values indicated waters considerably under-saturated with respect to aragonite (Fig. 5.3a). Specific conductivity of groundwater obtained from wells located near these sites was at least 5x greater than stream samples, indicating that this deeper groundwater is not the source of local baseflow in the upstream sites (Table 5.1). Specific conductivity, pH, and discharge were relatively constant throughout the reach where *A. heterodon* are found (~river km 5-17; Table 5.1) and log (SI) for aragonite was generally  $> 0$  (Fig. 5.3a), indicating conditions favorable for aragonite precipitation during summer baseflow conditions. Laboratory calcium and bicarbonate measurements for October baseflow samples were in agreement ( $\pm 2\%$ ) with the specific conductance-based regression equations (Table 5.1), verifying the use of these equations to calculate calcium and bicarbonate for the August 24, 2011 samples and the calculation of  $SI_{\text{aragonite}}$ .

### 5.4.2. Spatial Variations in Bed Substrate Mobility

The furthest upstream sites (upstream of river km 30) are relatively shallow and contain large, poorly sorted sediment particles, indicated on Fig. 5.3c as the  $D_{50}$ ,  $D_{16}$ , and  $D_{84}$  grain sizes (Table 5.2; Figs. 5.3b, c). These morphological features contribute to a  $MI \ll 1$ , indicating stable beds during bankfull floods (Table 5.2; Fig. 5.3d). As the river progresses downstream it deepens and large particles occupy less



**Figure 5.3** Water chemistry calculations, geomorphic characteristics, and August 2010 mean daily temperatures as a function of distance upstream from the mouth of Flat Brook. Shown are A) log saturation index for aragonite, B) width to depth ratio and particle sorting, C) bed grain size, D) dimensionless shear stress ratio where values > 1 indicate bed mobility at bankfull stage, and E) mean daily water temperature (latter from C. Campbell, USGS, unpublished data).



of the channel bed. The MI is  $\sim 1$  for the reach just upstream of Little Flat Brook ( $\sim$ river km 21) and  $> 1$  for the steep reach upstream of the mouth ( $<$  river km 2.5), indicating bed mobility for bankfull and higher floods in these regions (Table 5.2; Fig. 5.3d).

The dimensionless shear stress ratios calculated for the 2011 hydrograph at the USGS gauge (river km 2.4) indicate bed mobility for all 3 floods, which had magnitudes greater than bankfull (Fig. 5.2b). Field observations near the USGS gauge indicate that cobbles and other bedload were transported from the channel onto the floodplain and just downstream of the gauge there was damage to a bridge over the river. Evidence of bed mobility was observed at some upstream sites, particularly just upstream of the *A. heterodon* reach ( $\sim$ river km 21; Table 5.2). Further upstream,  $>$  river km 30, there was no evidence of bed material on the floodplain and algae-covered cobbles were not overturned on the streambed (Table 5.2).

## 5.5 Discussion

### 5.5.1. Stream Bed Stability

*A. heterodon* are confined to the lowest gradients in the river, found downstream of the confluence with Little Flat Brook. Similarly, a study of *Margaritifera falcata* within the South Fork Eel River basin in Northern California found that *M. falcata* densities were highest where the average channel gradients were lowest, suggesting a relationship to geomorphology (Howard and Cuffey 2003). My geomorphically-derived mobility indices indicated stable stream beds throughout the *A. heterodon* reach, as well as in upstream reaches. Previous research in the Neversink River, another tributary of the upper Delaware River, suggested that stable

habitats can serve as refuges from high flows (Strayer 1999). Hydrodynamic models developed for three reaches of the mainstem Delaware River support this hypothesis and found persistent *A. heterodon* populations at sites with stable substrates (Maloney et al. 2012). Similarly, other studies that developed mobility indices similar to mine found the availability of stable stream beds essential for mussel survival of high flow events (Morales et al. 2006; Allen and Vaughn 2010). Thus, the steep, incised reaches immediately upstream and downstream of the *A. heterodon* reach in Flat Brook (bankfull mobility indices approaching or exceeding one) were unsuitable mussel habitat.

The moderate stream gradients, shallow depths, and large particles found in the upper reaches (> river km 30) combined to create stable channel beds with MI << 1.0 (Table 5.2). During high magnitude floods the wide adjacent floodplains provide temporary storage of water, contributing to streambed stability (Leopold et al. 1964), and there was little field evidence of cobble or larger particle movement during the 2011 floods. If bed mobility was the sole determinant of *A. heterodon* occurrence, I might expect to find some individuals in these upper reaches, but none were found. Previous studies of *A. heterodon* indicate a preferred microhabitat of fine sediment and moderate depths, therefore, the large particles and shallow depths in these upper reaches may provide unsuitable habitat (Strayer and Ralley 1993; Michaelson and Neves 1995). My field data, however, suggest that these reaches might also be unsuitable due to their water chemistry, which indicates highly unsaturated conditions with respect to aragonite saturation. Without fine sediments to burrow into, mussels

in the upper reaches are exposed to unsaturated, turbulent flow, which may be difficult conditions in which to survive.

#### 5.5.2. Aragonite Saturation

*A. heterodon* has previously been determined to occur in calcium-poor streams with a distribution related to some factor correlated with calcium content (Strayer 1993). Calcium concentrations alone do not determine whether waters are saturated with respect to aragonite, which is also sensitive to pH, temperature, and carbonate concentrations (calculated from bicarbonate dissociation). The low calcium concentrations I found throughout the study area (3 – 26 mg/L) were comparable to those found in Strayer (1993), however I also found *A. heterodon* constrained to waters that supported aragonite ( $\text{CaCO}_3$ ) precipitation during summer baseflow minima (when temperature and solute concentrations from groundwater should be at their highest). Unionid shells are composed primarily of aragonite (Wilbur 1964), which is precipitated by mussels as seasonal growth bands of varying width from which seasonal and inter-annual environmental and climatic conditions are often inferred (Dettman and Lohmann 1993; Goewert et al. 2007; Versteegh et al. 2009). I am unaware of any study that has examined spatial distributions of aragonite saturation indices to define habitat ranges of a mussel species that favors relatively dilute waters. Freshwater mussels maintain calcium carbonate stores in different organs that are later used for growth and reproduction (Pynnönen 1991). For *A. heterodon* in Flat Brook, baseflow aragonite may be vital during the first 1-2 years of life when growth rates for the species are generally highest (Michaelson and Neves 1995) and also in reproducing individuals whose calcium carbonate stores are

directed toward shell growth in the developing larvae (Pynnönen 1991). If conditions become unfavorable for aragonite saturation, recruitment could become limited resulting in an aging, potentially unsustainable, population (Pynnönen 1991). However, species differ in their ability to store calcium carbonate (Pynnönen 1991) which may explain why *E. complanata* were found in beaver ponds upstream of river km 30 (W. Lellis, U.S. Geological Survey, unpublished data). In southern Ontario, *E. complanata* occurred in waters with alkalinities ranging from 2 – 172 mg CaCO<sub>3</sub>/L and calcium hardness values of 4 – 125 mg CaCO<sub>3</sub>/L, suggesting that aragonite saturation may not be limiting growth or reproduction (Mackie and Flippance 1983). Without sampling throughout the year, however, and calculating aragonite saturation for a range of conditions, it is difficult to understand the implications of geochemical data to mussel habitat. Furthermore, water chemistry can be markedly different between hyporheic zones and well-mixed turbulent stream waters. Thus, further research examining the chemical microhabitats and chemical requirements of various freshwater mussel species is warranted.

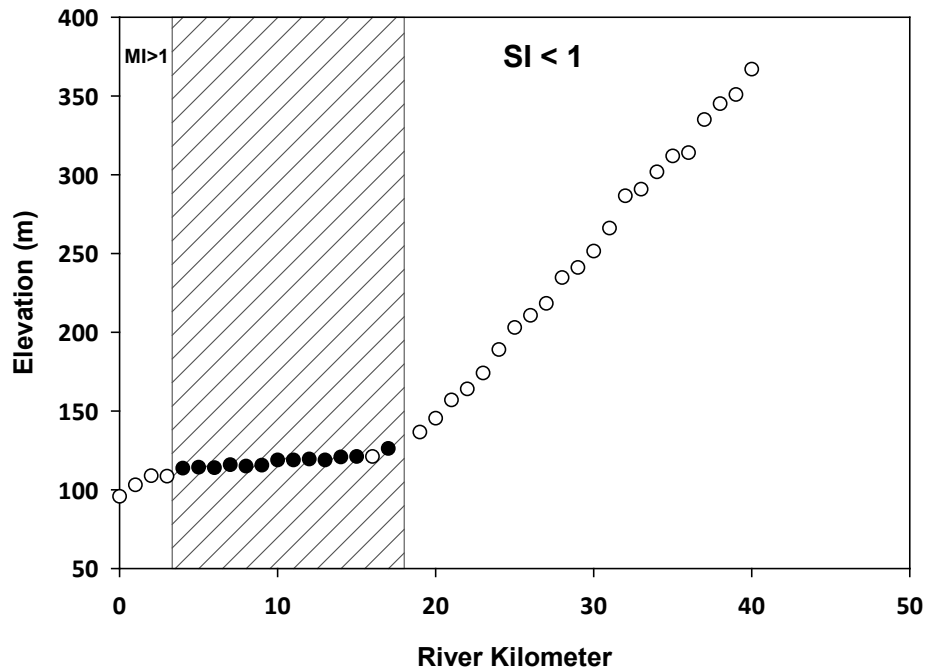
The sources of groundwater contributions to base flow could be responsible for the abrupt change in water chemistry found upstream of the *A. heterodon* reach. Upstream of river km 17.8, dilute waters unfavorable for aragonite precipitation were in stark contrast to the more alkaline and solute-rich (conductive) groundwater from nearby water supply wells. This difference suggests that deeper groundwater sources are not contributing significantly to baseflow in the upstream reaches and that baseflow is derived from shallow groundwater flow through the surrounding glacial till. The abrupt change to higher solute water favoring aragonite precipitation could

indicate incoming groundwater from deeper flow systems (Tóth 1963). In these downstream reaches, the river is cut through fractured bedrock rather than glacial till; spring discharge from these rock fractures is conveyed to streams (R. Evans, National Park Service, personal communication). This possible influx of deep, aragonite-saturated water in the downstream reaches of Flat Brook is also supported by the sharp decrease in mean daily temperatures (measured in August 2010) around river km 17.8 (Fig. 5.3e; C. Campbell, U.S. Geological Survey, unpublished data). The higher temperatures in the upstream reaches might reflect shallow groundwater sources warmed by air temperatures (Bogan et al. 2003). I suggest that this influx altered the water chemistry downstream throughout the section of Flat Brook where *A. heterodon* is observed.

#### 5.5.3. Habitat Window

The longitudinal patterns of bed mobility and water chemistry along Flat Brook have created an *A. heterodon* “habitat window” where bed sediment is stable at bankfull and lower flows and water chemistry is saturated with respect to aragonite during summer baseflow (Fig. 5.4). Although upstream reaches have stable channel beds, the water chemistry is too dilute to support aragonite precipitation, even during base flow minima. Thus, dilute water chemistry along with coarse grain sizes may limit *A. heterodon* occurrence in the headwaters of Flat Brook. The opposite condition prevails near the confluence of Flat Brook with the Delaware River; water chemistry is consistent with aragonite precipitation during summer baseflow, but the channels are steep and although coarsely grained, bed mobility indices and field observations indicate bed mobility at bankfull and higher discharges. Thus, bed

particle mobility and bed scour likely constrain *A. heterodon* occurrences in lower Flat Brook as they do elsewhere in the Delaware River Basin (Maloney et al. 2012).



**Figure 5.4** The habitat window (hatched) for *A. heterodon* is controlled by water chemistry in the upstream reaches (saturation index is  $< 1.0$ ) and by bed mobility in the lower reach (mobility index  $> 1.0$  for bankfull conditions). The location of *A. heterodon* is indicated with dark circles and mussel data is aggregated at the kilometer-scale for display (W. Lellis, USGS, unpublished data).

*A. heterodon* are susceptible to changes in climate that affect bed mobility or aragonite saturation. In the Northeast, changes in climate are predicted to increase temperatures and shift precipitation patterns toward wetter winters, drier summers, and more extreme precipitation events (Arnell 1999; Diffenbaugh et al. 2005; Hayhoe et al. 2008). This may reduce the duration of snow cover and switch the timing of runoff from a spring snowmelt to winter runoff which, depending on the size and hydraulic characteristics of the river, could affect the recruitment success of mussel populations (Arnell 1999; Hastie et al. 2003). If these changes in the annual

distribution of precipitation are insufficient for recharge to offset increases in evapotranspiration, water table levels can eventually drop and decrease stream discharge (Sophocleous 2002; Brolsma et al. 2010). Reduced groundwater levels can lead to a loss of riparian vegetation, increased frequency and magnitude of floods, increased stream bank erosion, and changes in water chemistry and quality (Naiman and Décamps 1997; Shafroth et al. 2000). These changes could create a “habitat squeeze” that could influence the viability of the *A. heterodon* population in Flat Brook.

## Chapter 6: Conclusions and implications

The purpose of this research was to use both modeling and field approaches to identify habitat characteristics for *Alasmidonta heterodon*, a federally endangered freshwater mussel. Quantifying species-habitat relationships is needed for conservation of at-risk species in order to: 1) identify undiscovered populations; 2) determine potentially suitable habitat; 3) forecast the potential effects of human activities and climate change on species distributions; and 4) enhance conservation and management planning (Farnsworth and Ogurcak 2006; Guisan et al. 2006; Lomba et al. 2010; Wilson et al. 2011). Predictive models are useful tools in the conservation of at-risk species because they develop statistical relationships between a species and a set of predictor variables to map the potential distribution of a species (Guisan et al. 2002). However, these models predict potential habitat based on the similarity between unknown habitat and known habitat (O’Conner 2002). The predictive ability of these landscape models can be hampered by their tendency to identify landscape proxies for the characteristics actually influencing mussel survival. For example, identifying an association between a species distribution and latitude and longitude does not mean anything *per se*, but can be suggestive of thermal constraints (Dunham et al. 1999). Thus, identifying causal mechanisms and constraints to species distributions requires finer-scaled field or laboratory approaches. In this study, I used a combination of community analyses and predictive modeling to identify topographic, geologic, hydrologic, and land cover characteristics associated with *A. heterodon* occurrence. Based on results from these models, I conducted exploratory



field work to evaluate physical, biogeochemical, and thermal controls on *A. heterodon* in reaches throughout the species' range.

### 6.1 Results from the Community Analyses

At-risk species are important to management agencies, yet their fragmented distributions, restricted geographic ranges, specialized habitat, and low numbers make quantifying species-habitat relationships and predicting occurrence difficult (Lomba et al. 2010). Regression models of mussel-habitat relationships are often highly significant, yet have low predictive power (Strayer and Ralley 1993; Arbuckle and Downing 2002). Therefore, scientists have turned to more complex modeling techniques to develop bivalve habitat descriptors that have predictive ability (Steuer et al. 2008; Hopkins 2009; Weber and Schwartz 2011; Jähnig et al. 2012). I evaluated whether biological surrogates (fish or mussel species) could be identified that would indicate an increased or decreased likelihood for *A. heterodon* to be present in a given reach of river. Thus, I combined community analyses and predictive modeling to identify potential suitable *A. heterodon* habitat in the Maryland Coastal Plain.

Community analyses are often used to define distinct assemblages of taxa and identify habitats influencing taxa assemblages (Ilmonen et al. 2009; Haag 2010; Pérez-Quintero 2013). Using standard approaches, I identified similar bivalve assemblages across both the Maryland Coastal Plain and within the subset of rivers that contain *A. heterodon*. With both data sets (entire Maryland Coastal Plain and in the subset of *A. heterodon* rivers) *A. heterodon* was in its own cluster which was not significantly associated with other mussel species. This strongly suggests that *A.*

*heterodon* has habitat requirements that differ from other Coastal Plain species, which may account for its endangered status.

Therefore, the community analyses were used to identify biological surrogates that could be used to enhance predictive models of *A. heterodon* occurrence.

Community analysis indicated three fish species associated with the *A. heterodon* cluster. Unfortunately, two of these species (*Notropis chalybaeus* and *Percina peltata*) are rare within Maryland (Jenkins and Burkhead 1993; Maryland Natural Heritage Program 2010; Ciccotto and Stranko 2011) and *Esox americanus* does not inhabit streams with characteristic *A. heterodon* habitat (Jenkins and Burkhead 1993). Landscape analysis indicated that the *A. heterodon* cluster was associated with agricultural lands, higher elevations, and Miocene-aged sediments and negatively associated with wetlands. Similar variables have been associated with mussel communities in other systems (Arbuckle and Downing 2002; Baldigo et al. 2003; Atkinson et al. 2012; Cao et al. 2013). Therefore, based on these results, I concluded that landscape rather than biological surrogates would be more useful predictors of suitable *A. heterodon* habitat in the Maryland Coastal Plain.

## 6.2 MaxEnt Modeling

The landscape variables associated with the mussel community structure in the ordinations served as input into the predictive occupancy models. The goal was to determine if landscape variables could predict suitable stream segments for *A. heterodon*. A maximum entropy model (MaxEnt) was used for this analysis because it has been shown to out-perform other methods for the low sample sizes commonly acquired for rare species (Hernandez et al. 2006; Pearson et al. 2007; Wisz et al.

2008). I used MaxEnt to develop predictions for stream segments rather than the more commonly used grid cells (e.g., Pearson et al. 2007). The final MaxEnt model suggests that habitat suitability for *A. heterodon* increases with increasing depth to the water table but decreases with increasing pasture/hay land cover, woody wetlands, Tertiary deposits, and minimum elevation. Suitable habitats also had low levels of development. Similar habitat characteristics have been previously identified with the occurrence of other mussel species (Hopkins 2009; Brown et al. 2010; Weber and Schwartz 2011; Wilson et al. 2011). Mapping the model predictions identified the suitability of segments to either currently contain or formerly support *A. heterodon* populations. When this map is given to resource managers familiar with the area, a survey scheme can be established in these stream segments to ground-truth model predictions and, potentially, discover unknown populations.

### 6.3 Suitable Landscape Habitats and Potential *A. heterodon* Constraints

The model was useful for identifying variables that affect habitat suitability for *A. heterodon* at the stream segment scale. I found low elevation stream segments with low to moderate amounts of Tertiary deposits and little low intensity development or woody wetlands in the local catchment to be the most suitable for *A. heterodon*. In addition, these segments generally have little low intensity development and low to moderate amounts of pasture/hay agriculture in cumulative watersheds with deeper average depths to the water table. *A. heterodon* are likely not responding to these variables *per se*, but rather to some abiotic or biotic factor that is a co-variable (Strayer 2008).

The amount of surrounding development indicates a possible association between the mussel and hydraulic and bed stability. Urbanization is associated with increased volume of runoff, flood peaks, erosion, and sedimentation (Wolman 1967; Leopold 1968). Channel incision and increased cross-sectional areas increase bankfull channel capacity and nearbed shear stresses during high flow events (Booth 1990; Gangloff and Feminella 2007). This decrease in hydraulic and bed stability accompanying urbanization may be a determinant factor of the low suitability of developed reaches for *A. heterodon* in the Coastal Plain. In addition, stream water temperatures can be influenced by many factors, some of which are affected by urbanization: riparian vegetation, stream discharge, stream surface area, and thermal discharges from point- and non-point sources (Edinger et al. 1968; LeBlanc et al. 1997; Gu et al. 1998; Bogan et al. 2003). Temperature tolerance limits may constrain the spatial distribution of many aquatic taxa (Sweeney and Vannote 1978; Milner et al. 2001; Brazner et al. 2005; Isaak et al. 2010).

Other landscape variables are suggestive of water chemistry as an important habitat characteristic for *A. heterodon*. The decrease in suitability with increasing pasture/hay lands supports a water chemistry limitation as tilled lands in the Coastal Plain are often limed with calcium to adjust pH levels and alter water chemistry toward calcium bicarbonate-type water (Goulding and Blake 1998; Oh and Raymond 2006); pasture/hay lands do not receive this benefit. Also, my model identified greater depths to the water table as suitable *A. heterodon* habitat. Where water moves through deposits containing shells or cement, dissolution of calcium carbonate in the sediments produces calcium bicarbonate-type water with a high pH (Chapelle 1983;

Hamilton et al. 1991). Woody wetlands were not predicted as suitable habitats, possibly due to their characteristic acidity in the Coastal Plain (Morgan and Good 1988). *A. heterodon* sites generally have a significantly higher pH than sites without the mussel (Ashton 2010). In addition, a primary host of *A. heterodon*, the tessellated darter (*Etheostoma olmstedi*; Michaelson and Neves 1995), is intolerant of high acidity and does not occur in blackwater streams with low pH (Jenkins and Burkhead 1993).

The results from the community and habitat modeling suggest that geomorphic, hydraulic, thermal, and chemical characteristics of the stream environment may influence *A. heterodon* occurrence. Therefore, detailed field investigations were conducted to examine the thermal regimes, chemical characteristics (associated with calcium), and geomorphic characteristics (associated with bed stability) of *A. heterodon* reaches at different locations throughout the species' range.

#### 6.4 Field Identification of Reach-Scale Habitat Characteristics for *A. heterodon*

The community analyses and predictive models identified suitable landscape-scale habitats that influence suitability for the mussel, but these are correlative and don't identify controlling mechanism(s) (Strayer 2008). Therefore, field work was conducted to identify potential constraints or essential habitat(s) at a finer scale than can be detected through landscape modeling. I specifically examined several factors associated with the survival of freshwater mussels: temperature (Pandolfo et al. 2010; Galbraith et al. 2012; Ganser et al. 2013), streambed stability (Vannote and Minshall 1982; Johnson and Brown 2000; Hastie et al. 2001), and water chemistry (Johnson

and Brown 2000; Strayer and Malcolm 2012). For temperature, I examined thermal regimes at *A. heterodon* sites throughout the species range, specifically looking for a potential thermal limit for the species. Bed stability and water chemistry were examined in one northern stream with a healthy *A. heterodon* population where the extent of the species along the length of the stream is known (W. Lellis, U.S. Geological Survey, unpublished data). Performing field assessments across these different extents provides information on potential habitat limiting *A. heterodon* occurrence and how this may differ throughout the species' range.

The approach for temperature was to take field measurements across the species' range to identify a potential thermal limit under natural (rather than laboratory) conditions. The 95<sup>th</sup> percentile temperatures at individual sites suggest that the mussel occurs in reaches with temperatures < 29°C. The higher maximum temperatures in southern sites combined with the very small rate of change (evaluated as the 95<sup>th</sup> percentile temperature change per hour) suggest that these populations are living in warmer thermal regimes. Further, groundwater source analysis and examination of air-water relationships suggest that southern sites might receive water primarily from intermediate to deep sources, whereas northern sites appeared to have a range of water sources (shallow to deep). These data suggest that changes in air temperature may affect some of the northern sites (particularly those with shallow groundwater contributions), whereas changes in hydrological processes that might accompany climate or land-use changes might affect the southern sites. The water temperatures of the southern sites may also be susceptible to climate changes that affect the timing of groundwater recharge.

Flat Brook, in the Delaware River basin, is a relatively pristine watershed that may have an intact distribution of *A. heterodon*. Thus, it provides a laboratory in which to evaluate physical and geochemical constraints on *A. heterodon* occurrence. Detailed longitudinal mussel surveys by the U.S. Geological Survey have identified the extent of *A. heterodon* throughout the stream and associated this range with a decrease in stream gradient (W. Lellis, U.S. Geological Survey, unpublished data). Changes in stream gradient can reflect geological or geomorphological boundaries that influence geomorphic characteristics (bed grain size, fluid shear stress, bed mobility, etc.), flow regimes, groundwater contributions to streams, and stream water chemistry (Tóth 1963; Tóth 1970; Boxall et al. 2008). Any confounding effects of land use in Flat Brook are considered negligible as water quality is considered unimpaired (Albert and Limbeck 2000). Grain size, hydraulic, and water chemistry measurements taken along the length of the stream identified a “habitat window” for *A. heterodon* in Flat Brook. The mussel occurs in the section of stream where water is saturated with respect to aragonite (i.e., calcium carbonate) during summer baseflow and the streambed is stable during bankfull and lower discharges. I am unaware of any previous study that has examined spatial distributions of aragonite saturation indices to define habitat ranges of a mussel species that favors relatively dilute waters (Strayer 1993).

#### 6.5 Integrating Field and Modeling Results

My predictive models suggest that stream characteristics at multiple spatial scales may influence *A. heterodon* occurrence, which is similar to recent findings for other mussel species (Hopkins 2009; Weber and Schwartz 2011). Suitable habitat was

strongly dependent on the underlying geology of the site and the amount and type of land use in the surrounding landscape. These variables have also been associated with the occurrence of other mussel species (Hopkins 2009; Brown et al. 2010; Cao et al. 2013). The community analyses defined *A. heterodon* as its own cluster which was not significantly associated with other mussel species. This suggests that *A. heterodon* may have some characteristics that lead to essential habitat requirements that are different from other mussel species in the Maryland Coastal Plain. For example, *P. cataracta* and *A. implicata* can float on muddy sediment that may provide solutes not found in the overlying water column. In contrast, *A. heterodon* burrows into fine sediments, thus needs to acquire significant  $\text{CaCO}_3$  to build and maintain its shell from the overlying water column. The variables in the final model suggest that land use activities that increase bed instability or alter water chemistry or quality (pH, calcium, or alkalinity) could reduce suitability for *A. heterodon*.

My field-based investigations identified more explicit habitat characteristics that need to be measured at a fine-scale. I found *A. heterodon* limited to a section of Flat Brook with streambeds that are stable at bankfull and lower stages. These areas can serve as refuges from high flows (Strayer 1999; Maloney et al. 2012). Bed stability during high flows is increasingly being used to describe and predict the occurrence, abundance, and distribution of other mussel species (Steuer et al. 2008; Zigler et al. 2008; Allen and Vaughn 2010). The availability of waters with low calcium concentrations have been suggested as a constraint to *A. heterodon* (Strayer 1993) and *Margaritifera margaritifera* (Bauer 1988), an occurrence possibly associated with eutrophication in waters with elevated calcium concentrations



(Strayer 1993; Bauer 1988). Calcium concentrations in Flat Brook were comparable to those seen in Strayer (1993) however, I suggest that the total water chemistry and the saturation with respect to aragonite (i.e., calcium carbonate) may constrain *A. heterodon* occurrences in Flat Brook. Water chemistry in equilibrium with aragonite saturation may be vital during summer baseflow in the first 1-2 years of life when *A. heterodon* growth rates are highest (Michaelson and Neves 1995) and also in reproducing individuals whose calcium carbonate stores are directed toward shell growth in the developing larvae (Pynnönen 1991). If conditions become unfavorable for aragonite saturation, recruitment could become limited resulting in an aging, potentially unsustainable, population (Pynnönen 1991).

The temperature data suggest that southern *A. heterodon* populations occupy warmer thermal regimes than northern populations. Southern sites might require water from intermediate to deep water sources and the water temperatures may reflect the timing of groundwater recharge. Previous studies of thermal tolerance indicate that susceptibility to high temperatures varies by species and life stage (Pandolfo et al. 2010; Galbraith et al. 2012; Ganser et al. 2013). Temperatures causing up to 50% mortality can vary by as little as  $\sim 5^{\circ}\text{C}$  (Pandolfo et al. 2010). Shifts in climate and landuse are predicted to cause temperature spikes averaging  $3.5^{\circ}\text{C}$ , with maximum increases reaching as high as  $\sim 7^{\circ}\text{C}$ , in Piedmont streams in the Chesapeake Bay watershed (Nelson and Palmer 2007). These temperature spikes will likely occur frequently at the most urbanized sites with headwater streams showing the most widespread impacts of urbanization (Nelson and Palmer 2007).

Urban and exurban sprawl will continue to tax stream ecosystems in the region, therefore work is needed to identify how bed instability, water chemistry, or water quality affect *A. heterodon* viability. Bed stability has already received attention (Strayer and Ralley 1993; Strayer 1999; Maloney et al. 2012), however little is known about the chemical and thermal requirements for *A. heterodon* and they would be fruitful areas for future research. The observations in Flat Brook indicate that water chemistry changes were also accompanied by a change in temperature, both indicators of a change in groundwater source to streamflow. Thus, the covariance of appropriate geochemical and thermal characteristics should also be evaluated.

#### 6.6 Implications for *A. heterodon* Management and Recovery

The goal of the *A. heterodon* recovery plan is to maintain and restore viable populations of the mussel to a significant portion of its historical range (U.S. Fish and Wildlife Service 1993). There are two major provisions: 1) establish and expand populations and 2) protect and enhance habitat (U.S. Fish and Wildlife Service 1993). The goal of this project was to use modeling and field approaches to identify habitats that could be used to support the two provisions of the recovery plan. To reclassify *A. heterodon* from endangered to threatened, thirteen viable populations (a population consists of a group of individuals in a stream) are needed and, of these, ten must support viable populations distributed widely enough within the stream to buffer the population against loss due to a single event (U.S. Fish and Wildlife Service 1993). The plan specifies seven existing populations that should remain viable, but specifies that at least any six other populations throughout the range must be shown viable for

reclassification (U.S. Fish and Wildlife Service 1993). Thus, identifying currently unknown populations could provide additional viable populations that could lead toward downlisting the species. Performing snorkel surveys throughout the species' range in search of unknown populations is not feasible, so I identified potential suitable habitat using modeling approaches. If followed up with field surveys, this could lead toward the discovery of unknown populations. The second provision involves the identification of essential habitat and identifying how different anthropogenic activities create conditions unsuitable for mussel survival (U.S. Fish and Wildlife Service 1993). Toward this goal, I applied field-based approaches at known locations of *A. heterodon* to identify potential essential habitat(s). Thus, my approach combined field and modeling approaches to generate a robust description of *A. heterodon* habitat at multiple-scales.

Under the *A. heterodon* recovery plan, downlisting can be accomplished through achieving a target number of viable populations. Thus, the species is considered one unit rather than distinct population segments as is allowed for vertebrate species under the Endangered Species Act (1973). These distinct population segments represent the genetic building blocks of the species as a whole and those that would represent significant loss to the ecological-genetic diversity if it went extinct (Waples 1995). My results suggest that these species-based targets may not be a valid management goal for *A. heterodon*. The species is sparsely populated along a wide swath of the Atlantic Slope (U.S. Fish and Wildlife Service 1993). This wide gradient of conditions could allow for adaptations that have enabled the species to survive (Ganser et al. 2013). My data suggests that mussels in the south may have

adapted to the warmer temperature regimes experienced in this region. There is an apparent geographical separation between the northern and southern streams. This separation occurs along an urban corridor encompassing Washington D.C., Baltimore, Philadelphia, and New York City. It is impossible to know if this area is truly devoid of *A. heterodon* or simply occurs due to a lack of survey effort in this region. If this separation is real, it may be recent and associated with land-use changes, however it also occurs along a major geomorphic boundary (glaciated north versus non-glaciated south). Thus, it is possible that the northern and southern sites have become genetically isolated. The historical distribution of the species indicates that *A. heterodon* once inhabited some portion of this corridor (U.S. Fish and Wildlife Service 1993). Urbanization has been associated with a loss of mussel species (Gillies et al. 2003; Lyons et al. 2007). Thus, continued growth of this urban corridor threatens local populations and potentially maintains, if not increases, any physical separation between northern and southern populations. This increases the chances of genetic divergence between the northern and southern populations.

The genetic structure of *A. heterodon* is not known across the Atlantic Slope, however, another freshwater mussel, *Lasmigona subviridis*, showed genetic differentiation between populations in the Susquehanna and Potomac Rivers and more southern populations (King et al. 1999). In fact, the authors suggested that the reproductive isolation between northern and southern populations constitutes evolutionary significant lineages and the two populations should be managed as separate conservation units (King et al. 1999). Similar genetic studies are warranted for *A. heterodon* to determine if northern and southern populations have become

genetically isolated or, perhaps, different species. The results would determine the management strategies that should be followed. For example, assuming the northern and southern populations remain a single species, transplants and relocations could be most advantageous in southern streams because the populations may have adaptations in place to deal with some amount of stream warming. These southern systems are also threatened from human development (Jantz et al. 2005; Utz et al. 2011). If these thermally resilient populations become eradicated, the species may lose any adaptations, which may affect species viability under changing environmental conditions. Also, temperature can influence the ability of mussels to recover (i.e., turn upright, move, and burrow) following disturbances associated with conservation activities such as relocation, stocking, and status surveys (Waller et al. 1999). Thus, the different thermal regimes in the two regions suggest that transplants and reintroductions would benefit from remaining within a geographic region rather than occurring between northern and southern regions.

With the focus of recovery on viable populations, emphasis should be given toward identifying any remaining potential suitable habitat in the southern part of the range. My predictive models identified the suitability of segments for *A. heterodon* in the Maryland Coastal Plain. The logistic predictions could provide a foundation for a prioritized sampling scheme for the species in the Maryland Coastal Plain. For example, the predicted habitat suitabilities could be stratified and random segments selected from each strata for sampling (e.g., 40 highly suitable, 20 moderately suitable, and 10 unsuitable). Sampling in this manner would allow for the potential discovery of unknown *A. heterodon* populations, the validation of the MaxEnt model,

and the collection of data for further model calibration. In addition, model results could be used to predict the suitability of other Coastal Plain areas for *A. heterodon* (e.g., streams segments within the Virginia Coastal Plain). Data for the seven variables in the final MaxEnt model would need to be assembled for the new stream segments to which the model will be applied, the model re-run using the original data, and suitability predictions generated for the new stream segments. A stratified random sampling scheme could be designed as described above and qualitative snorkel surveys conducted to look for unknown populations. Survey results would serve to further validate the model. Additionally, the model predictions could be used for species' transplants and reintroductions. Strayer et al. (1996) suggested that *A. heterodon* population sizes can vary greatly. Animals from the larger populations could be transplanted or reintroduced into segments within the Coastal Plain according to their suitability using the above stratifications. Follow up surveys to monitor the animal's survival could identify individual stream segments that show the greatest potential for successful *A. heterodon* reintroduction. These surveys could also uncover unknown *A. heterodon* populations.

One of the main objectives of the *A. heterodon* recovery plan is to identify and protect essential habitats. Suitable forms of micro- and hydraulic habitat have been identified in the literature for *A. heterodon* (Strayer and Ralley 1993; Michaelson and Neves 1995; Maloney et al. 2012), but the components of essential habitat remains unclear. My results, when combined with other studies, provide several possibilities: (1) habitats with stable streambeds during bankfull and lower flows; (2) waters temporarily in equilibrium with aragonite (i.e., calcium carbonate) precipitation; and

(3) habitats with temperatures below 29°C and stable thermal regimes. These habitat characteristics have support in the literature (Strayer 1993; Strayer 1999; Maloney et al. 2012; Ganser et al. 2013), but additional field and laboratory experiments are needed to verify if they are truly essential to *A. heterodon* survival. If essential habitats are identified, policies and plans can be developed to protect key processes influencing these habitats. In the meantime, maintaining suitable *A. heterodon* habitat and the viability of individual populations will likely require limiting activities that modify stream channel geomorphology, riparian vegetation, groundwater levels, the timing or magnitude of floods, and water chemistry and quality. However, many of these parameters may be affected by climate changes. Until essential habitats are identified and management plans instituted, all populations should be similarly protected and the loss of individual populations prevented.

## Bibliography

- Albert, R. and R.L. Limbeck. 2000. High flow management objectives for New Jersey non-coastal waters. Delaware River Basin Commission, West Trenton, NJ.
- Allen, D.C. and C.C. Vaughn. 2010. Complex hydraulic and substrate variables limit freshwater mussel species richness and abundance. *Journal of the North American Benthological Society* 29:383-394.
- Arbuckle, K.E. and J.A. Downing. 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. *Canadian Journal of Fisheries and Aquatic Sciences* 59:310-316.
- Archambault, J.M., W.G. Cope, and T.J. Kwak. 2014. Survival and behaviour of juvenile unionids mussels exposed to thermal stress and dewatering in the presence of a sediment temperature gradient. *Freshwater Biology* 59:601-613.
- Arnell, N.W. 1999. Climate change and global water resources. *Global Environmental Change* 9:S31-S49.
- Ashton, M.J. 2010. Freshwater mussel records collected by the Maryland Department of Natural Resources' Monitoring and Non-tidal Assessment Division (1995-2009): investigating environmental conditions and potential host fish of select species. Publication No. 12-3112010-443, Maryland Department of Natural Resources, Annapolis.
- Atkinson, C.L., J.P. Julian, and C.C. Vaughn. 2012. Scale-dependent longitudinal patterns in mussel communities. *Freshwater Biology* 57:2272-2284.
- Bakker, J.D. 2008. Increasing the utility of Indicator Species Analysis. *Journal of Applied Ecology* 45:1829-1835.
- Baldigo, B.P., K.R. Riva-Murray, and G.E. Schuler. 2003. Effects of environmental and spatial features on mussel populations and communities in a North American river. *Walkerana* 14(31):1-32.
- Balfour, D.L. and L.A. Smock. 1995. Distribution, age structure, and movements of the freshwater mussel *Elliptio complanata* (Mollusca: Unionidae) in a headwater stream. *Journal of Freshwater Ecology* 10:255-268.
- Bauer, G. 1988. Threats to the freshwater pearl mussel *Margaritifera margaritifera* L. in Central Europe. *Biological Conservation* 45:239-253.



- Bauer, G. 1992. Variation in the life span and size of the freshwater pearl mussel. *Journal of Animal Ecology* 61:425-436.
- Beitinger, T.L. and L.C. Fitzpatrick. 1979. Physiological and ecological correlates of preferred temperature: preferenda versus optima. *American Zoologist* 19:319-329.
- Benitez, J.A. and T.R. Fisher. 2004. Historical land-cover conversion (1665-1820) in the Choptank watershed, eastern United States. *Ecosystems* 7:219-232.
- Beyer, H.L. 2004. Hawth's analysis tools for ArcGIS. (Available at: <http://www.spatialecology.com/htools>)
- Bogan, A.E. 1993a. Freshwater bivalve extinctions (Mollusca: Unionoida): A search for causes. *American Zoologist* 33:599-609.
- Bogan, A.E. 1993b. Workshop of freshwater bivalves of Pennsylvania. Carnegie Museum of Natural History, Pittsburgh.
- Bogan, A. 2008. Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater. *Hydrobiologia* 595:139-147.
- Bogan, T., O. Mohseni, and H.G. Stefan. 2003. Stream temperature-equilibrium temperature relationship. *Water Resources Research* 39:1245.
- Böhlke, J.K., M.E. O'Connell, and K.L. Prestegard. 2007. Ground water stratification and delivery of nitrate to an incised stream under varying flow conditions. *Journal of Environmental Quality* 36:664-680.
- Booth, D.B. 1990. Stream channel incision following drainage-basin urbanization. *Water Resources Bulletin* 26:407-417.
- Boxall, G.D., G.R. Giannico, and H.W. Li. 2008. Landscape topography and the distribution of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) in a high desert stream. *Environmental Biology of Fishes* 82:71-84.
- Braby, C.E. and G.N. Somero. 2006. Following the heart: temperature and salinity effects on heart rate in native and invasive species of blue mussels (genus *Mytilus*). *Journal of Experimental Biology* 209:2554-2566.
- Brazner, J.C., D.K. Tanner, N.E. Detenbeck, S.L. Batterman, S.L. Stark, L.A. Jagger, and V.M. Snarski. 2005. Regional, watershed, and site-specific environmental influences on fish assemblage structure and function in western Lake Superior tributaries. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1254-1270.

Briggs, M.A., E.B. Voytek, F.D. Day-Lewis, D.O. Rosenberry, and J.W. Lane. 2013. Understanding water column and streambed thermal refugia for endangered mussels in the Delaware River. *Environmental Science & Technology* 47:11423-11431.

Brolsma, R.J., M.T.H. van Vliet, and M.F.P. Bierkens. 2010. Climate change impact on a groundwater-influenced hillslope ecosystem. *Water Resources Research* 46:W11503.

Brown, K.M., G. George, and W. Daniel. 2010. Urbanization and a threatened freshwater mussel: evidence from landscape scale studies. *Hydrobiologia* 655:189-196.

Caissie, D. 2006. The thermal regime of rivers: a review. *Freshwater Biology* 51:1389-1406.

Candy, I., M. Stephens, J. Hancock, and R. Waghorne. 2011. Palaeoenvironments of ancient humans in Britain: The application of oxygen and carbon isotopes to the reconstruction of Pleistocene environments. Pages 23-37 *In* N.M. Ashton, S.G. Lewis and C.B. Stringer (eds.) *The Ancient Human Occupation of Britain. Developments in Quaternary Science*, Vol. 14. Elsevier, Amsterdam.

Cao, Y., J. Huang, K.S. Cummings, and A. Holtrop. 2013. Modeling changes in freshwater mussel diversity in an agriculturally dominated landscape. *Freshwater Science* 32:1205-1218.

Cavalli, M., P. Tarolli, M. Lorenzo, and G. Dalla Fontana. 2008. The effectiveness of airborne LiDAR data in the recognition of channel-bed morphology. *Catena* 73:249-260.

Chapelle, F.H. 1983. Groundwater geochemistry and calcite cementation of the aquia aquifer in southern Maryland. *Water Resources Research* 19:545-558.

Chen, L., A.G. Heath, and R.J. Neves. 2001. Comparison of oxygen consumption in freshwater mussels (Unionidae) from different habitats during declining dissolved oxygen concentration. *Hydrobiologia* 450:209-214.

Ciccotto, P. and S. Stranko. 2011. Patterns of shield darter, *Percina peltata*, distribution in the Eastern Piedmont of Maryland, USA. *Environmental Biology of Fishes* 92:141-150.

Clancy, K. and K. Prestegard. 2006. Quantifying particle organization in boulder bed streams. Pages 71-77 *In* G. Parker and M.H. Garcia (eds.) *River, Coastal, and Estuarine Morphodynamics: RCEM 2005*. Taylor & Francis Group, plc., London.

Clarke, A.H. 1981a. The tribe Alasmidontini (Unionidae: Anodontinae), Part I: Pegias, Alasmidonta, and Arcidens. *Smithsonian Contributions to Zoology* No. 326.

- Clarke, A.H. 1981*b*. The freshwater mollusks of Canada. National Museum of Natural Sciences, National Museums of Canada.
- Clarke, A.H. and C.O. Berg. 1959. The freshwater mussels of central New York, with an illustrated key to the species of northeastern North America. Cornell University Agricultural Experiment Station Memoir 367:1-79.
- Clawges, R.M. and C.V. Price. 1999. Digital data sets describing principal aquifers, surficial geology, and ground-water regions of the conterminous United States. U.S. Geological Survey Open-File Report 99-77. U.S. Geological Survey, Reston, Virginia.
- Cleaves, E.T., J. Edwards, and J.D. Glaser. 1968. Geologic map of Maryland. Maryland Geological Survey, Baltimore, Maryland, scale 1:250,000.
- Cook, G.H. 1868. Geology of New Jersey. New Jersey Geological Survey, Newark.
- Crowley, T.E. 1957. Age determination in *Anodonta*. Journal of Conchology 24:201-207.
- Coutant, C.C. 1987. Thermal preference: when does an asset become a liability? Environmental Biology of Fishes 18:161-172.
- De'ath, G. and K.E. Fabricius. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology 81:3179-3192.
- Dettman, D.L. and K.C. Lohmann. 1993. Seasonal change in Paleogene surface water  $\delta^{18}\text{O}$ : Fresh-water bivalves of western North America. Geophysical Monograph 78:153-163.
- Di Maio, J. and L.D. Corkum. 1995. Relationship between the spatial distribution of freshwater mussels (Bivalvia: Unionidae) and the hydrological variability of rivers. Canadian Journal of Zoology 73:663-671.
- Dicken, C.L., S.W. Nicholson, J.D. Horton, S.A. Kinney, G. Gunther, M.P. Foote, and J.A.L. Mueller. 2005. Integrated geologic map databases for the United States: Delaware, Maryland, New York, Pennsylvania, and Virginia. U.S. Geological Survey Open-File Report 2005-1325, US. Geological Survey, Reston, Virginia.
- Diffenbaugh, N.S., J.S. Pal, R.J. Trapp, and F. Giorgi. 2005. Fine-scale processes regulate the response of extreme events to global climate change. Proceedings of the National Academy of Sciences of the United States of America 102:15774-15778.
- Dimock, R.V. and A.H. Wright. 1993. Sensitivity of juvenile freshwater mussels to hypoxic, thermal and acid stress. Journal of the Elisha Mitchell Scientific Society 109:183-192.

- Douda, K., P. Horký, and M. Bílý. 2012. Host limitation of the thick-shelled river mussel: Identifying the threats to declining affiliate species. *Animal Conservation* 15:536-544.
- DuBoys, M.P. 1879. Le Rhone et les rivieres a lit affouillable. *Annales de Pontset Chausses* 18 (sec.5), p. 141-195.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- Dunham, J.B., M.M. Peacock, B.E. Rieman, R.E. Schroeter, and G.L. Vinyard. 1999. Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout. *Transactions of the American Fisheries Society* 128(5):875-889.
- Dunne, T. and L.B. Leopold. 1978. *Water in Environmental Planning*. W.H. Freeman and Co., San Francisco, California.
- Edinger, J.E., D.W. Duttweiler, and J.C. Geyer. 1968. The response of water temperatures to meteorological conditions. *Water Resources Research* 4:1137-1143.
- Edren, S.M.C., M.S. Wisz, J. Teilmann, R. Dietz, and J. Soderkvist. 2010. Modeling the spatial patterns in harbor porpoise satellite telemetry data using maximum entropy. *Ecography* 33:698-708.
- Elith, J., S.J. Phillips, T. Hastie, M. Dudík, Y.E. Chee, and C.J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17:43-57.
- Elliott, J.M. 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology* 25:61-70.
- Endangered Species Act of 1973, as amended (16 U.S.C. 1531 *et seq.*).
- Erickson, T.R. and H.G. Stefan. 2000. Linear air/water temperature correlations for streams during open water periods. *Journal of Hydrologic Engineering* 5:317-321.
- Farnsworth, E.J. and D.E. Ogurcak. 2006. Biogeography and decline of rare plants in New England: Historical evidence and contemporary monitoring. *Ecological Applications* 16:1327-1337.
- Fisher, T.R., J.D. Hagy, W.R. Boynton, and M.R. Williams. 2006. Cultural eutrophication in the Choptank and Patuxent estuaries of Chesapeake Bay. *Limnology and Oceanography* 51:435-447.

Foresman, T.W., S.T.S. Pickett, and W.C. Zipperer. 1997. Methods for spatial and temporal land use and land cover assessment for urban ecosystems and application in the greater Baltimore-Chesapeake region. *Urban Ecosystems* 1:201-216.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management* 10:199-214.

Fuller, S.L.H. 1977. Freshwater and terrestrial mollusks. Pages 143-194 *In* J.E. Cooper et al. (eds.) *Endangered and threatened plants and animals of North Carolina*. North Carolina State Museum of Natural History, Raleigh, North Carolina.

Gagnon, P., W. Michener, M. Freeman, and J. Brim-Box. 2006. Unionid habitat and assemblage composition in Coastal Plain tributaries of Flint River (Georgia). *Southeastern Naturalist* 5:31-52.

Galbraith, H.S., C.J. Blakeslee, and W.A. Lellis. 2012. Recent thermal history influences thermal tolerance in freshwater mussel species (Bivalvia:Unionoida). *Freshwater Science* 31:83-92.

Galbraith, H.S., D.E. Spooner, and C.C. Vaughn. 2010. Synergistic effects of regional climate patterns and local water management on freshwater mussel communities. *Biological Conservation* 143:1175-1183.

Galbraith, H.S. and C.C. Vaughn. 2009. Temperature and food interact to influence gamete development in freshwater mussels. *Hydrobiologia* 636:35-47.

Galbraith, H.S. and C.C. Vaughn. 2011. Effects of reservoir management on abundance, condition, parasitism and reproductive traits of downstream mussels. *River Research and Applications* 27:1535-1467.

Gangloff, M.M. and J.W. Feminella. 2007. Stream channel geomorphology influences mussel abundance in southern Appalachian streams, U.S.A. *Freshwater Biology* 52:64-74.

Gangloff, M., L. Siefferman, W. Seesock, and E.C. Webber. 2009. Influence of urban tributaries on freshwater mussel populations in a biologically diverse Piedmont (USA) stream. *Hydrobiologia* 636:191-201.

Ganser, A.M., T.J. Newton, and R.J. Haro. 2013. The effects of elevated water temperature on native juvenile mussels: Implications for climate change. *Freshwater Science* 32:1168-1177.

Gillies, R.R., J. Brim Box, J. Symanzik, and E.J. Rodemaker. 2003. Effects of urbanization on the aquatic fauna of the Line Creek watershed, Atlanta--a satellite perspective. *Remote Sensing of Environment* 86:411-422.

- Gioria, M., A. Schaffers, G. Bacaro, and J. Feehan. 2010. The conservation value of farmland ponds: Predicting water beetle assemblages using vascular plants as a surrogate group. *Biological Conservation* 143:1125-1133.
- Goewert, A., D. Surge, S.J. Carpenter, and J. Downing. 2007. Oxygen and carbon isotope ratios of *Lampsilis cardium* (Unionidae) from two streams in agricultural watersheds of Iowa, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 252:637-648.
- Gordon, N.D., T.A. McMahon, B.L. Finlayson, C.J. Gippel, and R.J. Nathan. 2004. *Stream hydrology: An introduction for ecologists*. John Wiley & Sons, Ltd, West Sussex.
- Gotelli, N.J. and A.M. Ellison. 2004. *A primer of ecological statistics*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Goulding, K.W.T. and L. Blake. 1998. Land use, liming and the mobilization of potentially toxic metals. *Agriculture, Ecosystems & Environment* 67:135-144.
- Gray, B.R., R.J. Haro, J.T. Rogala, and J.S. Sauer. 2005. Modelling habitat associations with fingernail clam (Family: Sphaeriidae) counts at multiple spatial scales using hierarchical count models. *Freshwater Biology* 50:715-729.
- Gray, E.V.S., W.A. Lellis, J.C. Cole, and C.S. Johnson. 2002. Host identification for *Strophitus undulatus* (Bivalvia: Unionidae), the creeper, in the upper Susquehanna River basin, Pennsylvania. *American Midland Naturalist* 147:153-161.
- Grinnell, J. 1917. The niche-relationships of the California thrasher. *Auk* 34:427-433.
- Gu, R., S. Montgomery, and T.A. Austin. 1998. Quantifying the effects of stream discharge on summer river temperature. *Hydrological Sciences Journal* 43:885-904.
- Guisan, A., O. Broennimann, R. Engler, M. Vust, N.G. Yoccoz, A. Lehmann, and N.E. Zimmermann. 2006. Using niche-based models to improve the sampling of rare species. *Conservation Biology* 20:501-511.
- Guisan, A., T.C. Edwards, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: Setting the scene. *Ecological Modelling* 157:89-100.
- Guisan, A. and W. Thuiller. 2005. Predicting species distribution: Offering more than simple habitat models. *Ecology Letters* 8:993-1009.
- Guisan, A. and N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147-186.

- Haag, W.R. 2010. A hierarchical classification of freshwater mussel diversity in North America. *Journal of Biogeography* 37:12-26.
- Haag, W.R. and M.L. Warren. 1998. Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. *Canadian Journal of Fisheries and Aquatic Sciences* 55:297-306.
- Hall, L.W., M.C. Scott, W.D. Killen, and R.D. Anderson. 1996. The effects of land-use characteristics and acid sensitivity on the ecological status of Maryland coastal plain streams. *Environmental Toxicology and Chemistry* 15:384-394.
- Hamilton, P.A., R.J. Shedlock, and P.J. Phillips. 1991. Water-quality assessment of the Delmarva Peninsula, Delaware, Maryland, and Virginia – Analysis of available ground-water-quality data through 1987. U.S. Geological Survey Water-Supply Paper 2355, United States Government Printing Office, Denver, Colorado.
- Hardison, B.S. and J.B. Layzer. 2001. Relations between complex hydraulics and the localized distribution of mussels in three regulated rivers. *Regulated Rivers: Research & Management* 17:77-84.
- Hardy, J.D. 1978. Development of fishes of the Mid-Atlantic Bight. An atlas of egg, larval and juvenile stages, volume 2. U.S. Fish and Wildlife Service Biological Services Program FWS-OBS-78/12.
- Hastie, L.C., P.J. Boon, M.R. Young, and S. Way. 2001. The effects of a major flood on an endangered freshwater mussel population. *Biological Conservation* 98:107-115.
- Hastie, L.C., P.J. Cosgrove, N. Ellis, and M.J. Gaywood. 2003. The threat of climate change to freshwater pearl mussel populations. *Ambio* 32:40-46.
- Hauer, C., G. Mandlbürger, and H. Habersack. 2009. Hydraulically related hydro-morphological units: description based on a new conceptual mesohabitat evaluation model (MEM) using LiDAR data as geometric input. *River Research and Applications* 25:29-47.
- Haukioja, E. and T. Hakala. 1978. Measuring growth from shell rings in populations of the mussel *Anodonta piscinalis* (Pelecypoda, Unionidae). *Annales Zoologici Fennici* 11:60-65.
- Hayhoe, K., C. Wake, B. Anderson, X.Z. Liang, E. Maurer, J. Zhu, J. Bradbury, A. DeGaetano, A.M. Stoner, and D. Wuebbles. 2008. Regional climate change projections for the Northeast USA. *Mitigation and Adaptation Strategies for Global Change* 13:425-436.

- Heglund, P.J. 2002. Foundations of species-environment relations. Pages 35-41 *In* J.M. Washington. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, and F.B. Samson (eds.) Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington, DC.
- Heinricher, J.R. and J.B. Layzer. 1999. Reproduction by individuals of a nonreproducing population of *Megaloniaias nervosa* (Mollusca: Unionidae) following translocation. *American Midland Naturalist* 141:140-148.
- Hernandez, P.A., C.H. Graham, L.L. Master, and D.L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773-785.
- Holste, L. and M.A. Peck. 2006. The effects of temperature and salinity on egg production and hatching success of Baltic *Acartia tonsa* (Copepoda: Calanoida): a laboratory investigation. *Marine Biology* 148:1061-1070.
- Homer, C., J. Dewitz, J. Fry, M. Coan, N. Hossain, C. Larson, N. Herold, A. McKerrow, J.N. VanDriel, and J. Wickham. 2007. Completion of the 2001 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing* 73:337-341.
- Hopkins, R.L. 2009. Use of landscape pattern metrics and multiscale data in aquatic species distribution models: a case study of a freshwater mussel. *Landscape Ecology* 24:943-955.
- Horsak, M. and M. Hajek. 2003. Composition and species richness of molluscan communities in relation to vegetation and water chemistry in the western Carpathian spring fens: The poor-rich gradient. *Journal of Molluscan Studies* 69:349-357.
- Howard, A.D. and B.J. Anson. 1922. Phases in the parasitism of the Unionidae. *Journal of Parasitology* 9:68-82.
- Howard, J.K. and K.M. Cuffey. 2003. Freshwater mussels in a California North Coast Range river: occurrence, distribution, and controls. *Journal of the North American Benthological Society* 22:63-77.
- Huebner, J.D. and K.S. Pynnönen. 1992. Viability of glochidia of two species of *Anodonta* exposed to low pH and selected metals. *Canadian Journal of Zoology* 70:2348-2355.
- Huff, D.D., S.L. Hubler, and A.N. Borisenko. 2005. Using field data to estimate the realized thermal niche of aquatic vertebrates. *North American Journal of Fisheries Management* 25:346-360.



- Huston M.A. 2002. Introductory essay: Critical issues for improving predictions. Pages 7-21 *In* J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, and F.B. Samson (eds.) Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington, DC.
- Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415-427.
- Ilmonen, J., L. Paasivirta, R. Virtanen, and T. Muotka. 2009. Regional and local drivers of macroinvertebrate assemblages in boreal springs. *Journal of Biogeography* 36:822-834.
- Isaak, D.J., C.H. Luce, B.E. Rieman, D.E. Nagel, E.E. Peterson, D.L. Horan, S. Parkes, and G.L. Chandler. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications* 20:1350-1371.
- Jackson, S.T. and J.T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26:194-220.
- Jähnig, S.C., M. Kuemmerlen, J. Kiesel, S. Domisch, Q. Cai, B. Schmalz, and N. Fohrer. 2012. Modelling of riverine ecosystems by integrating models: conceptual approach, a case study and research agenda. *Journal of Biogeography* 39:2253-2263.
- Jantz, P., S. Goetz, C. Jantz. 2005. Urbanization and the loss of resource lands in the Chesapeake Bay watershed. *Environmental Management* 36:808-825.
- Jaynes, E.T. 1957. Information theory and statistical mechanics. *Physical Review* 106:620-630.
- Jenkins, R.E. and N.M. Burkhead. 1993. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.
- Johnson, P.D. and K.M. Brown. 2000. The importance of microhabitat factors and habitat stability to the threatened Louisiana pearl shell, *Margaritifera hembeli* (Conrad). *Canadian Journal of Zoology* 78:271-277.
- Johnstone, H.C. and F.J. Rahel. 2003. Assessing temperature tolerance of Bonneville cutthroat trout based on constant and cycling thermal regimes. *Transactions of the American Fisheries Society* 132:92-99.
- Kat, P.W. 1982. Effects of population density and substratum type on growth and migration of *Elliptio complanata* (Bivalvia: Unionidae). *Malacological Review* 15:119-127.

- Kaushal, S.S., G.E. Likens, N.A. Jaworski, M.L. Pace, A.M. Sides, D. Seekell, K.T. Belt, D.H. Secor, and R.L. Wingate. 2010. Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment* 8:461-466.
- Kelleher, C., T. Wagener, M. Gooseff, B. McGlynn, K. McGuire, and L. Marshall. 2012. Investigating controls on the thermal sensitivity of Pennsylvania streams. *Hydrological Processes* 26:771-785.
- King, T.L., M.S. Eackles, B. Gjetvaj, and W.R. Hoeh. 1999. Intraspecific phylogeography of *Lasmigona subviridis* (Bivalvia: Unionidae): Conservation implications of range discontinuity. *Molecular Ecology* 8(Supp. 1):S65-S78.
- Lance, G.N. and W.T. Williams. 1967. A general theory of classificatory sorting strategies 1. Hierarchical systems. *The Computer Journal* 9:373-380.
- Layzer, J.B. and L.M. Madison. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. *Regulated Rivers: Research & Management* 10:329-345.
- LeBlanc, R.T., R.D. Brown, and J.E. FitzGibbon. 1997. Modeling the effects of land use change on the water temperature in unregulated urban streams. *Journal of Environmental Management* 49:445-469.
- Lefsky, M.A., W.B. Cohen, G.G. Parker, and D.J. Harding. 2002. Lidar remote sensing for ecosystem studies. *BioScience* 52:19-30.
- Legendre, P. and L. Legendre. 1998. *Numerical Ecology*. Second edition. Elsevier Science B.V., Amsterdam.
- Lellis, W.A., B.S. White, J.C. Cole, C.S. Johnson, J.L. Devers, E.V.S. Gray, and H.S. Galbraith. 2013. Newly documented host fishes for the eastern elliptio mussel *Elliptio complanata*. *Journal of Fish and Wildlife Management* 4:75-85.
- Lenzi, M.A., L. Mao, F. Comiti. 2006. When does bedload transport begin in steep boulder-bed streams? *Hydrological Processes* 20:3517-3533.
- Leopold, L.B. 1968. *Hydrology for urban land planning: A guidebook on the hydrologic effect of urban land uses*. Geological Survey Circular 554. U.S. Geological Survey, Washington D.C.
- Leopold, L.B., M.G. Wolman, and J.P. Miller. 1964. *Fluvial processes in geomorphology*. W.H. Freeman Company, San Francisco.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73(6):1943-1967.

- Locke, A., J.M. Hanson, G.J. Klassen, S.M. Richardson, and C.I. Aube. 2003. The damming of the Petitcodiac River: Species, populations, and habitats lost. *Northeastern Naturalist* 10:39-54.
- Lohr, S.C., P.A. Byorth, C.M. Kaya, and W.P. Dwyer. 1996. High-temperature tolerances of fluvial arctic grayling and comparisons with summer river temperatures of the Big Hole River, Montana. *Transactions of the American Fisheries Society* 125:933-939.
- Lomba, A., L. Pellissier, C. Randin, J. Vicente, F. Moreira, J. Honrado, and A. Guisan. 2010. Overcoming the rare species modelling paradox: A novel hierarchical framework applied to an Iberian endemic plant. *Biological Conservation* 143:2647-2657.
- Lopes-Lima, M., A. Lopes, P. Casaca, I. Nogueira, A. Checa, and J. Machado. 2009. Seasonal variations of pH, pCO<sub>2</sub>, pO<sub>2</sub>, HCO<sub>3</sub><sup>-</sup> and Ca<sup>2+</sup> in the haemolymph: implications on the calcification physiology in *Anodonta cygnea*. *Journal of Comparative Physiology B* 179:279-286.
- Lydeard, C., R.H. Cowie, W.F. Ponder, A.E. Bogan, P. Bouchet, S.A. Clark, K.S. Cummings, T.J. Frest, O. Gargominy, D.G. Herbert, R. Hershler, K.E. Perez, B. Roth, M. Seddon, E.E. Strong, and F.G. Thompson. 2004. The global decline of nonmarine mollusks. *BioScience* 54:321-330.
- Lyons, M.S., R.A. Krebs, J.P. Holt, L.J. Rundo, and W. Zawiski. 2007. Assessing causes of change in the freshwater mussels (Bivalvia: Unionidae) in the Black River, Ohio. *The American Midland Naturalist* 158:1-15.
- Mackie, G.L. and L.A. Flippance. 1983. Intra- and interspecific variations in calcium content of freshwater mollusca in relation to calcium content of the water. *Journal of Molluscan Studies* 49:204-212.
- Maloney, K.O., W.A. Lellis, R.M. Bennett, and T.J. Waddle. 2012. Habitat persistence for sedentary organisms in managed rivers: the case for the federally endangered dwarf wedgemussel (*Alasmodonta heterodon*) in the Delaware River. *Freshwater Biology* 57:1315-1327.
- Martin, S.M. 1997. Freshwater mussels (Bivalvia: Unionoida) of Maine. *Northeastern Naturalist* 4:1-34.
- Maryland Natural Heritage Program. 2010. Rare, threatened, and endangered animals of Maryland. April 2010 edition. Maryland Department of Natural Resources, Wildlife and Heritage Service, Annapolis.

Master, L.L. 1986. *Alasmidonta heterodon*, dwarf wedgemussel: results of a global status survey and proposal to list as an endangered species. Final report, U.S. Fish and Wildlife Service, Newton Corner, Massachusetts.

McCune, B. and J.B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McLain, D.C. and M.R. Ross. 2005. Reproduction based on local patch size of *Alasmidonta heterodon* and dispersal by its darter host in the Mill River, Massachusetts, USA. Journal of the North American Benthological Society 24:139-147.

McMahon, R.F. 1999. Invasive characteristics of the freshwater bivalve, *Corbicula fluminea*. Pages 315-343 In R. Claudi and J.H. Leach (eds.) Nonindigenous freshwater organisms: vectors, biology and impacts. Lewis Publishers, Boca Raton, FL.

McMahon, R.F. 2002. Evolutionary and physiological adaptations of aquatic invasive animals: r selection versus resistance. Canadian Journal of Fisheries and Aquatic Resources 59:1235-1244.

McMahon, R.F. and A.E. Bogan. 2001. Mollusca: Bivalvia. Pages 331-429 In J.H. Thorp and A.P. Covich (eds.) Ecology and classification of North American freshwater invertebrates 2<sup>nd</sup> Edition. Academic Press, Inc., San Diego.

McRae, S.E., J.D. Allan, and J.B. Burch. 2004. Reach and catchment-scale determinants of the distribution of freshwater mussels (Bivalvia: Unionidae) in southeastern Michigan, USA. Freshwater Biology 49:127-142.

Meisner, J.D., J.S. Rosenfeld, and H.A. Regier. 1988. The role of groundwater in the impact of climate warming on stream salmonines. Fisheries 13(3):2-8.

Michaelson, D.L. and R.J. Neves. 1995. Life history and habitat of the endangered dwarf wedgemussel *Alasmidonta heterodon* (Bivalvia: Unionidae). Journal of the North American Benthological Society 14:324-340.

Milner, A.M., J.E. Brittain, E. Castella, and G.E. Petts. 2001. Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: a synthesis. Freshwater Biology: 46:1833-1847.

Morales, Y., L.J. Weber, A.E. Mynett, and T.J. Newton. 2006. Effects of substrate and hydrodynamic conditions on the formation of mussel beds in a large river. Journal of the North American Benthological Society 25:664-676.

- Morgan, M.D. and R.E. Good. 1988. Stream chemistry in the New Jersey pinelands: The influence of precipitation and watershed disturbance. *Water Resources Research* 24:1091-1100.
- Morris, T.J. and L.D. Corkum. 1996. Assemblage structure of freshwater mussels (Bivalvia:Unionidae) in rivers with grassy and forested riparian zones. *Journal of the North American Benthological Society* 15:576-586.
- Mynsberge, A.R., M.P. Strager, J.M. Strager, and P.M. Mazik. 2009. Developing predictive models for freshwater mussels (Mollusca: Unionidae) in the Appalachians: Limitations and directions for future research. *Ecoscience* 16:387-398.
- Naiman, R.J. and H. Décamps. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* 28:621-658.
- Nedean, E.J. 2008. Freshwater mussels and the Connecticut River watershed. Connecticut River Watershed Council, Greenfield, Massachusetts.
- Negishi, J.N. and Y. Kayaba. 2010. Size-specific growth patterns and estimated longevity of the unionid mussel (*Pronodularia japonensis*). *Ecological Research* 25:403-411.
- Negus, C.L. 1966. A quantitative study of the growth and production of unionid mussels in the River Thames at Reading. *Journal of Animal Ecology* 36:513-532.
- Nelson, K.C. and M.A. Palmer. 2007. Stream temperature surges under urbanization and climate change: Data, models, and responses. *Journal of the American Water Resources Association* 43:440-452.
- Nelson, K.C., M.A. Palmer, J.E. Pizzuto, G.E. Moglen, P.L. Angermeier, R.H. Hilderbrand, M. Dettinger, and K. Hayhoe. 2009. Forecasting the combined effects of urbanization and climate change on stream ecosystems: from impacts to management options. *Journal of Applied Ecology* 46:154-163.
- Newton, T.J., D.A. Woolnough, and D.L. Strayer. 2008. Using landscape ecology to understand and manage freshwater mussel populations. *Journal of the North American Benthological Society* 27:424-439.
- Nordlie, F.G. and A. Mirandi. 1996. Salinity relationships in a freshwater population of eastern mosquitofish. *Journal of Fish Biology* 49:1226-1232.
- Norton, M.M. and T.R. Fisher. 2000. The effects of forest on stream water quality in two coastal plain watersheds of the Chesapeake Bay. *Ecological Engineering* 14:337-362.

- O'Conner, R.J. 2002. Introduction to Part 1: The conceptual basis of species distribution modeling: Time for a paradigm shift? Pages 25-33 *In* J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, and F.B. Samson (eds.) *Predicting species occurrences: Issues of accuracy and scale*. Island Press, Washington, DC.
- O'Driscoll, M.A. and D.R. DeWalle. 2006. Stream–air temperature relations to classify stream–ground water interactions in a karst setting, central Pennsylvania, USA. *Journal of Hydrology* 329:140-153.
- O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. *A hierarchical concept of the ecosystem*. Princeton University Press, Princeton, NJ.
- Oh, N.H. and P.A. Raymond. 2006. Contribution of agricultural liming to riverine bicarbonate export and CO<sub>2</sub> sequestration in the Ohio River basin. *Global Biogeochemical Cycles* 20:GB3012.
- Olden, J.D., N.L. Poff, and K.R. Bestgen. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs* 76:25-40.
- Pandolfo, T.J., W.G. Cope, and C. Arellano. 2009. Heart rate as a sublethal indicator of thermal stress in juvenile freshwater mussels. *Comparative Biochemistry and Physiology* 154A:347-352.
- Pandolfo, T.J., W.G. Cope, C. Arellano, R.B. Bringolf, M.C. Barnhart, and E. Hammer. 2010. Upper thermal tolerances of early life stages of freshwater mussels. *Journal of the North American Benthological Society* 29:959-969.
- Parker, B. 1978. Self-formed straight rivers with equilibrium banks and mobile bed. Part 2. The gravel river. *Journal of Fluid Mechanics* 89:127-146.
- Pearson, R.G., C.J. Raxworthy, M. Nakamura, and A.T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* 34:102-117.
- Pérez-Quintero, J.C. 2013. Mollusc communities along upstream–downstream gradients in small coastal basins of the south-western Iberian Peninsula. *Hydrobiologia* 703:165-175.
- Peterson, J.T., J.M. Wisniewski, C.P. Shea, and C.R. Jackson. 2011. Estimation of mussel population response to hydrologic alteration in a southeastern U.S. stream. *Environmental Management* 48:109-122.
- Phillips, S.J. 2006. A brief tutorial on Maxent. AT&T Research. Available at <http://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc>.

- Phillips, S.J., R.P. Anderson, and R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231-259.
- Phillips, S.J. and M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161-175.
- Phillips, S.J., M. Dudík, J. Elith, C.H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19:181-197.
- Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16:391-409.
- Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegard, B.D. Richter, R.E. Sparks, and J.C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769-784.
- Power, G., R.S. Brown, and J.G. Imhof. 1999. Groundwater and fish—insights from northern North America. *Hydrological Processes* 13:401-422.
- Prestegard, K.L. 1983. Variables influencing water-surface slopes in gravel-bed streams at bankfull stage. *Geological Society of America Bulletin* 94:673-678.
- Preston, S.D. 2000. Statistical identification of hydrochemical response units for hydrologic monitoring and modeling in Maryland. U.S. Geological Survey Water-Resources Investigations Report 00-4232. U.S. Geological Survey, Reston, Virginia.
- Pynnönen, K. 1991. Accumulation of  $^{45}\text{Ca}$  in the freshwater unionids *Anodonta anatina* and *Unio tumidus*, as influenced by water hardness, protons, and aluminum. *The Journal of Experimental Zoology* 260:18-27.
- Pynnönen, K. 1995. Effect of pH, hardness, and maternal pre-exposure on the toxicity of Cd, Cu, and Zn to the glochidial larvae of a freshwater clam *Anodonta cygnea*. *Water Research* 29:247-254.
- Randhir, T.O. and A.G. Hawes. 2009. Watershed land use and aquatic ecosystem response: Ecohydrologic approach to conservation policy. *Journal of Hydrology* 364:182-199.
- Rashleigh, B. and D.L. DeAngelis. 2007. Conditions for coexistence of freshwater mussel species via partitioning of fish host resources. *Ecological Modelling* 201:171-178.

- Salisbury, R.D., H.B. Kummel, C.E. Peet, and G.N. Knapp. 1902. The glacial geology of New Jersey. MacCrellish & Quigley, Trenton, N.J.
- Schiff, R. and G. Benoit. 2007. Effects of impervious cover at multiple spatial scales on coastal watershed streams. *Journal of the North American Water Resources Association* 43:712-730.
- Schmidt, M.F. 1993. Maryland's geology. Schiffer Publishing, Ltd., Atglen, Pennsylvania.
- Schofield, C.L. and C.T. Driscoll. 1987. Fish species distribution in relation to water quality gradients in the North Branch of the Moose River basin. *Biogeochemistry* 3:63-85.
- Schwalb, A.N., T.J. Morris, N.E. Mandrak, and K. Cottenie. 2013. Distribution of unionid freshwater mussels depends on the distribution of host fishes on a regional scale. *Diversity and Distributions* 19:446-454.
- Sepkoski, J.J. and M.A. Rex. 1974. Distribution of freshwater mussels: Coastal rivers as biogeographical islands. *Systematic Zoology* 23:165-188.
- Sethi, S.A., A.R. Selle, M.W. Doyle, E.H. Stanley, and H.E. Kitchel. 2004. Response of unionid mussels to dam removal in Koshkonong Creek, Wisconsin (USA). *Hydrobiologia* 525:157-165.
- Shafroth, P.B., J.C. Stromberg, and D.T. Patten. 2000. Woody riparian vegetation response to different alluvial water table regimes. *Western North American Naturalist* 60:66-76.
- Shedlock, R.J., J.M. Denver, M.A. Hayes, P.A. Hamilton, M.T. Koterba, L. Joseph Bachman, P.J. Phillips, and W.S.L. Banks. 1999. Water-quality assessment of the Delmarva Peninsula, Delaware, Maryland, and Virginia: results of investigations, 1987-91. U.S. Geological Survey Water-Supply Paper 2355-A, U.S. Geological Survey, Reston, Virginia.
- Shields A. 1936. Application of the theory of similarity and turbulence research to the bedload movement. *Transl.QMSaleh. Mitt.Preuss.Vers.WasserbauSchiffbau*, 26th, Berlin.
- Shrode, J.B., K.E. Zerba, and J.S. Stephens. 1982. Ecological significance of temperature tolerance and preference of some inshore California fishes. *Transactions of the American Fisheries Society* 111:45-51.



- Sims, J.T. and F.J. Coale. 2002. Solutions to nutrient management problems in the Chesapeake Bay watershed, USA. Pages 345-372 in P.M. Haygarth and S.C. Jarvis (editors). Agriculture, Hydrology and Water Quality, CABI Publishing, New York, New York.
- Smith, D.G. 1985. Recent range expansion of the freshwater mussel *Anodonta imbecilis* and its relationship to clupeid fish restoration in the Connecticut River system. *Freshwater Invertebrate Biology* 4:105-108.
- Sophocleous, M. 2002. Interactions between groundwater and surface water: the state of the science. *Hydrogeology Journal* 10:52-67.
- Spooner, D.E. and C.C. Vaughn. 2006. Context-dependent effects of freshwater mussels on stream benthic communities. *Freshwater Biology* 51:1016-1024.
- Spooner, D.E. and C.C. Vaughn. 2008. A trait-based approach to species' roles in stream ecosystems: Climate change, community structure, and material cycling. *Oecologia* 158:307-317.
- Spooner, D.E. and C.C. Vaughn. 2009. Species richness and temperature influence mussel biomass: A partitioning approach applied to natural communities. *Ecology* 90:781-790.
- Steuer, J.J., T.J. Newton, and S.J. Zigler. 2008. Use of complex hydraulic variables to predict the distribution and density of unionids in a side channel of the Upper Mississippi River. *Hydrobiologia* 610:67-82.
- Stevens, C.E., C.A. Paszkowski, and A.L. Foote. 2007. Beaver (*Castor Canadensis*) as a surrogate species for conserving anuran amphibians on boreal streams in Alberta, Canada. *Biological Conservation* 134:1-13.
- Stockwell, D.R.B. and A.T. Peterson. 2002. Effects of sample size accuracy on species distribution models. *Ecological Modelling* 148:1-13.
- Strayer, D.L. 1993. Macrohabitats of freshwater mussels (Bivalvia:Unionacea) in streams of the northern Atlantic Slope. *Journal of the North American Benthological Society* 12:236-246.
- Strayer, D.L. 1999. Use of flow refuges by unionid mussels in rivers. *Journal of the North American Benthological Society* 18:468-476.
- Strayer, D.L. 2008. Freshwater mussel ecology: A multifactor approach to distribution and abundance. University of California Press, Berkeley.

Strayer, D.L., J.A. Downing, W.R. Haag, T.L. King, J.B. Layzer, T.J. Newton, and S.J. Nichols. 2004. Changing perspectives on pearly mussels, North America's most imperiled animals. *BioScience* 54:429-439.

Strayer, D.L. and K.J. Jirka. 1997. The pearly mussels of New York State. New York State Museum Memoir 26. The New York State Education Department, Albany.

Strayer, D.L. and H.M. Malcom. 2012. Causes of recruitment failure in freshwater mussel populations in southeastern New York. *Ecological Applications* 22:1780-1790.

Strayer, D.L. and J. Ralley. 1991. The freshwater mussels (Bivalvia: Unionoidea) of the upper Delaware River drainage. *American Malacological Bulletin* 9:21-25.

Strayer, D.L. and J. Ralley. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. *Journal of the North American Benthological Society* 12:247-258.

Strayer, D.L., S.J. Sprague, and S. Claypool. 1996. A range-wide assessment of populations of *Alasmidonta heterodon*, an endangered freshwater mussel (Bivalvia:Unionidae). *Journal of the North American Benthological Society* 15:308-317.

Sweeney, B.W. and R.L. Vannote. 1978. Size variation and the distribution of Hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science* 200:444-446.

Thoma, D.P., S.C. Gupta, M.E. Bauer, and C.E. Kirchoff. 2005. Airborne laser scanning for riverbank erosion assessment. *Remote Sensing of Environment* 95:493-501.

Thompson, W.L. 2004. Sampling rare or elusive species. Island Press, Washington, DC.

Tiner, R.W. and D.G. Burke. 1995. Wetlands of Maryland. U.S. Fish and Wildlife Service, Ecological Services, Region 5, Hadley, Massachusetts and Maryland Department of Natural Resources, Annapolis, Maryland.

Tóth, J. 1963. A theoretical analysis of groundwater flow in small drainage basins. *Journal of Geophysical Research* 68:4795-4812.

Tóth, J. 1970. A conceptual model of the groundwater regime and the hydrogeologic environment. *Journal of Hydrology* 10:164-176.

- Urban, D.L., R.V. O'Neill, and H.H. Shugart. 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. *BioScience* 37:119-127.
- U.S. Army Corps of Engineers. 2008. National inventory of Dams. U.S. Army Corps of Engineers. (Available from: <http://geo.usace.army.mil/pgis/f?p=397:1:0>).
- U.S. Census Bureau. 2001. Census 2000 TIGER/Line® files. U.S. Census Bureau. (Available from: <http://www.census.gov/geo/www/tiger/tiger2k/tgr2000.html>).
- U.S. Department of Agriculture. 2008. U.S. General Soil Map (STATSGO2). U.S. Department of Agriculture, Washington, DC. (Available from: <http://soildatamart.nrcs.usda.gov/>).
- U.S. Environmental Protection Agency. 2003. Level III ecoregions of the conterminous United States. U.S. EPA Office of Research & Development, National Health and Environmental Effects Research Laboratory, Corvallis, Oregon.
- U.S. Environmental Protection Agency. 2006. National Hydrography Dataset Plus (NHDPlus). Version 1.0. U.S. Environmental Protection Agency, Washington, DC. (Available from: [http://www.horizon-systems.com/NHDPlus/NHDPlusV1\\_home.php](http://www.horizon-systems.com/NHDPlus/NHDPlusV1_home.php)).
- U.S. Environmental Protection Agency. 2008. Catchment attribute allocation & accumulation tool (CA3T). Version 1.009. U.S. Environmental Protection Agency, Washington, DC. (Available from: [http://www.horizon-systems.com/NHDPlus/NHDPlusV1\\_tools.php](http://www.horizon-systems.com/NHDPlus/NHDPlusV1_tools.php)).
- U.S. Fish and Wildlife Service. 1993. Dwarf wedge mussel (*Alasmidonta heterodon*) recovery plan. US Fish and Wildlife Service, Northeast Region, Hadley, Massachusetts. 52pp.
- U.S. Fish and Wildlife Service. 2007. Dwarf wedgemussel (*Alasmidonta heterodon*) 5-year review: summary and evaluation. U.S. Fish and Wildlife Service, Concord, New Hampshire.
- Utz, R., K. Eshleman, and R. Hilderbrand. 2011. Variation in hydrologic, chemical and thermal responses to urbanization in streams between two physiographic regions of the Mid-Atlantic United States. *Ecological Applications* 21:402-415.
- Vannote, R.L. and G.W. Minshall. 1982. Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. *Proceedings of the National Academy of Sciences of the United States of America* 79:4103-4107.
- Vaughn, C.C. 1997. Regional patterns of mussel species distributions in North American rivers. *Ecography* 20:107-115.

- Vaughn, C.C., K. Gido, and D. Spooner. 2004. Ecosystem processes performed by unionid mussels in stream mesocosms: Species roles and effects of abundance. *Hydrobiologia* 527:35-47.
- Vaughn, C.C. and C.M. Taylor. 2000. Macroecology of a host-parasite relationship. *Ecography* 23:11-20.
- Versteegh, E.A.A., S.R. Troelstra, H.B. Vonhof, and D. Kroon. 2009. Oxygen isotope composition of bivalve seasonal growth increments and ambient water in the rivers Rhine and Meuse. *Palaaios* 24:497-504.
- Waller, D.L., S. Gutreuter, and J.J. Rach. 1999. Behavioral responses to disturbance in freshwater mussels with implications for conservation and management. *Journal of the North American Benthological Society* 18:381-390.
- Walsh, M.C., J. Deeds, and B. Nightingale. 2007*a*. User's manual and data guide to the Pennsylvania aquatic community classification. Pennsylvania Natural Heritage Program, Western Pennsylvania Conservancy, Middletown, PA, and Pittsburgh, PA.
- Walsh, M.C., J. Deeds, and B. Nightingale. 2007*b*. Classifying lotic systems for conservation: methods and results of the Pennsylvania aquatic community classification. Pennsylvania Natural Heritage Program, Western Pennsylvania Conservancy, Middletown, PA, and Pittsburgh, PA.
- Waples, R.S. 1995. Evolutionary significant units and the conservation of biological diversity under the Endangered Species Act. Pages 8-27 *In* J.L. Nielsen (ed.) *Evolution and the aquatic ecosystem: Defining unique units in population conservation*. American Fisheries Society Symposium 17, Bethesda, Maryland.
- Watters, G.T. 1992. Unionids, fishes, and the species-area curve. *Journal of Biogeography* 19:481-490.
- Weber, T.C. and M. Schwartz. 2011. Maximum entropy habitat modeling of four endangered mussels in the Ohio River basin, USA. *Journal of Conservation Planning* 7:13-26.
- Wehrly, K.E., L. Wang, and M. Mitro. 2007. Field-based estimates of thermal tolerance limits for trout: Incorporating exposure time and temperature fluctuation. *Transactions of the American Fisheries Society* 136:365-374.
- Wehrly, K.E., M.J. Wiley, and P.W. Seelbach. 2003. Classifying regional variation in thermal regime based on stream fish community patterns. *Transactions of the American Fisheries Society* 132:18-38.

Wilbur, K.M. 1964. Shell formation and regeneration. Pages 243-282 *In* K.M. Wilbur and C.M. Yonge (eds.) Physiology of Mollusca. Academic Press, New York.

Williams, J.D., M.L. Warren, K.S. Cummings, J.L. Harris, and R.J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries* 18:6-22.

Wilson, C.D., D. Roberts, and N. Reid. 2011. Applying species distribution modelling to identify areas of high conservation value for endangered species: A case study using *Margaritifera margaritifera* (L.). *Biological Conservation* 144:821-829.

Wisz, M.S., R.J. Hijmans, J. Li, A.T. Peterson, C.H. Graham, and A. Guisan. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14:763-773.

Wolman, M.G. 1954. A method of sampling coarse river-bed material. *Transactions of the American Geophysical Union* 35:951-956.

Wolman, M.G. 1967. A cycle of sedimentation and erosion in urban river channels. *Geografiska Annaler. Series A, Physical Geography* 49:385-395.

Yang, L., C. Huang, C. Homer, B. Wylie, and M. Coan. 2002. An approach for mapping large-area impervious surfaces: Synergistic use of Landsat 7 ETM+ and high spatial resolution imagery. *Canadian Journal of Remote Sensing* 29:230-240.

Zale, A.V. and R.J. Neves. 1982. Fish hosts of four species of lampsiline mussels (Mollusca: Unionidae) in Big Moccasin Creek, Virginia. *Canadian Journal of Zoology* 60:2535-2542.

Zigler, S.J., T.J. Newton, M. Davis, and J.T. Rogala. 2012. Patterns in species richness and assemblage structure of native mussels in the Upper Mississippi River. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22:577-587.

Zigler, S.J., T.J. Newton, J.J. Steuer, M.R. Bartsch, and J.S. Sauer. 2008. Importance of physical and hydraulic characteristics to unionid mussels: A retrospective analysis in a reach of a large river. *Hydrobiologia* 598:343-360.